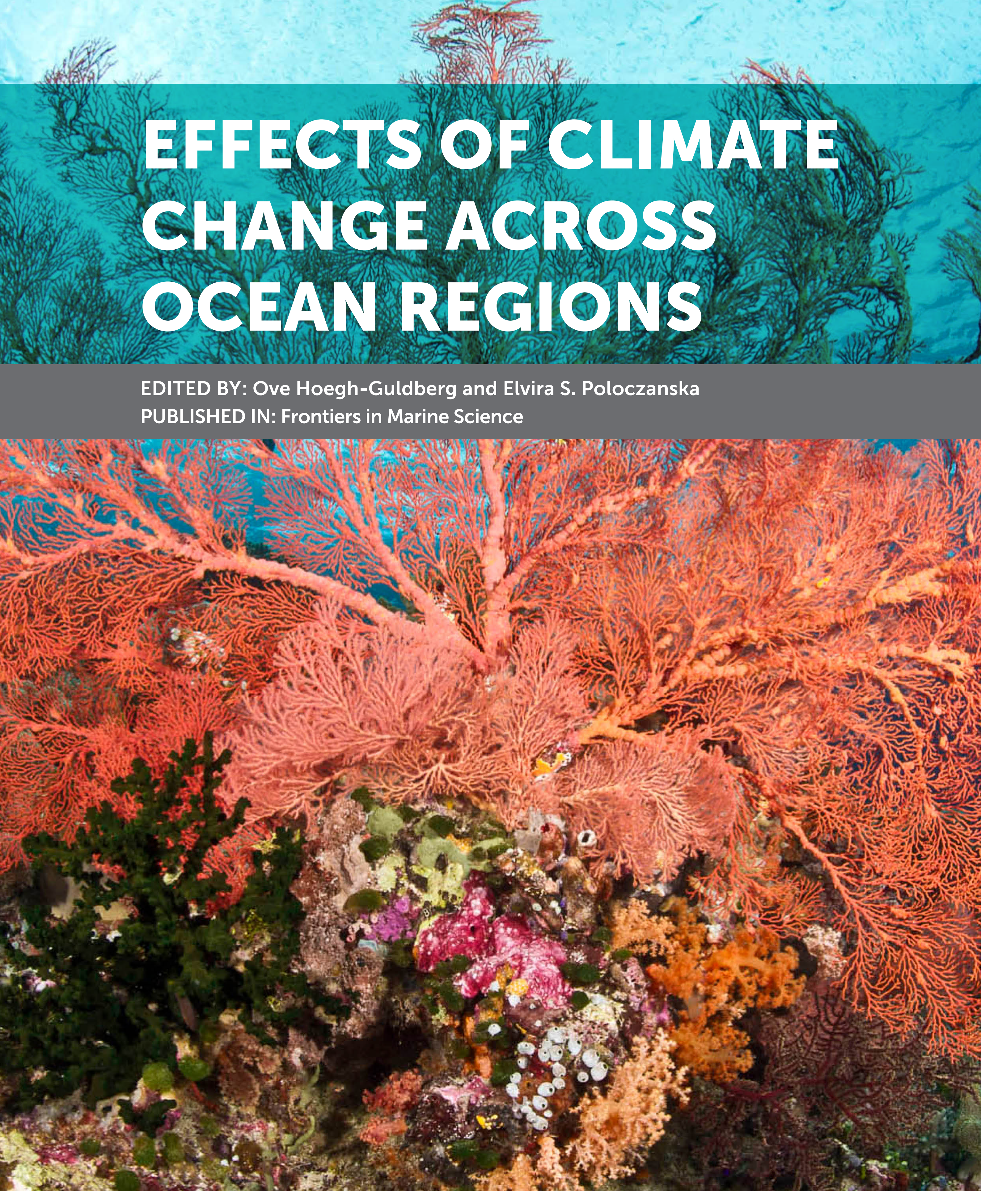

EFFECTS OF CLIMATE CHANGE ACROSS OCEAN REGIONS

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EFFECTS OF CLIMATE CHANGE ACROSS OCEAN REGIONS

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Table of Contents

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EDITORIAL
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Editorial: The Effect of Climate Change across Ocean Regions

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Keywords: corals, deep sea, cold water, climate change, symbiotic, mass coral bleaching, ocean acidification, ocean warming

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Editorial on the Research Topic

The Effect of Climate Change across Ocean Regions

According to the consensus of the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC, 2014), conditions within Earth's ocean are changing at rates that are greater than any of other time during the past 65 million years. As a result, major changes have begun to occur in ocean systems that have serious consequences for geophysical, ecological, and human systems. This research topic expands on discussions held as part of AR5 on past, present and future changes across ocean regions (**Figure 1**), drawing on literature published since the AR5 cut-off dates for literature (March to October 2013, depending on IPCC Working Group) as well as new analyses.

The papers in this collection present a global overview of the geophysical to ecological changes (Howes et al.) in the following sub-regions: sub-tropical gyres (Signorini et al.), the Mediterranean semi-enclosed sea (Marbà et al.), the North Atlantic High latitude spring bloom system (Sundby et al.), eastern boundary upwelling systems (García-Reyes et al.). Risks to specific ecosystems are presented by Hoegh-Guldberg et al.(warm- and cold-water coral reefs) and Steckbauer et al.(the benthic ecosystem in the EBUE along the coast of Chile). Boyd presents a modeling exercise of impacts on the ocean "biological pump" which has consequences for the ocean carbon cycle. Poloczanska et al. focus on distribution shifts of species as a response to climate change and synthesize information across the ocean regions while Weatherdon et al. provide an update of the assessment on social and economic impacts arising from changes in ocean ecosystems.

Changes in ocean primary production are explored by Boyd using a 1-D model to investigate the impacts of changing temperature on components of the "biological pump," (the roles of marine microbes in moving carbon from surface waters into deep ocean). The study shows that climate-driven shifts in surface and subsurface structure of plankton communities reduce the efficiency of the biological pump, thus an important feedback loop to the global carbon cycle. The potential of ocean warming to impact the global carbon cycle is also highlighted in the contribution of Signorini et al. who analyzed the trends in chlorophyll-*a* and derived net primary production in the surface waters of the five sub-tropical ocean gyres: the North Pacific, South Pacific, Indian Ocean, North Atlantic, and South Atlantic. These gyre systems occupy around 40% of the surface of the Earth so although they are oligotrophic (low biomass and low productivity) they make an important contribution to the global carbon cycle given their immense size. In all gyres, significant downwards trends in chlorophyll-*a* (except South Pacific) and net primary production were found, measured over 1998–2013.

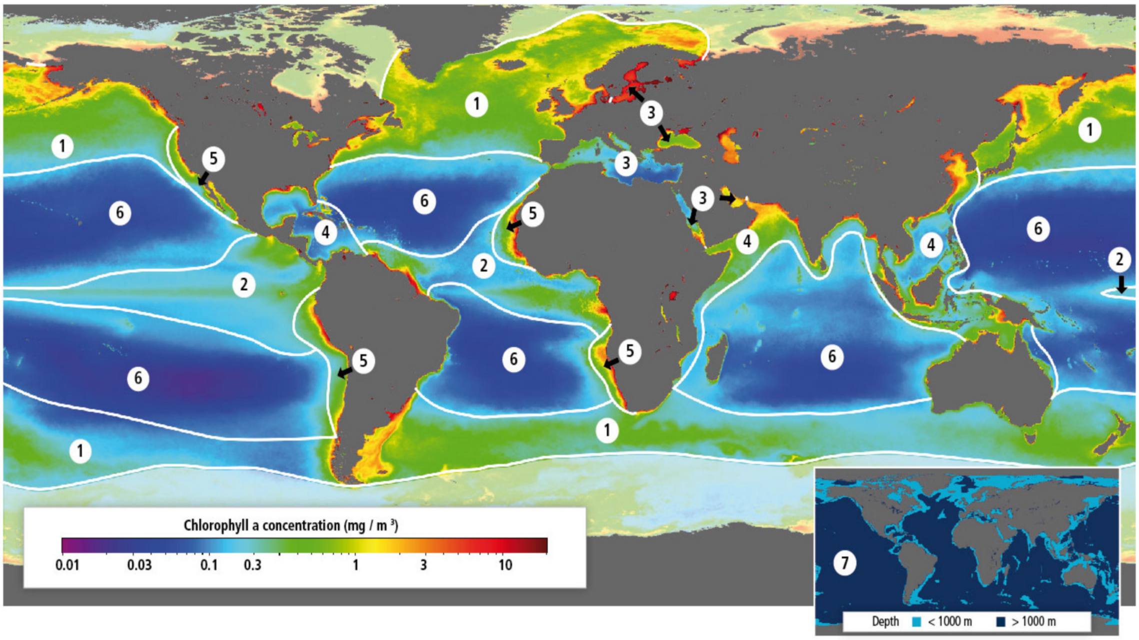

FIGURE 1 | Separation of the world's oceans into seven major sub-regions (excluding an eighth area, Polar Oceans; white shaded area). The chlorophyll-*a* signal measured by SeaWIFS and averaged over the period from Sep 4, 1997 to 30 Nov 2010 (NASA) provides a proxy for differences in marine productivity. Ecosystem structure and functioning, as well as key oceanographic features, provided the basis for separating the Ocean into the sub-regions shown. The map insert shows the distribution of the Deep Sea (DS) habitat (>1,000 m; Bathypelagic and Abyssopelagic habitats combined).

García-Reyes et al. synthesize the current state of knowledge of the dynamics of the Eastern Boundary Upwelling Systems (EBUE) and provide evidence that coastal upwelling-favorable changes in the poleward portions of these systems (with the exception of the Canary EBUE) have intensified. This synthesis also considers future effects on coastal biogeochemistry and concludes that, although confidence in the projected changes is currently low, observed decreases in pH and oxygen concentrations in the upper waters of EBUE are expected to continue. These are highly productive ecosystems and hence changes in their physical and biogeochemical properties are likely to have ecological impacts with severe economic and social consequences for coastal fisheries and communities. The ecological repercussions are highlighted in the paper by Steckbauer et al., who experimentally show that the combined effects of decreased pH (ocean acidification) and decreased oxygen concentration enhance negative impacts on invertebrates from the coastline of Chile in the Humboldt Current EBUE. However, the authors point out that the invertebrates are likely to be adapted to short-term exposures to these stressors.

The compound risks from warming temperatures and ocean acidification were reviewed Hoegh-Guldberg et al. with respect to cold- and warm-water corals. Their assessment highlights the high vulnerability of these ecosystems to climate change, and warns that warm-water coral reefs may be eliminated by mid-century without urgent and drastic mitigation. This consensus stemming from the AR5 is emphasized the recent catastrophic heating events driving mass coral bleaching and mortality in many parts of the world including the Indo-Pacific and Caribbean, and key sites such as the Great Barrier Reef (Hughes et al., 2017). Marbà et al. synthesize evidence of the effects of warming temperatures on the Mediterranean Sea ecosystems and show widespread changes in migration, abundance, survival, and phenology of species, among other factors, which are particularly evident during marine heat waves. The study highlights the high sensitivities of many Mediterranean species to warming, which are likely due to direct metabolic impacts of temperature and indirect impacts on nutrient availabilities. Sundby et al. and Poloczanska et al. also focus on distribution shifts on marine species. Sundby et al. look at the north Atlantic HLSBS where warming has been rapid, and consider influence of climate variability, such as the North Atlantic Oscillation and Atlantic Multidecadal Oscillation on ecosystem attributes including phytoplankton and zooplankton production and fish stock productivity. In particular, they focus on observations of, and the potential for, climate-driven distribution shifts of key species in the region drawing out the underlying mechanisms. They present evidence that there are limits to poleward migration of temperate species into the polar region under future climate change. The transition to extreme seasonality in the light cycle at latitudes strongly influences primary production and north of the "critical latitudes" (63–68°N) where life cycles adapted for low food availability during long, dark winters are required. Poloczanska et al. show graphically how regional warming and light seasonality can influence the potential for shifts the

TABLE 1 | Relationship between area (millions km^2), primary productivity, and fish catch (as millions of tons yr^{-1}) for the period 1970–2006 for each ocean sub-region shown in **Figure 1** (numbers in **Figure 1** correspond to numbers in this table).

Area		Description	Area (%)	Primary productivity (%)	Fisheries productivity (%)
1. High Latitude Spring Bloom Systems (HLSBS)	Northern Section	From 35°N and 35°S to the edge of the winter ice. Strong seasonal cycle of primary productivity that is nutrient limited at times and which becomes more pronounced toward higher latitudes where primary production shifts to a single peak during early spring and decreases to near zero in winter (numbered references)	10.6	22.6	29.6
	Southern Section		14.4	20.4	6.8
2. Equatorial Upwelling Systems (EUS)		Consist of highly productive regions along eastern edge of the Pacific and Atlantic oceans	8.2	9.0	5
3. Semi Enclosed Seas (SES)		Defined here as large landlocked seas (>200,000 km^2) with single narrow passageways (<120 km) includes Arabian Gulf, Red, Mediterranean, Black, and Baltic seas	1.1	2.3	3.3
4. Western Boundary Systems (WBS)		Include diverse marine ecosystems that are influenced by different location-specific oceanographic processes and primary productivity values. Like the EBUE, light is abundant although nutrients may be restricted spatially and temporally by a number of different factors (e.g., stratification, coastal run-off)	6.2	10.6	28
5. Eastern Boundary Upwelling Ecosystems (EBUE)		Consist of four major components; the canary Current and Benguela Current in the Atlantic: Ocean, and the California Current and the Humboldt Current in the Pacific Ocean. In contrast to the high latitude spring-bloom systems, large levels of primary production tends to occur continuously, driven by regional wind systems that drive the upwelling of nutrients from the deep to surface	1.7	7.0	20
6. Subtropical Gyres (STG)		Found in all three oceans and exhibit low productivity due to warm and highly stratified water columns which restricts nutrient supply to euphotic layer ("ocean nutrient deserts")	41.0	22.0	8
7. Deep Ocean (DO)		Defined here as habitats below 1,000 m representing the largest habitat on Earth. Despite its large size, our understanding of the deep ocean is minimal. Interacts strongly with the upper ocean through the sedimentation of biogenic material, remineralization, vertical mixing, upwelling, downwelling, and vertical migrations (including ontogenetic)	88.0	0	0.5

*The top three bars (sub-regions HLSBS-North, CBS, and EBUE) cover 19% of the world oceans' area and provide 76% of the world's fish catches. Both **Figure 1** and **Table 1** modified from Hoegh-Guldberg et al. (2014).*

distribution of species across latitudes. In the tropics, species may need to shift distributions large distances to track optimal temperatures but will experience little change in light seasonality, while at high latitudes, a short shift in distance can mean exposure to very different light seasonality. Poloczanska et al. also assess the evidence for climate-driven distribution shifts across ocean regions and discuss the factors facilitating or limiting responses.

Howes et al. present a synthesis of literature from physics and chemistry to ecology. In particular, they present updates for the evidence of impacts and vulnerabilities across taxonomic groups: microbes, macroalgae, and seagrasses, and animals, to changes in temperature, dissolved oxygen, and ocean acidification. Weatherdon et al. review the literature and expand discussions to consider the impacts on the goods and services provided by marine ecosystems such as the risks from ocean acidification to shellfish fisheries and aquaculture, and the impacts of warming on the distributions of fish stocks and fisheries catches. They consider regional impacts on tropical, temperature and subtropical and polar fisheries. They assess the recent evidence for risks to coastal tourism, human health and food security from climate-driven shifts in species distributions and other climate change impacts.

Overall, we hope that the group of papers that we have drawn together here will be useful for understanding the current and unprecedented changes that are occurring in the world's oceans. In many cases, the observed phenomena are in the earliest stages of being understood, suggesting that the literature and understanding in each of these fundamental areas is set to grow rapidly over the coming years.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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REVIEW
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An updated synthesis of the observed and projected impacts of climate change on the chemical, physical and biological processes in the oceans

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The 5th Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) states with very high certainty that anthropogenic emissions have caused measurable changes in the physical ocean environment. These changes are summarized with special focus on those that are predicted to have the strongest, most direct effects on ocean biological processes; namely, ocean warming and associated phenomena (including stratification and sea level rise) as well as deoxygenation and ocean acidification. The biological effects of these changes are then discussed for microbes (including phytoplankton), plants, animals, warm and cold-water corals, and ecosystems. The IPCC AR5 highlighted several areas related to both the physical and biological processes that required further research. As a rapidly developing field, there have been many pertinent studies published since the cut off dates for the AR5, which have increased our understanding of the processes at work. This study undertook an extensive review of recently published literature to update the findings of the AR5 and provide a synthesized review on the main issues facing future oceans. The level of detail provided in the AR5 and subsequent work provided a basis for constructing projections of the state of ocean ecosystems in 2100 under two the Representative Concentration Pathways RCP4.5 and 8.5. Finally the review highlights notable additions, clarifications and points of departure from AR5 provided by subsequent studies.

Keywords: oceans and climate change, IPCC AR5, biological processes, physical processes, warming, ocean acidification, anoxia

Introduction

Working Groups I and II (WGI and WGII) of the Intergovernmental Panel on Climate Change's (IPCC's) Fifth Assessment Report (AR5) synthesized research regarding observed and projected impacts of climate change on physical and biological processes in the oceans at both global and regional levels. The impacts of these changes on human health and socio-economics were also discussed (reviewed by Cheung et al., submitted). Key findings on physical processes highlighted, with an extremely high certainty, that the upper ocean had warmed over the last 40 years and predicted with *very high confidence* that this trend would continue over the coming century (Ciais et al., 2013; Rhein et al., 2013). It was considered *very likely* that this increase in temperature contributed to significant global mean sea level rise (Rhein et al., 2013). High agreement amongst data provided evidence that stratification caused by increasing sea temperatures has caused declining seawater oxygen concentrations (Rhein et al., 2013). The report expressed *high confidence* that the oceans are absorbing anthropogenic carbon and that the resulting chemical reactions cause ocean acidification (Ciais et al., 2013; Rhein et al., 2013).

Key findings on biological processes highlighted the effect of ocean warming on the geographical distribution of organisms with observations lending evidence to poleward migrations of species (Poloczanska et al., 2014; Pörtner et al., 2014). Temperature has already affected the timing of life history events (phenology) such as reproduction and migration, and caused irreversible regime shifts in warm water coral reef and Arctic ecosystems (*medium confidence*; Field et al., 2014). Net primary productivity (NPP) was projected to decrease moderately by 2100 in the open ocean under both low- and high-emission scenarios, paralleled by an increase in NPP at high latitudes and a decrease in the tropics (Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). Despite a lack of field observations, ocean acidification was predicted to have a significant effect on many aspects of organisms' physiology, behavior, and population dynamics (Pörtner et al., 2014). There was *medium confidence* that expansion of suboxic zones would benefit anaerobic microbes and limit oxygen dependent species (Pörtner et al., 2014). There was *high confidence* that the various environmental drivers would act simultaneously on organisms causing complex, interacting effects (Pörtner et al., 2014).

AR5 also identified key uncertainties regarding potential climate-related impacts on biological and physical systems. In particular, it highlighted the need for an updated understanding regarding the following aspects:

(1) The extent of warming in deep water masses (below 700 m) and limited observational coverage of the ocean, hampering more robust estimates of ocean heat and carbon content.
(2) While acknowledged as a critical process influencing ecosystem productivity, the likelihood of climate-induced changes to major upwelling systems (i.e., increased or decreased upwelling) is still uncertain (Lluch-Cota et al., 2014).
(3) Ways in which climate-induced changes in the physiology and biogeography of an individual species may alter ecosystem structures, species interactions, and food webs (Pörtner et al., 2014).
(4) An improved understanding of climate sensitivity at the ecosystem level that considers multiple drivers (e.g., ocean warming, acidification, and hypoxia) and synergistic impacts (Pörtner et al., 2014; Wong et al., 2014).
(5) The degrees to which species can track changes in climate as well as the influence of multiple stressors on their capacities to respond remained uncertain (Poloczanska et al., 2014).
(6) The capacity for phenotypic and evolutionary adaptation over generations to respond to long-term climate change (Pörtner et al., 2014).

The objective of this review is to draw together the various sections of the AR5 that address the physical and biological impacts of climate change on the ocean. We focus on the physical processes that will have the greatest direct impacts on biota, namely warming, acidification, and deoxygenation. Papers published after the AR5 cutoff dates (15/03/2013 for working group I and 31/08/2013 for working group II) were then reviewed to update the understanding of the observed and projected impacts of climate change on physical and biological processes. The review endeavors to highlight key developments with respect to our scientific understanding of the relationships among different anthropogenic and climatic drivers on marine ecosystems. Lastly, the review calls attention to areas of agreement with, and points of departure from AR5. Throughout the text, where possible, the review strives to employ the same language of certainty as the AR5, summarized in **Table 1** and **Figure 1**.

Physical Science

Since the start of the Industrial Era (1750 onwards), anthropogenic activities have resulted in increased concentrations of greenhouse gases and it is now *virtually certain* that atmospheric concentrations of greenhouse gases are at their highest in the last 800,000 years (Ciais et al., 2013). Concentrations of CO_2, CH_4 and N_2O rose by 40, 150, and 20%, respectively, between 1970 and 2011. Accumulation of these gases in the atmosphere act to increase radiative forcing and, of the three, CO_2 has the greatest effect (Ciais et al., 2013). This has resulted in a measureable increase in global air and sea temperatures (**Figure 2**) with the beginning of the 21st century having the warmest years on record since 1880 (IPCC, 2013; **Table 2**).

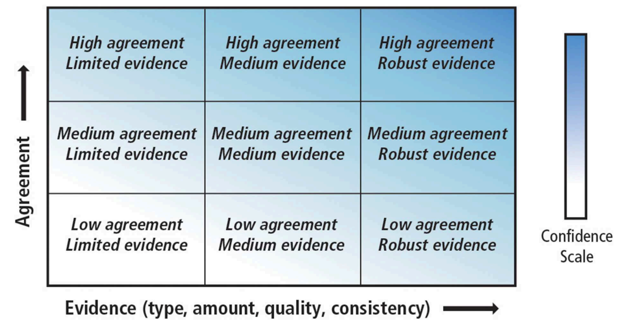
Over the last 800,000 years, concentrations of atmospheric CO_2 have been relatively stable, oscillating between 180 ppm during glacial periods and 300 ppm during interglacial periods (Ciais et al., 2013). Between 1750 and 2013, atmospheric CO_2 levels rose from 278 ppm to 395.31 ppm (Le Quéré et al., 2014), exceeding 400 ppm for much of 2014 (http://www.esrl.noaa.gov/gmd/ccgg/trends/). Total anthropogenic emissions between 1870 and 2014 amounted to 545 ± 55 Pg C (Le Quéré et al., 2014). The AR5 states with *very high confidence* that burning of fossil fuels and land use changes are the dominant cause of the increase in atmospheric CO_2 (Ciais et al., 2013), contributing 395 ± 20 Pg C (including emissions from cement production of 8 Pg C) and 185 ± 65 Pg C, respectively (Le Quéré et al., 2014).

The accumulation of greenhouse gases in the atmosphere and the oceans produces widespread, global, and long-lasting physical changes in the ocean environment. These changes are summarized below, focusing on those that are anticipated to

TABLE 1 | Breakdown of the IPCC AR5 confidence and likelihood terminology.

Confidence terminology		Likelihood terminology	
Very high confidence	At least 9 out of 10 chance	*Virtually certain*	99–100% probability of occurring
High confidence	About 8 out of 10 chance	*Very likely*	90–100% probability
Medium confidence	About 5 out of 10 chance	*Likely*	66–100% probability
Low confidence	About 2 out of 10 chance	*About as likely as not*	33–66% probability
Very low confidence	Less than 1 out of 10 chance	*Unlikely*	0–33% probability
		Very unlikely	1–10% probability
		Exceptionally unlikely	0–1% probability

Source: Stocker et al. (2013).



High agreement Limited evidence	*High agreement Medium evidence*	*High agreement Robust evidence*
Medium agreement Limited evidence	*Medium agreement Medium evidence*	*Medium agreement Robust evidence*
Low agreement Limited evidence	*Low agreement Medium evidence*	*Low agreement Robust evidence*

FIGURE 1 | A depiction of evidence and agreement statements and their relationship to confidence. Confidence increases toward the top right corner as suggested by the increasing strength of shading. Generally, evidence is most robust when there are multiple, consistent independent lines of high quality. Source: Stocker et al. (2013).

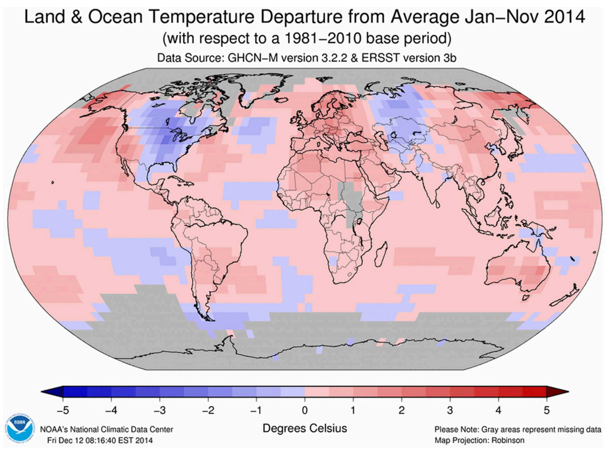


FIGURE 2 | Global temperature anomaly means for January to November 2014 (2014 was the warmest year ever recorded for this period). Source: http://www.ncdc.noaa.gov/sotc/global/2014/11#temp.

TABLE 2 | List of the 10 warmest years between 1880 and 2014.

Rank 1 = warmest	Year	Anomaly (°C)
1	2014	0.69
2 (tie)	2010	0.65
2 (tie)	2005	0.65
4	1998	0.63
5 (tie)	2013	0.62
5 (tie)	2003	0.62
7	2002	0.61
8	2006	0.60
9 (tie)	2009	0.59
9 (tie)	2007	0.59

Source: http://www.ncdc.noaa.gov/sotc/global/2014/13.

have the greatest effect on organism and ecosystem functioning. It is *virtually certain* that the oceans have sequestered 155 ± 30 Pg C (28% of total emissions) of anthropogenic CO_2 since the Industrial Revolution, *very likely* at a rate of between 0.1 and 3.2 Pg C yr^{-1} (Ciais et al., 2013). The increased CO_2 absorbed by the ocean is in response to the increasing concentrations of CO_2 in the atmosphere. Without ocean uptake, atmospheric CO_2 would be much higher, thus the oceans play an important role in mediating global climate change effects (Ciais et al., 2013).

Model projections show that an increase in atmospheric CO_2 will always lead to an increase in ocean carbon storage, all other things being held constant (Ciais et al., 2013). The proportion of carbon that remains in the atmosphere will increase with increasing input of carbon in the atmosphere-ocean system as the oceans' buffer capacity diminishes (Ciais et al., 2013). The excess carbon will continue to invade the ocean for centuries, perturbing dissolved inorganic carbon (DIC), the partial pressure of pCO_2 in seawater and pH, also in the deep oceans (Ciais et al., 2013). Model projections show a widespread increase of CO_2 in the upper mixed layer from 0.1 to 0.2 mol m^{-3} in year 1990 to 0.2–0.4 mol m^{-3} in year 2100 under a high emissions scenario (Cocco et al., 2013).

Warming

AR5 Summary

There is *high confidence* that 93% of the excess heat in Earth's energy inventory from 1971 and 2010 ended up in the oceans (Rhein et al., 2013). The upper ocean has warmed between 1971 and 2010; globally averaged increases from 0 to 200 m between 1971 and 2010 are 0.25°C, accounting for approximately 64% of the total warming occurring in the ocean (Rhein et al., 2013). Warming is most pronounced at the surface; between 1971 and 2010, temperatures in the upper 75 m are estimated to have increased by approximately 0.11°C decade^{-1} (Rhein et al., 2013). It is also *very likely* that warming was occurring earlier, between the 1870's and 1971 (Rhein et al., 2013). It is *virtually certain* that the heat content of the upper oceans has increased; estimates for the heating rate between 1971 and 2010 vary between 74 and 137 TW (Rhein et al., 2013). It is *very likely* that warming has increased the stratification of upper 200 m of the oceans by about 4% during the period 1971–2010; in turn there is *medium confidence* that this has reduced the dissolved oxygen concentration and decreased the availability of inorganic nutrients (Rhein et al., 2013).

Regionally, the average sea surface temperature (SST) of the Indian, Atlantic and Pacific Oceans has increased by 0.65, 0.41, and 0.31°C, respectively, between 1950 and 2009 (Hoegh-Guldberg et al., 2014). There is *high confidence* that sea surface temperatures in sub-tropical gyres of the Atlantic, Pacific, and Indian Oceans have increased (Hoegh-Guldberg et al., 2014). In the Indian Ocean, there is *medium confidence* that 90% of the warming trend can be attributed to external forcing. Average sea temperatures have increased between 1950 and 2009 by 0.43 and 0.54°C in the Pacific and Atlantic equatorial upwelling systems, respectively (Hoegh-Guldberg et al., 2014). It is *likely* that North Atlantic surface waters have warmed by 0.07°C decade^{-1} between 1950 and 2009 (Hoegh-Guldberg et al., 2014), which has been suggested to be a contributing factor to the retreat of the Greenland ice sheet (Straneo and Heimbach, 2013).

Warming can be observed in all the sub-regions of coastal boundary systems (CBS), overall, CBS warmed by 0.14–0.80°C from 1950 to 2009 (Hoegh-Guldberg et al., 2014). Key sub-regions within the CBS such as the Coral Triangle and Western Indian Ocean warmed by 0.79 and 0.60°C, respectively, from 1950–2009 (Hoegh-Guldberg et al., 2014). It is *very likely* that the Gulf of Mexico and Caribbean Sea have warmed by 0.31 and 0.50°C, respectively from 1982 to 2006 (Hoegh-Guldberg et al., 2014).

Due to undersampling, uncertainties assessing warming in the deep ocean are much higher than for the surface waters; before 2005, the data are too sparse to produce reliable estimates. Studies confirm warming between 0 and 1500 m since 2005 and it is *likely* that waters between 700 and 2000 m have warmed, on average between 1957 and 2009 (Rhein et al., 2013). Conversely, it is *likely* that there has been no significant global warming trend between 2000 and 3000 m (1992–2005), although steep vertical gradients and water mass movements confound sparse sampling at mid-depths (Rhein et al., 2013). Globally, waters from 3000 m to the bottom are thought *likely* to have experienced a warming trend greater than zero (Rhein et al., 2013). Some regions are better sampled than others, allowing a more detailed assessment of temperature changes. It is *very likely* that N. Atlantic deep waters below 2000 m have a net cooling trend of -4 TW between 1955 and 2005 (Rhein et al., 2013). It is considered *likely* that waters of Antarctic origin have warmed below 3000 m by 0.01°C decade^{-1} between 1992 and 2005 and that waters south of the Sub-Antarctic polar front have warmed by 0.03°C decade^{-1} for the same period (Rhein et al., 2013).

For deep waters, warming of between 0.3°C (RCP2.6) to 0.6°C (RCP8.5) are projected (**Figure 3**; Ciais et al., 2013). Depending on the emission scenario, global ocean warming between 0.5°C (RCP2.6) and 1.5°C (RCP8.5) will reach a depth of about 1 km by the end of the century (Ciais et al., 2013). There is *high confidence* that the largest warming of deep waters will occur in the Southern Ocean (Ciais et al., 2013).

Updates to AR5

The 2000's were the warmest decade on record and the 1990's the second warmest (Trenberth and Fasullo, 2013; Goddard, 2014). Nonetheless, several estimates used in the AR5 reported that the increase in upper ocean heat content (OHC) has slowed between 2003 and 2010, compared to previous decades (Rhein et al., 2013). Work published since the AR5 suggested that there may be an impact of large scale natural climate variability, a reduced radiative forcing, or a smaller warming response to atmospheric CO_2 concentrations (Lewis, 2013). The central and eastern Pacific have exhibited the greatest slowing in warming trend (Trenberth et al., 2014) and it has been suggested that variations in both the Pacific Decadal Oscillation (PDO) and the Atlantic Multidecadal Oscillation may be responsible for this (Trenberth and Fasullo, 2013; Goddard, 2014; Trenberth et al., 2014; Steinman et al., 2015). Two recent studies suggest that the warming hiatus is caused by heat transported to deeper layers in ocean basins, although there is debate as to which basins are the main drivers (Chen and Tung, 2014; Trenberth et al., 2014).

Despite the recent hiatus in the global mean surface air temperature trend, the consensus is that this can be attributed to natural variability (Trenberth and Fasullo, 2013) and OHC continues to increase (Goddard, 2014; Huber and Knutti, 2014; Schmidt et al., 2014b; Trenberth et al., 2014). Data from Argo floats for the period 2006 to 2013 show no warming pause and estimate increases in OHC between 0 and 2000 m depth, at a rate of 0.4–0.6 W m^2. The Argo data show that the heat is evenly distributed between the upper 500 m and 500–2000 m with the Southern Hemisphere gaining more heat than the Northern (Roemmich et al., 2015). At the same time, Steinman et al. (2015) combined climate observations and model simulations and found that a modest positive peak in the Atlantic multidecadal variability and a substantially negative-trending Pacific multidecadal variability are seen to produce a slowdown or "false pause" in warming of the past decade.

Durack et al. (2014) argue that the AR5 estimates for increases in OHC might be biased low due to limited sampling of the Southern Hemisphere compared to the Northern Hemisphere. Satellite observations of sea surface height were used as a model parameter to calculate changes in OHC, showing a more homogeneous warming, with larger magnitudes in the South Pacific and South Atlantic basins compared to IPCC estimates. The results yielded an increase in global upper OHC of 2.2 to 7.1×10^{22} J above existing estimates for 1970 to 2004.

Work published since the AR5 has found that the Arctic Ocean has exhibited one of the strongest (but variable) warming trends. In areas where the warming trend is high, a novel study using isotope proxy analysis found up to 3.7°C increase between 1920 and 2011. This is approximately 6 times higher than

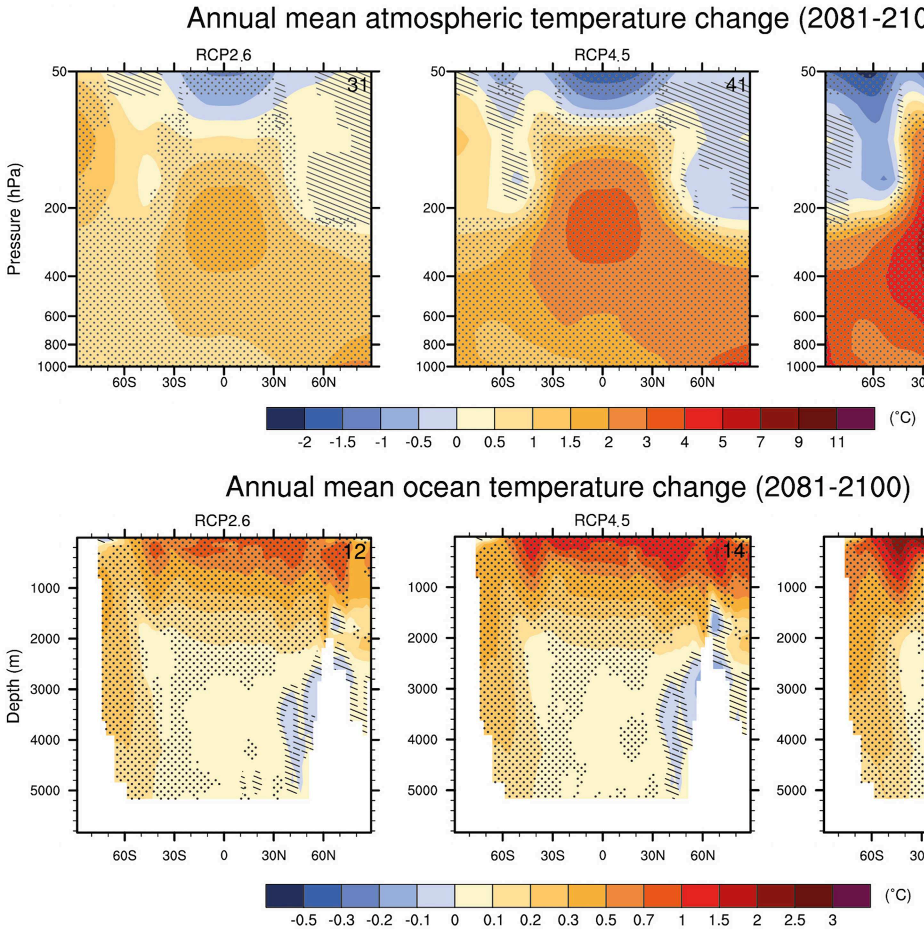


FIGURE 3 | CMIP5 multi-model changes in annual mean zonal mean temperature in the atmosphere and ocean relative to 1986–2005 for 2081–2100 under the RCP2.6 (left), RCP4.5 (center) and RCP8.5 (right) forcing scenarios. Hatching indicates regions where the multi model mean is less than one standard deviation of internal variability. Stippling indicates regions where the multi model mean is greater than two standard deviations of internal variability and where 90% of the models agree on the sign of change Source: Collins et al. (2013).

the observed global warming trend and double the previously suggested rate of warming for the area (Brand et al., 2014). Conversely, SST measurements have decreased in the Southern Ocean, particularly around the sea ice margins, possibly due to runoff from melting shelf ice cooling and freshening surface waters in the surrounding areas (Bintanja et al., 2013).

A recent estimate suggested that, in the last decade, about 30% ocean warming has occurred below 700 m, contributing significantly to an acceleration of the warming trend (Balmaseda et al., 2013). Warming of deep waters is thought to be particularly strong in the Southern Ocean with a rate of up to 0.05°C decade^{-1} (Patara and Böning, 2014). The warming of deep Antarctic waters, may, in turn, strengthen the large-scale meridional overturning of the Atlantic Ocean (Patara and Böning, 2014).

Results from recent studies agree with the AR5 in predicting high variability for future SSTs: the strongest warming trends are predicted in the Arctic Ocean, the tropics and the North Pacific with increases larger than 4°C in all 3 regions, under scenario RCP8.5 (**Figure 3**; Bopp et al., 2013). Model projections of surface ocean warming are projected to be +2.73 ±0.72, +1.58 ±0.48, +1.28 ±0.56 and +0.71 ±0.45°C for RCP8.5, RCP6.0, RCP4.5 and RCP2.6, respectively by the end of the 21st century (**Figure 3**; Bopp et al., 2013).

Upwelling

AR5 Summary

There is considerable debate as to whether climate change will drive a universal intensification of upwelling (Hoegh-Guldberg et al., 2014). There is *robust evidence* and *medium agreement* that the California Current has experienced a decrease in the number of upwelling events (23–40%), but *high confidence* that there has been an increase in the intensity of upwelling events between 1967 and 2010 (Hoegh-Guldberg et al., 2014). In the Canary Current, there is *low agreement* on whether the strength of the upwelling has intensified over the last 60 years (Hoegh-Guldberg et al., 2014).

It is considered *very likely* that continued warming would continue to increase thermal stratification (Ciais et al., 2013), potentially decreasing the availability of inorganic nutrients to surface waters. It is *likely* that the response will vary geographically, as complex systems govern these water mass movements (Ciais et al., 2013). Intensification of upwelling is predicted in the Southern Ocean, however, there is *low confidence* in the current understanding of how eastern upwelling systems will be altered under future climate change (Ciais et al., 2013). In the Benguela Current there is *medium agreement* and *limited evidence*, that upwelling will change as a result of climate change (Hoegh-Guldberg et al., 2014). It is considered *likely* that warming in the Atlantic equatorial upwelling systems will weaken upwelling (Hoegh-Guldberg et al., 2014).

Updates to AR5

Meta analysis of the last 60 years found intensification of upwelling favorable winds over the California, Benguela, and Humboldt upwelling systems (Sydeman et al., 2014). Jacox et al. (2014) reported an increase in nearshore ($\leq$50 km from the shore) upwelling in the California Current System between 1988 and 2010 but a decrease in off shore (50–200 km) upwelling for the same period. The authors attribute these differences to large-scale climate mode fluctuations.

New model projections predict strong changes in in the intensity, timing and spatial heterogeneity of Eastern Boundary Upwelling Systems (EBUS) by 2100 (Wang et al., 2015). The projections show earlier onset and later end of the upwelling season, as well as an increase in upwelling intensity at higher latitudes. These predictions were consistent for the Benguala, Canary and Humboldt Current systems but not for the California Current System.

Sea Level Rise

AR5 Summary

Sea level varies relative to changes in temperature (thermosteric sea level rise) and fluxes of water between the oceans and the continents and ice sheets (mass sea level rise). Global mean sea level (GMSL) has risen by 0.19 $\pm$ 0.02 m over the period 1901–2010 (Rhein et al., 2013). It is *very likely* that the mean rate was 1.7 $\pm$ 0.2 mm yr^{-1} between 1901 and 2010 and increased to 3.2 $\pm$ 0.4 mm yr^{-1} between 1993 and 2010. Ocean thermal expansion and melting of glaciers have accounted for over 80% of the GMSL rise over the latter part of the time series (Church et al., 2013). Although records for the deep sea are sparser, it is possible to estimate that warming below 2000 m contributed 0.1 [0.0 to 0.2] mm yr^{-1} to GMSL rise between about 1992 and 2005 (Rhein et al., 2013). The component of sea level rise that is attributed to changes in fluxes of water between the oceans and the continents and ice sheets has been increasing at a rate between 1 and 2 mm yr^{-1} since 2002 (Rhein et al., 2013).

There is *very high confidence* that there is high regional variability in sea level rise, with relative sea level rise sometimes exceeding global mean sea level rise by an order of magnitude, reaching more than 10 cm yr^{-1} (Church et al., 2013). This variation is partly due to fluctuations in ocean circulation, tectonic activity and interactions with climate mode variability such as the ENSO in the Pacific (Church et al., 2013). Anthropogenic activities such as oil and gas extraction and changes to the coastal sediment delivery via damming or consolidation from building work have also contributed to localized changes in relative sea level (Church et al., 2013). Sea level rise in coastal boundary systems is variable but, in some regions, has risen by up to 10 mm yr^{-1} between 1950 and 2009 (Hoegh-Guldberg et al., 2014). In the Pacific, changes in sea level have been highly variable, in the warm pool of the western Pacific, rates of sea level rise are up to three times higher than the global average (Rhein et al., 2013), while the eastern equatorial Pacific has been declining by -10 mm yr^{-1} (Hoegh-Guldberg et al., 2014).

It is *virtually certain* that sea level rise will continue beyond the 21st Century (Church et al., 2013). Future rates of GMSL rise over the 21st century are projected to exceed the observed rate for the period between 1971 and 2010 of 2.0 $\pm$ 0.3 mm yr^{-1} (Church et al., 2013) for all RCP scenarios.

Updates to AR5

The AR5 reports *low agreement* on the projected magnitude of sea level rise due to the use of different models, some of which take into account ice sheet dynamics (Church et al., 2013). The IPCC AR5 predicts with *medium confidence* that the mean sea level rise will be 0.44 m under RCP2.6, 0.53 m under RCP4.5, 0.55 m under RCP6.0, and 0.74 m under RCP8.5 (Church et al., 2013). Less conservative estimates of projected sea level rise have been published since and a more recent study suggested it *very likely* that GMSL would reach 0.5–1.2 m under RCP8.5 and 0.4–0.9 m under RCP4.5 (Kopp et al., 2014; Slangen et al., 2014).

Oxygen

AR5 Summary

Due to the solubility effect, warmer waters contain less dissolved oxygen. Increased stratification, as a result of warming, decreases ventilation of water masses, also causing decreased oxygen concentration. When [O$_2$] are below 60 μmol kg^{-1} conditions become hypoxic, below 4.5 μmol kg^{-1}, waters are termed suboxic and waters without measurable dissolved oxygen are termed anoxic (**Figure 4**; Pörtner et al., 2014).

There is *medium confidence* that dissolved oxygen concentrations generally decreased since 1960 but with strong regional variations (Rhein et al., 2013). The mean annual global oxygen loss during 1970–1990 between 100 and 1000 m is calculated as 0.55 $\pm$ 0.13 $\times$ 10^{14} mol yr^{-1} (Rhein et al., 2013). Stratification-induced reduced ventilation is thought to be the major cause of this decline, with solubility effect accounting for only 15% of the decrease (Rhein et al., 2013). Naturally occurring, periodic hypoxic events may be exacerbated by climate change (Rhein et al., 2013).

Decreases in [O$_2$] have been observed over the last 50 years in tropical basins (-2 to -3 μmol kg^{-1} decade^{-1}), the subpolar North Pacific and below the thermocline in the southern Indian Ocean east of 75°E (Hoegh-Guldberg et al., 2014). Over the same period, [O$_2$] decreased in North Atlantic surface waters but increased in intermediate waters (Hoegh-Guldberg et al., 2014). Conversely, it increased in the thermocline in the Indian Ocean and South Pacific Oceans between the 1990's and 2000's (Hoegh-Guldberg et al., 2014). Results for the Southern

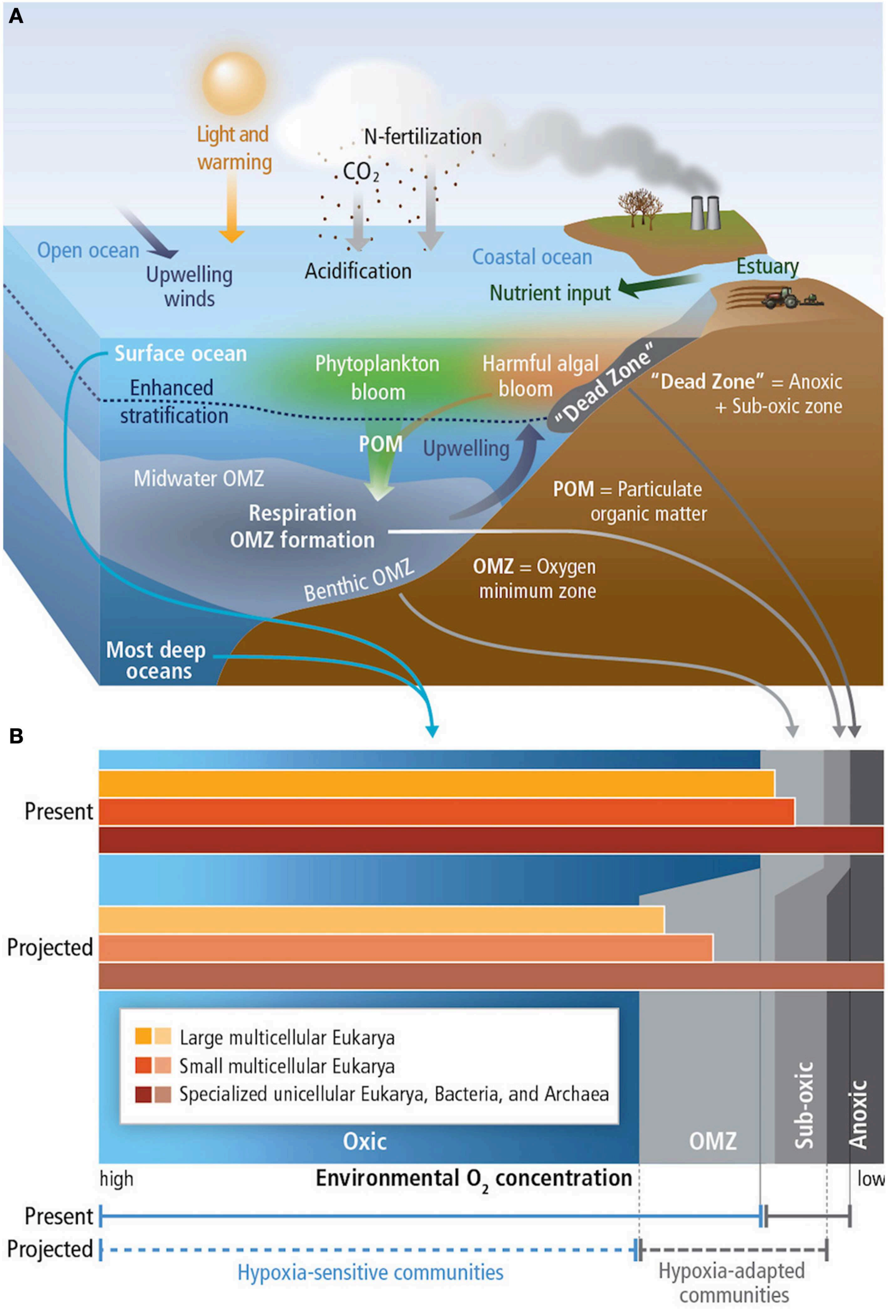


FIGURE 4 | (A) Principal mechanisms underlying the formation of hypoxic conditions and their biological background. The buoyant, fresh input from rivers produces sharp density stratification at the base of the freshened layer (also valid for ice melt and high precipitation) near the surface and, hence, vertical mixing is greatly reduced. In consequence, the nutrient inputs from the river and the atmosphere accumulate in a narrow upper layer, leading to blooms of phytoplankton. The increased oxygen consumption due to aerobic decomposition of sinking particulate organic matter (POM) results in hypoxic conditions of benthic and mid-water oxygen minimum zones (OMZs). Enrichment of nutrients (eutrophication) results in coastal dead zones. In the open oceans, heating of the upper layer increases stratification, while the wind-driven upwelling of hypoxic, nutrient-rich water from deeper layers adds to the formation of the OMZs. **(B)** Distribution of free-living marine organisms (microbes such as archaea, bacteria), in various water layers. Hypoxia tolerance is enhanced in small compared to large organisms, allowing unicellular species and small animals to thrive in extremely hypoxic habitats. Species richness and body size of animals decrease with falling O_2 levels. Source: Pörtner et al. (2014).

Ocean are contradictory depending on region and time period and require further clarification (Rhein et al., 2013). Along the continental shelf, large regions of the Eastern Pacific are low in dissolved oxygen and oxygen minimum zones (OMZ) are found at around 300 m depth (Hoegh-Guldberg et al., 2014).

The shoaling lysocline as a result of ocean acidification means that it is *likely* that upwelling waters will be both depleted in oxygen and acidified (Rhein et al., 2013). Coastal regions, particularly along the west coast of North America, have exhibited decreases in $[O_2]$ due to increased stratification and it has been suggested that oxygen concentrations in coastal areas may be declining approximately 10 times faster than the open ocean, although more data are needed to confirm this hypothesis (Hoegh-Guldberg et al., 2014). Due to the greater solubility of O_2 in cold waters and the low microbial activity, deep sea waters are relatively well oxygenated (Hoegh-Guldberg et al., 2014). However, oxygen concentration is decreasing in the deep sea, with the largest decline at intermediate water depths (<1000 m), some deeper waters are also decreasing in O_2 (Hoegh-Guldberg et al., 2014).

Ocean warming will *very likely* lead to further declines in dissolved O_2, estimates of global decline range between 6 and 12 μmol kg^{-1} by 2100, depending on the RCP scenario (Ciais et al., 2013). The regions most affected by decreasing O_2 are the intermediate to deep waters of the North Atlantic, North Pacific and Southern Ocean with declines between 20 and 200 μmol kg^{-1} by 2100 (Hoegh-Guldberg et al., 2014).

Updates to AR5

Recent model projections agree with AR5, suggesting a decrease in oxygen concentration under every RCP scenario. The modeled mean reduction in global ocean $[O_2]$ is -3.4, -2.5, -2.3, and -1.8% by the end of the century relative to the 1990s, for RCP8.5, RCP6.0, RCP4.5, and RCP2.6, respectively (Bopp et al., 2013).

Models have been limited in their simulation of present day O_2 concentration (Cocco et al., 2013) and as a result there is uncertainty surrounding the expansion of hypoxic and suboxic zones, the AR5 report considers it *as likely as it is unlikely* that they will expand (Ciais et al., 2013). Cocco et al. (2013) used models representing the interactions between the physical climate system, biogeochemical cycles and ecosystems and predicted a decrease in total ocean dissolved oxygen inventory of 2–4% between 1870 and 2100. The authors found relatively small changes were projected in the volume of hypoxic and suboxic waters. Suboxic waters were projected to decrease in volume by $\leq$10%. There were discrepancies between model results for more oxygenated waters; the majority of models predict an expansion of between 2 and 16% for regions with less than 80 mmol m^{-3} and a decrease in volume of between 0.4 and 4.5% for water with less than 50 mmol m^{-3}.

Ocean Acidification

AR5 Summary

CO_2 absorbed by the ocean reacts with the seawater and causes a decrease in pH, changing the relative abundances of the dissolved inorganic carbonate species: the concentration of bicarbonate ions (HCO_3^-) increases while the concentration of carbonate ions (CO_3^{2-}) decreases, lowering the saturation state (Ω) of $CaCO_3$. The carbonate system of seawater, including saturation state, is affected by temperature, salinity and pressure and, thus, varies regionally and with depth. The chemical response of the oceans to increasing CO_2 is well understood with *very high confidence* (Rhein et al., 2013). There is *high confidence* that surface ocean pH has declined by 0.1 pH units since the beginning of the Industrial Era, corresponding to a 26% increase in the concentrations of H^+ ions (Rhein et al., 2013). Direct measurements show that the rate of pH decrease is between -0.0014 and -0.0024 units yr^{-1} in surface waters (Rhein et al., 2013).

Regional estimates vary, with some areas better sampled than others. There is a paucity of time series measurements in the Southern Ocean surface waters; however, the available data suggest rates similar to those seen globally (Rhein et al., 2013). Anthropogenic CO_2 has reached at least 1000 m in all three ocean basins and deeper in the Atlantic (Hoegh-Guldberg et al., 2014). As the waters at the bottom of some oceans basins are very old, it will take many centuries for full equilibration of deep ocean waters to recent global warming and CO_2 perturbation (Cao et al., 2014; Hoegh-Guldberg et al., 2014). In upwelling areas, upwelled water is high in dissolved CO_2, exacerbating ocean acidification driven by anthropogenic activities (Hoegh-Guldberg et al., 2014).

It is *virtually certain* that the continued uptake of CO_2 by the oceans will increase ocean acidification (Ciais et al., 2013). Global decreases in seawater pH are projected to be 0.065 for RCP2.6, 0.145 for RCP4.5, 0.203 for RCP6.0 and 0.31 for RCP8.5 in 2081–2100 compared to 1986–2005 (Ciais et al., 2013). The extent of ocean acidification will vary regionally and seasonally with undersaturated conditions first reached in wintertime (Ciais et al., 2013). The largest decreases in the concentration of CO_3^{2-} will be in warmer low and mid-latitudes, as these areas are naturally high in CO_3^{2-} concentration but high latitudes and coastal upwelling areas are projected to be the first to become undersaturated (Ciais et al., 2013).

Updates to AR5

It has recently been demonstrated that anthropogenic trends in ocean acidification emerge quickly from the background noise of natural variability on the local-to-regional scale. Anthropogenic trends in surface ocean pH (and pCO_2) emerge within roughly 12 years, for the majority of the global ocean area, compared to between 10 and 30 years for surface ocean DIC and 45–90 years for SST (Keller et al., 2014). This implies that anthropogenic carbon emissions have already forced surface pH values beyond the range of 20th century natural variability.

Baseline monitoring of the Western Arctic Ocean estimates that 20% of Canadian Basin surface waters are undersaturated with respect to aragonite (Robbins et al., 2013) and that the saturation horizon is shoaling; over 67 and 22% of the bottom water of Hudson Bay was undersaturated with respect to aragonite and calcite, respectively (Azetsu-Scott et al., 2014). In the Arctic, Ω decreases during ice formation and increases during ice melt, resulting in a five times larger seasonal amplitude of the carbonate system in the upper 20 m compared to what is observed in sea ice free systems (Fransson et al., 2013). Calculated pH trends for the North Atlantic Gyre suggest a decrease of -0.0022 ± 0.0004 units yr^{-1} over the period 1981–2007 (Lauvset and Gruber, 2014). In the North Pacific, a pH decrease of -0.0011 ± 0.0004 units yr^{-1} from 1997 to 2011 has been calculated (**Table 3**; Wakita et al., 2013).

It is *unlikely* that more than 10% of global surface waters will maintain Ω_a higher than 3 if atmospheric CO$_2$ exceeds 550 ppm by 2100 (Steinacher et al., 2013). It is predicted that when atmospheric CO$_2$ reaches four times its pre-industrial level, global mean saturation state of aragonite (Ω_a) horizon will shoal from the pre-industrial levels of 1288 m to 143 m (Cao et al., 2014).

Under RCP8.5, pH reductions exceeding 0.2, units are projected in 23% of North Atlantic deep-sea canyons and ~8% of seamounts (Gehlen et al., 2014). Recent work has found intermediate waters to be twice as sensitive to increased carbon concentrations as surface waters and project higher rates (-0.0008 to -0.0023 ± 0.0001 units yr^{-1}, the depending on RCP) of acidification in intermediate waters than surface waters over centennial timescales (Resplandy et al., 2013).

Recent projections of future ocean acidification in Polar Regions estimate that increased ice melt in the Arctic would lead to enhanced oceanic uptake of inorganic carbon to the surface layer (Fransson et al., 2013; Reisdorph and Mathis, 2014). Within 10 years, 10% of its waters will be undersaturated with respect to aragonite, and by 2025, under all RCP scenarios, 10% of its waters are projected to be undersaturated with respect to calcite (Popova et al., 2014). It is considered *likely* that large regions of Antarctic and Sub-Antarctic surface waters will become undersaturated with respect to aragonite by 2030 (Mattsdotter Björk et al., 2014).

Biological Impacts of Climate Change and Ocean Acidification

In the following sections the main findings for the impacts of changes in temperature, dissolved oxygen and ocean acidification are summarized for microbes, plants, animals and ecosystems. Corals and coral reefs are treated separately as they represent a unique and important habitat that is particularly sensitive to the effects of climate change and ocean acidification.

Impacts of Ocean Warming

The AR5 states that all organisms have an optimum range of temperature at which physiological processes are most efficient. The impact of changing temperature depends on the organism's specific window of thermal tolerance and ability to acclimate or adapt to changing conditions, both of which vary greatly among species. Exceeding these limits can have effects on a wide range of physiological processes (Poloczanska et al., 2014; Pörtner et al., 2014).

Organism-specific temperature ranges dictate the distribution of organisms. A common adaptation to changing temperature is the displacement of a species to areas of more favorable temperature (Poloczanska et al., 2014; Pörtner et al., 2014). Hence, under a warming scenario, poleward migrations are expected; however, possibilities for migration are limited for polar organisms. Organisms also respond to temperature-driven changes in the physical environment such as stratification, reduced sea-ice cover and freshening (Pörtner et al., 2014). Unfortunately, for many organisms, poleward movement may be limited by other factors that restrict migration (Pörtner et al., 2014).

According to the AR5 there is *high confidence* that polar and tropical species are most, and temperate species least vulnerable, to changes in temperature (Pörtner et al., 2014). As ocean temperatures are less variable in the Southern Hemisphere than the Northern Hemisphere, species from the polar regions of the Southern Hemisphere are predicted to be the most vulnerable to increasing temperature (Larsen et al., 2014) and more recent studies add weight to this statement, highlighting

TABLE 3 | Long-term trends of atmospheric (pCO$_2$ atm) and seawater carbonate chemistry (i.e., surface-water pCO$_2$, and corresponding calculated pH, CO$_3^{2-}$ and aragonite saturation state (Ω_a) at four ocean time series in the North Atlantic and North Pacific oceans: (1) Bermuda Atlantic Time-series Study (BATS, 31°40′N, 64°10′W) and Hydrostation S (32°10′N, 64°30′W) from 1983 to present; (2) Hawaii Ocean Time series (HOT) at Station ALOHA (A Long-term Oligotrophic Habitat Assessment; 22°45′N, 158°00′W) from 1988 to the present); (3) European Station for Time series in the Ocean (ESTOC, 29°10′N, 15°30′W) from 1994 to the present; and (4) Iceland Sea (IS, 68.0°N, 12.67°W) from 1985 to 2006.

Site	Period	pCO$_2^{atm}$(μ atm yr^{-1})	pCO$_2^{sea}$(μ atm yr^{-1})	pH$_T$(yr^{-1})	[CO$_3^{2-}$](μ mol kg^{-1} yr^{-1})	Ω_a(yr^{-1})
BATS	1983–2009	1.66 ± 0.01	1.92 ± 0.08	−0.0019 ± 0.0001	−0.59 ± 0.04	−0.0091 ± 0.0006
	1985–2009	1.67 ± 0.01	2.02 ± 0.08	−0.0020 ± 0.0001	−0.68 ± 0.04	−0.0105 ± 0.0006
	1988–2009	1.73 ± 0.01	2.22 ± 0.11	−0.0022 ± 0.0001	−0.87 ± 0.05	−0.0135 ± 0.0008
	1995–2009	1.90 ± 0.01	2.16 ± 0.18	−0.0021 ± 0.0001	−0.80 ± 0.08	−0.0125 ± 0.0013
ALOHA	1988–2009	1.73 ± 0.01	1.82 ± 0.07	−0.0018 ± 0.0001	−0.52 ± 0.04	−0.0083 ± 0.0007
	1995–2009	1.92 ± 0.01	1.58 ± 0.13	−0.0015 ± 0.0001	−0.40 ± 0.07	−0.0061 ± 0.0028
ESTOC	1995–2009	1.88 ± 0.02	1.83 ± 0.15	−0.0017 ± 0.0001	−0.72 ± 0.05	−0.0123 ± 0.0015
IS	1985–2009	1.75 ± 0.01	2.07 ± 0.15	−0.0024 ± 0.0002	−0.47 ± 0.04	−0.0071 ± 0.0006
	1988–2009	1.70 ± 0.01	1.96 ± 0.22	−0.0023 ± 0.0003	−0.48 ± 0.05	−0.0073 ± 0.0008
	1995–2009	1.90 ± 0.01	2.01 ± 0.37	−0.0022 ± 0.0004	−0.40 ± 0.08	−0.0062 ± 0.0012

Modified from Rhein et al. (2013).

the vulnerability of Southern Hemisphere polar organisms to temperature changes (Chambers et al., 2013; Constable et al., 2014; McBride et al., 2014).

Microbes

AR5 summary

According to the AR5, warming will enhance microbial growth. As thermal tolerances are species-specific, continued warming causes changes in species compositions with warmer conditions favoring smaller sized species (Pörtner et al., 2014).

Updates to AR5

Recent work by De Senerpont Domis et al. (2014) supports the assertions of the AR5; showing warming to enhance phytoplankton growth rates (2014). However, several studies find that growth is strongly modulated by nutrient availability, suggesting that under more stratified conditions warming may have a net negative effect on phytoplankton growth (Chust et al., 2014; Lewandowska et al., 2014; Marañón et al., 2014). New model results predict that warming of 2.3°C leads to a 6% reduction in phytoplankton biomass (Chust et al., 2014). Recent work supports the IPCC findings that phytoplankton, including those that cause harmful algal blooms (HABs), are the taxon that has displayed the largest latitudinal range shifts concurrent with climate change, with average distribution shifts of over 400 km decade^{-1} (Glibert et al., 2014; Poloczanska et al., 2014). In line with the findings of AR5, Calbet et al. (2014) observed shifts in microplankton species compositions, suggesting implications for the global carbon pump, as small size cells are likely to be re-mineralized to inorganic carbon at shallower depths. Recent work has shown that the coccolithophore *Emiliania huxleyi* is capable of evolutionary adaptation to ocean warming similar to that predicted under RCP8.5 (Benner et al., 2013; Schluter et al., 2014).

Rising temperature has been shown to influence host-pathogen interactions, increasing infectious disease outbreaks with pathogens moving polewards (Baker-Austin et al., 2013; Burge et al., 2014).

Macroalgae and Seagrasses

AR5 summary

There is *high confidence* that macrophytes are limited in thermal tolerance and, thus, sensitive to warming, especially in lower latitudes (Pörtner et al., 2014). Thermal stress has been shown to affect photosynthesis, growth, reproduction and survival, with subsequent consequences for macrophyte abundance, distribution, and productivity. Sea ice retreat in polar areas has allowed an expansion of macroalgal distribution, via increased habitat availability (Pörtner et al., 2014).

Updates to AR5

Recent publications support the assertions of the AR5, observing different distribution shifts and responses to warming in warm and cold-water species (Brodie et al., 2014; Komatsu et al., 2014) However, there are some inconsistencies in the literature as Brodie et al. (2014) predict, "seagrass will proliferate" in the North Atlantic under future warming. Recent publications add further evidence that, in temperate regions, kelp mortality, spore mortality and germination will be negatively affected by projected temperature increases under RCP8.5 (Brodie et al., 2014; Gaitán-Espitia et al., 2014). Warming has also been found to increase the incidence and/or severity of marine diseases affecting eelgrass (Bockelmann et al., 2013). Increased warming increases the Mg levels in the calcite of crustose coralline algae although, no significant trend was observed in samples collected between 1850 and 2010 (Williamson et al., 2014).

Animals

AR5 summary

There is *high confidence* that surpassing species-specific heat tolerance limits during warming causes reduced abundance, mortality, shifts in the seasonal timing, and changes in individual growth, development, calcification and immunity (Poloczanska et al., 2014; Pörtner et al., 2014). Although laboratory studies commonly use temperature means, there is evidence that extreme temperatures events illicit greater species response than sustained temperature means, causing mortality and/or latitudinal/depth range distribution shifts that can cause localized extinctions (*high confidence*; Pörtner et al., 2014). During early life, owing to incomplete development, or as adult spawners, due to large body size, animals can become more sensitive to warming (Pörtner et al., 2014).

Updates to AR5

More recent work continues to strongly support the findings of AR5 that many species are undergoing geographical and phenological shifts as a result of warming (Vehmaa et al., 2013; Goberville et al., 2014; Kamya et al., 2014; Mackenzie et al., 2014a; Church et al., 2013; Mackenzie et al., 2014a,b,c; Queirós et al., 2014; Rice et al., 2014). The AR5 found that zooplankton have exhibited some of the most extreme geographic range shifts of over 100 km decade^{-1} (Poloczanska et al., 2014). Subsequent work has observed significant distribution shifts of copepod species in the North Sea and North Atlantic in conjunction with warming between 1958 and 2009 (Beaugrand et al., 2014). Latitudinal range shifts have also been observed in benthic cnidarians, molluscs and crustacea, non-bony fish and bony fish (Engelhard et al., 2014; Poloczanska et al., 2014; Potts et al., 2014).

Temperature also governs the distribution and abundance of large pelagic fish in the Indian, Pacific and Atlantic Oceans and the work of Mackenzie et al. (2014a) adds weight to the *high confidence* of the statement in the AR5 that temperature anomalies caused a major shift in tuna distribution in these areas. This may cause high vulnerability in seasonally spawning fish species (Crozier and Hutchings, 2014; Elettra et al., 2014). There is *medium confidence* that warming also causes a decrease in the body size of some marine fishes (Rice et al., 2014).

Warming has been shown to increase disease incidence in many marine organisms (reviewed in Burge et al., 2014) and impair immune responses in host organisms, including shellfish (Travers et al., 2009), corals (Harvell et al., 2009), and finfish (reviewed in Bowden, 2008). Recent reemergence of *Vibrio tubiashii*, a bacterial pathogen of larval Pacific oysters, was linked to warming and upwelling of low pH waters (Elston et al., 2008). In some cases, though, adaptation to warming may reduce disease, as heat-resistant Pacific oysters were more resistant to infection by a herpesvirus (Dégremont, 2011).

Recent work continues to highlight the effects of secondary drivers such as ocean acidification, hypoxia and food availability on the capacity of an organism to adapt to changing temperatures and increasing numbers of recent studies are highlighting the interactive effects of temperature and secondary drivers (Vehmaa et al., 2013; Ko et al., 2014; Mackenzie et al., 2014b,c; Madeira et al., 2014; Pope et al., 2014). A recent study has demonstrated that trans-generational plasticity can mediate the effects of warming in a fish species (Shama et al., 2014); however, there remains *low confidence* in our understanding of the potential evolutionary adaptation to warming.

Warm and Cold Water Coral Communities

AR5 summary

Thermal tolerance and recovery capacity of the coral host and the symbiotic dinoflagellates varies with geography and among species (Wong et al., 2014). Mass bleaching has more widespread during the last 20 years; 7% of the reef locations exhibited at least one bleaching event between 1985 and 1994 compared to 38% between 1995 and 2004 (Wong et al., 2014). There is *very high confidence* that bleaching has the potential to cause up to 50% mortality, resulting in declining coral abundance (**Figure 5**; Wong et al., 2014).

There is *high confidence* that mass coral bleaching events have occurred in all three sub-tropical gyre (STG) regions, in conjunction with warming (Hoegh-Guldberg et al., 2014). In the Pacific, there has been a steady decline in coral cover on coastal coral reef ecosystems ranging between 0.5 and 2.0% yr^{-1} (Hoegh-Guldberg et al., 2014). High temperature in the Atlantic STG caused coral mortality in the eastern Caribbean (Eakin et al., 2010a,b), and in the Indian Ocean, coral cover declined by an average of 38% following the 1998 and 2010 temperature extremes (*high confidence*; Hoegh-Guldberg et al., 2014).

Studies of the thermal sensitivity of cold-water corals are scarce. One species, *Lophelia pertusa*, responds to 3°C warming with a three-fold increase in metabolic rate, indicating a narrow thermal window (Pörtner et al., 2014).

Updates to AR5

Studies continue to find that thermal tolerance and recovery capacity of the coral host and the symbionts varies geographically and among species (Alemu and Clement, 2014; Cantin and Lough, 2014; Comeau et al., 2014c; Falter et al., 2014; McClanahan and Muthiga, 2014). Nevertheless, mass bleaching events are becoming more predictable due to their relationship with sustained temperature anomalies of 1 to 2°C above the long-term summer maximum (Liu et al., 2014).

Several coral diseases and resultant mortalities have increased with ocean warming (see review in Burge et al., 2014). Population crashes of two key reef-building corals (*Acropora cervicornis* and *Acropora palmata*) in the Caribbean (Gladfelter, 1982; Aronson and Precht, 2001) have now been linked to ocean warming (Randall and Van Woesik, 2015) and have had drastic impacts on coral reef ecosystems throughout the region, leading to listing of the species as Threatened under the United States' Endangered Species Act (Weijerman et al., 2014). Temperature increases of 6°C have also been observed to reduce the production of mucous, which may increase susceptibility to coral diseases (Pratte and Richardson, 2014). Dispersal of coral larva is also reduced under high temperatures, which will weaken connectivity among populations, thus potentially slowing recovery if local populations are severely affected (Figueiredo et al., 2014).

Some thermally tolerant species are able to divert cellular energy into mechanisms for survival and recovery of short-term heat stress but at the expense of growth and biomineralization (Maor-Landaw et al., 2014). Studies have shown that repeat bleaching may impact thermal tolerance; some species are able to rapidly acclimatize while others become more susceptible (Grottoli et al., 2014). Models also provide limited evidence that corals have some capacity to acclimatize to high temperatures but even considering possible adaptation, it is projected that under RCP4.5, two thirds of the world's reefs will be subject to long-term degradation (Grottoli et al., 2014; Logan et al., 2014; Palumbi et al., 2014).

Recent work has also suggested that increased temperature and [CO_2] may cause cold-water corals to accumulate dimethylsulphoniopropionate (DMSP) from the water column. It has been suggested corals use DMSP in response to environmental challenges, implying an acclimation response to CO_2 stress (Burdett et al., 2014).

Ecosystems

AR5 summary

Ecosystems that are built around heat sensitive organisms such as coral reef or kelp forests, may be at increased risk from warming-induced habitat loss. Within ecosystems, different tolerances of individual species can cause changes in inter-specific competition, trophic dynamics and species compositions. There is *low confidence* in predicting how ecosystems will react to immigration of animals as a result of climate change (Pörtner et al., 2014).

There is *medium confidence* that in most semi-enclosed seas, temperature induced faunal latitudinal range shifts have occurred and in the Mediterranean, Black, and Baltic Seas, increased temperatures have prompted colonization by invasive warmer water species (Hoegh-Guldberg et al., 2014). There is *medium confidence* that loss of summer sea ice and increased ocean temperature will enhance secondary pelagic production in some regions of the Arctic). There is *high confidence* that these changes will alter the species composition and carrying capacity with subsequent effects on fish and shellfish populations (*medium confidence*; Larsen et al., 2014).

Updates to AR5

New evidence continues to add to the *high confidence* level that observed changes in distribution, phenology and reproduction of plants and animals in marine ecosystems are, at least partially, temperature induced (Chambers et al., 2013; Beaugrand et al., 2014; Goberville et al., 2014; Hiddink et al., 2014; Jones and Cheung, 2014; Kim et al., 2014; Lambert et al., 2014; Montero-Serra et al., 2014; Rice et al., 2014). As different species and

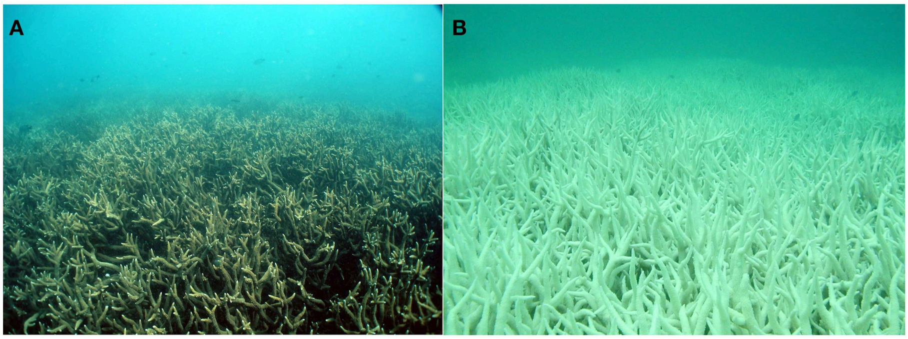


FIGURE 5 | The same coral community (A) before and (B) after a bleaching event in February 2002 at 5 m depth, Halfway Island, Great Barrier Reef. Approximately 95% of the coral community was severely bleached in 2002. Source: Elvidge et al. (2004).

groups have differential responses to warming, effects are seen at every trophic level and can also be amplified up the food chain (Pinsky et al., 2013; Chust et al., 2014). Changes in phenology are not synchronous among phyla and can cause predator-prey mismatches (Arula et al., 2014; Behrenfeld, 2014; Lewandowska et al., 2014), changes to species compositions (Albouy et al., 2014), alterations in food web body size (Gibert and Delong, 2014) and changes in food web composition (Verges et al., 2014). Recent work has suggested that this maybe most pronounced in systems governed by seasonal blooms (Behrenfeld, 2014).

Changes in the frequency, intensity, and geographic distribution of marine diseases have had significant impacts on many ecosystems, particularly if they affect keystone species (Burge et al., 2014).

Sea Level Rise

AR5 Summary

Vegetated habitats such as mangroves, seagrass meadows, intertidal rocky reefs and wetlands are the natural systems most affected by changes in sea level. There is *high confidence* that these habitats are in decline with the loss estimated to release 0.04–0.28 PgC yr^{-1} (Wong et al., 2014). Increasing sea levels as a result of warming have also caused reductions and range shifts in seagrass and mangrove systems in the Pacific region (Hoegh-Guldberg et al., 2014).

Updates to AR5

Recent research adds weight to the findings of AR5 by identifying vegetated habitats as being particularly vulnerable to sea level rise (Cazenave and Cozannet, 2014; Di Nitto et al., 2014; Murray et al., 2014b; Saintilan et al., 2014; Thorner et al., 2014). There is *medium confidence* that some coral reefs will be able to keep up with the projected rate of sea level rise (Hamylton et al., 2014; Woodroffe and Webster, 2014). However, increasing evidence suggests increased erosion and export of land-based sediments and pollutants will exacerbate existing stress to nearshore corals (Storlazzi et al., 2011). Because even small populations of humans in close proximity to coral reefs can be deleterious (Knowlton and Jackson, 2008), evacuation of low-lying islands may reduce stress to some reefs.

Decreasing Dissolved Oxygen Concentration

Under hypoxic conditions, species with higher O_2 demands are lost and, if hypoxic conditions are sustained, communities that thrive in low O_2 environments replace them (Pörtner et al., 2014). Oxygen demand depends on species, body size, life stage, metabolic activity and temperature. In extreme temperatures, critical O_2 concentration is almost the same as fully O_2 saturated water, indicating increased sensitivity to hypoxia in increased temperatures (Pörtner et al., 2014).

Microbes

AR5 summary

OMZs form habitat for both anaerobic and aerobic microbes that can utilize very low ($<1\ \mu mol\ kg^{-1}$) [O_2]. In OMZs, microbial respiration drives O_2 concentration down and maintains low concentrations. There is *high confidence* that microbial life will benefit from expanding OMZs (Pörtner et al., 2014).

Updates to AR5

Storch et al. (2014) observed communities shifting to smaller, multicellular Eukarya, Bacteria and Archaea under diminished O_2.

Animals and Plants

AR5 summary

Special adaptations to hypoxia and lower energy demand are present in animals that live permanently in OMZs but this is only possible for animals of small size (<1 mm), in cold temperatures (Pörtner et al., 2014). There is little information on the sensitivity of macrophytes to hypoxia; however, negative responses have been observed in eelgrasses so there is *medium confidence* that expanding benthic OMZs will constrain the distribution of macrophytes (Pörtner et al., 2014).

Updates to AR5

Few animals have developed strategies to temporarily cope with hypoxic conditions and recent research adds weight to the *high confidence* level that hypoxia-adapted life forms, such as the jumbo squid, will benefit from expanding OMZs (Stewart et al., 2014). Range expansion of hypoxia adapted squid has been observed (Stewart et al., 2014) and meta-analysis supported the oxygen- and capacity-limited thermal tolerance (OCLTT) theory on the interactive effect of O_2 and temperature (Portner, 2010), limiting the depth distributions of non-hypoxia adapted fish and invertebrates (Brown and Thatje, 2014).

Ecosystems

AR5 summary

There is *medium confidence* that expansions of OMZs, will result in habitat and abundance losses for taxa with high O_2 demands (Pörtner et al., 2014). As many pelagic species migrate vertically on a daily and seasonal basis, the shoaling of OMZs will affect migrations and shift microbial and faunal compositions to organisms that can tolerate brief exposure to hypoxia (*medium confidence*; Pörtner et al., 2014). Larval stages are particularly sensitive, suggesting that the impacts could threaten population survival and affect higher trophic levels (Pörtner et al., 2014). There is *high confidence* that, as a result of increased energy demand, calcifiers are particularly sensitive to hypoxia (Pörtner et al., 2014). Expansions of OMZs are predicted to compress habitat depth for hypoxia-intolerant fish (Hoegh-Guldberg et al., 2014). Oxidation reactions in OMZs release nitrogen into the atmosphere meaning that less fixed nitrogen is available to primary producers as a result there is *medium confidence* expansion of OMZs will limit primary productivity (Pörtner et al., 2014).

Updates to AR5

Observed range changes in non-hypoxia tolerant halibut, adds weight to the findings of AR5 (Sadorus et al., 2014). The work of Cheung et al. (2014) supports the assertions of the AR5, finding high sensitivity in the larvae of benthic invertebrates. Decreases in coral photosynthesis observed under hypoxic conditions suggest that decreasing oxygen concentrations could have potential negative implications for reef ecosystems (Wijgerde et al., 2014).

Ocean Acidification

A wide range of organismal functions are affected by ocean acidification including: membrane transport, calcification, photosynthesis, neuronal processes, growth, reproductive success and survival. Due to the direct effect of decreased Ω, calcifying species are thought to be at greatest risk from decreasing pH. Very little is known about the capacity for evolutionary adaptation as most experiments investigating the effects of ocean acidification are run over relatively short time periods (Pörtner et al., 2014). Here, the term ocean acidification primarily refers to the reduction in pH, the reduction in carbonate ion concentration Ω, and the increase in bicarbonate ion concentration and dissolved CO_2 concentration in response to carbon dioxide uptake.

Microbes

AR5 summary

Due to insufficient field observations there is *limited evidence* and *low agreement* on how future conditions will affect microorganisms. Ocean acidification can drastically alter the species composition of phytoplankton assemblages, and has been linked to increased occurrences of harmful algal blooms (HAB) of diatoms and dinoflagellates. There is *low* to *medium confidence* on the effects of ocean acidification on nitrogen (N_2) fixing cyanobacteria due to the wide range of N_2 fixation responses observed in laboratory experiments. There is *medium* to *high confidence* that foraminiferal calcification is negatively affected by acidification (Pörtner et al., 2014).

Updates to AR5

New research suggests that ocean acidification might benefit bacterial communities by elevating growth (Endres et al., 2014) and increased benthic bacterial diversity has been observed along natural CO_2 gradients (Taylor et al., 2014). Other studies have found no detectable effects of ocean acidification on natural bacterial communities (Ahrendt et al., 2014; Gazeau et al., 2014). There is *low* to *medium confidence* on the effects of ocean acidification on nitrogen (N_2) fixing cyanobacteria. A wide range of N_2 fixation responses under RCP8.5 conditions have been observed in laboratory experiments (Böttjer et al., 2014; Eichner et al., 2014; Gradoville et al., 2014), possibly due to species-specific differences in the mechanisms of N_2 fixation (Eichner et al., 2014).

There is *medium evidence* and *low agreement* on how coccolithophore growth and calcification will be affected as they exhibit highly varied responses depending on species, strain and secondary environmental controls such as irradiance, bloom species composition and nutrient availability (Benner et al., 2013; Horigome et al., 2014; Muller and Nisbet, 2014; Poulton et al., 2014; Sett et al., 2014; Young et al., 2014). There is evidence that the coccolithophore, *Emiliania huxleyi*, has the capacity to evolve genetic adaptions to both warming and ocean acidification expected under RCP8.5 (Benner et al., 2013; Lohbeck et al., 2014; Schluter et al., 2014).

Khanna et al. (2013) adds to the *medium* to *high confidence* that foraminiferal calcification is negatively affected by acidification. The severity of effects on benthic foraminifera are species and symbionts-specific (Doo et al., 2014). Planktonic foraminifera are predicted to experience the greatest decrease in diversity and abundance in sub-polar and tropical areas, under RCP8.5 (Roy et al., 2014).

Macroalgae and Seagrasses

AR5 summary

Non-calcifying species generally exhibit positive growth responses to increasing [CO_2] (Pörtner et al., 2014). There is *high confidence* that conditions of 720–1800 μatm CO_2 stimulate increases in primary production, shoot density, reproductive output and below ground biomass (Pörtner et al., 2014). There is *medium confidence* that impacts on calcification and respiration are observed when species-specific pCO_2 thresholds are surpassed (Pörtner et al., 2014).

Updates to AR5

Non-calcifying species generally exhibit positive growth responses to increasing [CO_2] although these responses are season and species specific (Longphuirt et al., 2013), although these effects can be modulated by nutrient availability (Martínez-Crego et al., 2014). The work of Betancor et al. (2014) adds more evidence to the *low confidence* levels of the AR5 that ocean acidification can impair the production of grazer-deterrent substances.

Recent work continues to find complex and varied responses to ocean acidification in calcifying macrophytes (James et al., 2014; Johnson et al., 2014b; McMinn et al., 2014). Changes in species composition along natural CO_2 gradients have been observed (Ordoñez et al., 2014) but negative effects on calcification can be mediated by inter-specific interactions (Reyes-Nivia et al., 2014; Short et al., 2014) and acclimatization (Johnson et al., 2014a). There is *medium confidence* that significant dissolution of living and dead maerl beds will occur, both of which provide important habitat for associated fauna (Brodie et al., 2014). Crustose coralline algae display species specific increases in calcification up to 900 μatm and decreases after the species-specific threshold is reached (McCoy and Kamenos, 2015). Greater instances of dissolution and deformities have also been observed in crustose coralline algae populations at natural CO_2 vent sites (Brinkman and Smith, 2015).

Animals

AR5 summary

Species-specific responses to ocean acidification are mixed (Pörtner et al., 2014). Amongst benthic invertebrates, calcifying organisms are more sensitive than non-calcifying. There is *medium confidence* that increased calcification under lowered pH increases energetic costs at the expense of other physiological processes (Pörtner et al., 2014). Early life stages are thought to be more sensitive to ocean acidification drivers and there is *high confidence* in attributing fatalities at oyster farms to upwelling, CO_2 rich waters. Despite experimental observation of ocean acidification effects, the AR5 highlights the lack of field evidence of current ocean acidification effects in natural communities (Pörtner et al., 2014).

Updates to AR5

Recent studies continue to find reduced calcification, reduced rates of repair calcification and weakened calcified structures under acidified conditions (Bressan et al., 2014; Coleman et al., 2014; Fitzer et al., 2014; Pörtner et al., 2014; Wei et al., 2015). Some species have been observed to increase calcification rates at $p\mathrm{CO}_2$ ranging from 600 to 900 μatm, before a decrease at higher $p\mathrm{CO}_2$ (Collard et al., 2014; Dery et al., 2014; Langer et al., 2014).

More evidence of the negative effects of decreasing pH on fertilization success of invertebrates has been found (Sewell et al., 2013; Bögner et al., 2014; Frieder, 2014; Scanes et al., 2014; Sung et al., 2014) and RCP8.5 acidification has been shown to have negative effects on clam larval dispersal (Clements and Hunt, 2014).

In the California Current System, pteropod shell dissolution due to undersaturated waters can already be observed (Bednaršek et al., 2014). Studies on non-calcifying zooplankton indicate a variety of sub-lethal effects under RCP8.5, including decreased egg production, lower hatch success and decreased survival of nauplii in copepods (Vehmaa et al., 2013; Zervoudaki et al., 2013; Pedersen et al., 2014). The AR5 has *high confidence* that embryos of Antarctic krill are vulnerable to increased seawater concentrations of CO_2 (Larsen et al., 2014) but Atlantic species have been found to be resilient (Sperfeld et al., 2014).

Fish, including some commercially important species such as cod and herring, have been shown to be reasonably resistant to the effects of ocean acidification (Jutfelt and Hedgärde, 2013; Chambers et al., 2014; Maneja et al., 2014). However, deformities in calcified structures (Pimentel et al., 2014) and damage to internal organs continue to be observed under conditions predicted for 2100 under RCP8.5 (Frommel et al., 2014). The strongest effects observed in fish are behavioral, lower pH has been observed to affect predator avoidance, prey detection, odor detection, retinal function, lateralization, boldness and swimming behaviors in fish (Caprio et al., 2014; Chung et al., 2014; Dixson et al., 2014; Domenici et al., 2014; Munday et al., 2014; Murray et al., 2014a; Welch et al., 2014).

Recently published reviews highlight the lack of long-term studies on ocean acidification and the lack of direct experimental evidence of evolutionary adaptation in animals (Reusch, 2014; Sunday et al., 2014). Nevertheless, evidence of a few examples of genetic variations are emerging and have been observed in sea urchins and polychaete worms (Calosi et al., 2013; Kelly et al., 2013; Pespeni et al., 2013), as well as genetic variations in fish that could illicit evolutionary adaptation (Malvezzi et al., 2015). Acclimatization and trans-generational phenotypic plasticity over longer-term experiments have been observed in sea urchins (Dupont et al., 2013) and carry over effects of brief exposure to acidification on growth of oyster larvae (Hettinger et al., 2013).

Warm and Cold Water Corals

AR5 summary

There is *high confidence* that warm-water corals will be sensitive to future ocean acidification, although the magnitude of response is species specific (**Figure 6**; Wong et al., 2014). Some species of warm-water and cold-water corals may display resistance to lowered pH and can maintain positive net calcification under aragonite saturation states <1 (Pörtner et al., 2014).

Updates to AR5

Observations of reductions in calcification continue to demonstrate a species-specific response in both cold and warm water species (Comeau et al., 2014d; Movilla et al., 2014), with fast calcifiers affected more than slow calcifiers (Comeau et al., 2014d). Holcomb et al. (2014) find that response is affected by the internal pH of the calcifying fluid. Despite inter-specific differences in pH tolerance, reef ecosystems may be disproportionately affected if keystone species are lost (Alvarez-Filip et al., 2013). The magnitude of calcification response to acidification is also highly geographically specific, suggesting that secondary factors such as irradiance, nutrient availability and interactions with other ecosystems, such as mangroves, can mediate the effects on calcification (Comeau et al., 2014a,c; Enochs et al., 2014; Gibbin et al., 2014; Tanaka et al., 2014; Wendel, 2014; Yates et al., 2014).

Ocean acidification has been shown to have significant effects on dissolution of warm-water corals, with up to 59% lower

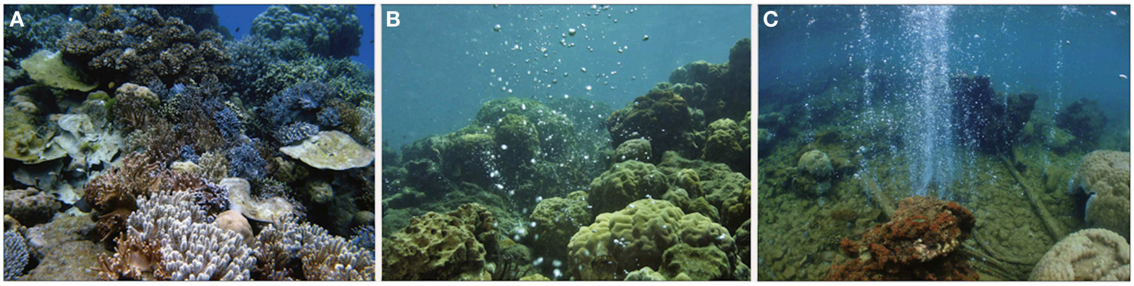


FIGURE 6 | Three CO_2 seeps in Milne Bay Province, Papua New Guinea show that prolonged exposure to high CO_2 is related to fundamental changes in the ecology of coral reefs. (A) Low pCO_2, $pH_T \sim 8.1$, **(B)** high pCO_2, $pH_T \sim 7.8$ to 8.0, **(C)** very high pCO_2, $pH_T < 7.7$. Source: Fabricius et al. (2011).

net community calcification (Comeau et al., 2014b; Silbiger and Donahue, 2014) observed under RCP8.5 conditions and already resulting in enhanced erosion of reef framework carbonates (Silbiger and Donahue, 2014). There is also evidence that acidified conditions can reduce fertilization and settling success of larvae (Uthicke et al., 2013).

Ecosystems

AR5 summary

As the effects of ocean acidification are complex and species specific, it is difficult to accurately assess the impacts at the ecosystem level. There is *high confidence* that ocean acidification will have a wide range of direct and indirect effects on ecosystems (Pörtner et al., 2014). There is *medium confidence* that naturally high CO_2 environments are associated with species compositions that favor non-calcifying species, suggesting that calcifiers are outcompeted once pH reaches 7.8–7.7 (Pörtner et al., 2014). There is *high confidence* that areas prone to low Ω, such as upwelling systems and the polar seas, will be strongly affected by ocean acidification. There is high confidence that Arctic ecosystems are also at high risk due to the exacerbating effects of freshwater from melting sea ice. There is *high confidence* that elevated CO_2 causes losses in diversity, biomass and trophic complexity of benthic marine communities (Pörtner et al., 2014).

Updates to AR5

A variety of recent publications further demonstrate that the severity and the magnitude of effects will vary with the type of ecosystem, geographical location, species composition and the influence of secondary environmental drivers (Garrard et al., 2014; Hendriks et al., 2014; Martínez-Crego et al., 2014; Park et al., 2014; Richier et al., 2014). There is added confidence that ecosystems built around heavily calcified structures such as coral and vermetid reefs or maerl beds are at high risk from ocean acidification (Alvarez-Filip et al., 2013; Brodie et al., 2014; Comeau et al., 2014b; Milazzo et al., 2014).

The Arctic food web is relatively simple, with pteropods acting as an important trophic link (AMAP, 2014). A recent assessment adds to the *medium confidence* of the AR5 that negative effects on pteropods will have wider consequences for the Arctic ecosystem, potentially affecting important fisheries (AMAP, 2014).

Effects of Multiple Drivers

There is *high confidence* that the effects of climate change will act on organisms and ecosystems as a suite of simultaneous environmental drivers which will interact with each other to have synergistic or antagonistic effects on the fitness of the individual or ecosystem. There is also growing evidence that the interactions of other environmental factors such as irradiance, nutrient availability geographic location and species community composition can strongly modulate the biological effects of warming, ocean acidification and hypoxia (Ko et al., 2014; Comeau et al., 2014a,c; Poulton et al., 2014; Pörtner et al., 2014).

Microbes

AR5 summary

Experiments and models show mixed responses to multiple drivers on microbial biota in the surface ocean. The effect of RCP8.5 levels of CO_2 on growth is species specific and these differences can alter bloom species compositions, with potential impacts on predator-prey interactions. Shifts to different phytoplankton species compositions can alter the sinking rates of particles, as bacteria decompose these particles, it can alter the levels of dissolved oxygen, potentially expanding OMZs (Pörtner et al., 2014).

Updates to AR5

Emiliania huxleyi has demonstrated the ability to adapt to concurrent warming and acidification (Lohbeck et al., 2014; Schluter et al., 2014). Recent work highlights that the effects of RCP8.5 levels of CO_2 on growth is species specific with and can be strongly modulated by nutrient availability (Hoppe et al., 2013; Marañón et al., 2014), light conditions and temperature (Errera et al., 2014; Sett et al., 2014).

Plants and Animals

AR5 summary

There is *high confidence* that the interaction among warming, acidification and hypoxia predicted for 2100 under RCP8.5 can have synergistic negative effects on organisms. There is *high confidence* that warming acts synergistically with CO_2 to decrease calcification and increase sensitivity to bleaching in warm-water corals (Comeau et al., 2014a; Pörtner et al., 2014). Combined warming and ocean acidification in mesocosms following approximately RCP4.5 and RCP8.5 scenarios caused losses of symbionts and corals, and a nocturnal decalcification of the reef community in summer (Pörtner et al., 2014). Hypoxia reduces heat tolerance and vice versa and there is *high confidence* that warming will expand the area of ecosystems affected by hypoxia, even if oxygen concentrations remain unchanged. This is likely to restrict geographic and depth ranges, particularly in upwelling areas (Pörtner et al., 2014).

Updates to AR5

It has been observed that increasing temperature increases the levels of Mg incorporated into crustose coralline algae calcite, with potentially synergistic negative effects with acidification as high Mg calcite dissolves more readily (Williamson et al., 2014). The combination of warming and high irradiance has been shown to increase bleaching in crustose coralline algae but recovery is possible if favorable conditions resume (McCoy and Kamenos, 2015).

Results continue to show interaction among warming, acidification and hypoxia effects under conditions predicted in 2100 under RCP8.5. Synergistic negative effects have been observed on the growth, survival, fitness, calcification and development of organisms (Padilla-Gamino et al., 2013; Vehmaa et al., 2013; Gaitán-Espitia et al., 2014; Gobler et al., 2014; Hyun et al., 2014; Mackenzie et al., 2014b; Madeira et al., 2014; Maugendre et al., 2014, Rastrick et al., 2014; Roy et al., 2014; Schram et al., 2014; Rosa et al., 2014a,b; Schmidt et al., 2014a). In some cases, hypoxic conditions have been observed to mediate the negative effects of ocean acidification (Mukherjee et al., 2013).

Ecosystems

AR5 summary

There is *high confidence* that the effects of climate change are already causing changes to the physical and chemical characteristics of habitats and altering food webs (Pörtner et al., 2014). There is *high confidence* that the indirect effects of climate change, such as shifts in stratification and productivity, expanding OMZs, and the changing composition and biomass of food are exacerbating the effects on ecosystems (Pörtner et al., 2014).

There is *high confidence* that the combined effects of increased temperature, hypoxia, and ocean acidification will have significant impacts on organisms that act as ecosystem engineers, such as coral or kelp (Dove et al., 2013; Pörtner et al., 2014). Thus, climate change could drastically alter ecosystems by reducing habitat quality and extent.

There is *high confidence* that species' range distributions and phenologies will be affected by climate change, altering the trophic interactions in a given area (Pörtner et al., 2014). It is likely that some of these changes may be irreversible as the effects of changes at the base of the food web can be amplified up trophic levels and drive the ecosystem to a new regime that may become permanent (**Figure 7**; Pörtner et al., 2014).

Updates to AR5

Recent studies have modeled the effects of multiple drivers on ecosystems highlighted implications for plankton biomass and trophic functioning (Chust et al., 2014; Guénette et al., 2014). Chust et al. (2014) predicted a global reduction in phytoplankton and zooplankton biomass by 6 and 11%, respectively, with negative tropic amplification of climate change effects for 47% of the ocean. A study focusing on the Scotian Shelf ecosystem found that the effects of climate change could be enhanced or ameliorated by predator–prey interactions and predicted a reduction in biomass of 19–29% by 2100 under RCP8.5 (Guénette et al., 2014).

Future Projections

Due to the relative lack of knowledge on the interacting effects of environmental drivers and the complexity of the marine trophic web, it is difficult to make ecosystem wide projections. It is *likely* that under both RCP4.5 and 8.5 there will be significant poleward migrations and phenological shifts in many groups of organisms (Pörtner et al., 2014). It is *very likely* that these effects will be amplified under RCP8.5 compared to RCP4.5 (**Figure 8**; Pörtner et al., 2014). It has also been suggested that there will be losses in biodiversity, particularly in the tropics (Pörtner et al., 2014). There may also be shifts to smaller body sizes due to thermal stress, exacerbated by interactions with other drivers (**Figure 8**; Pörtner et al., 2014).

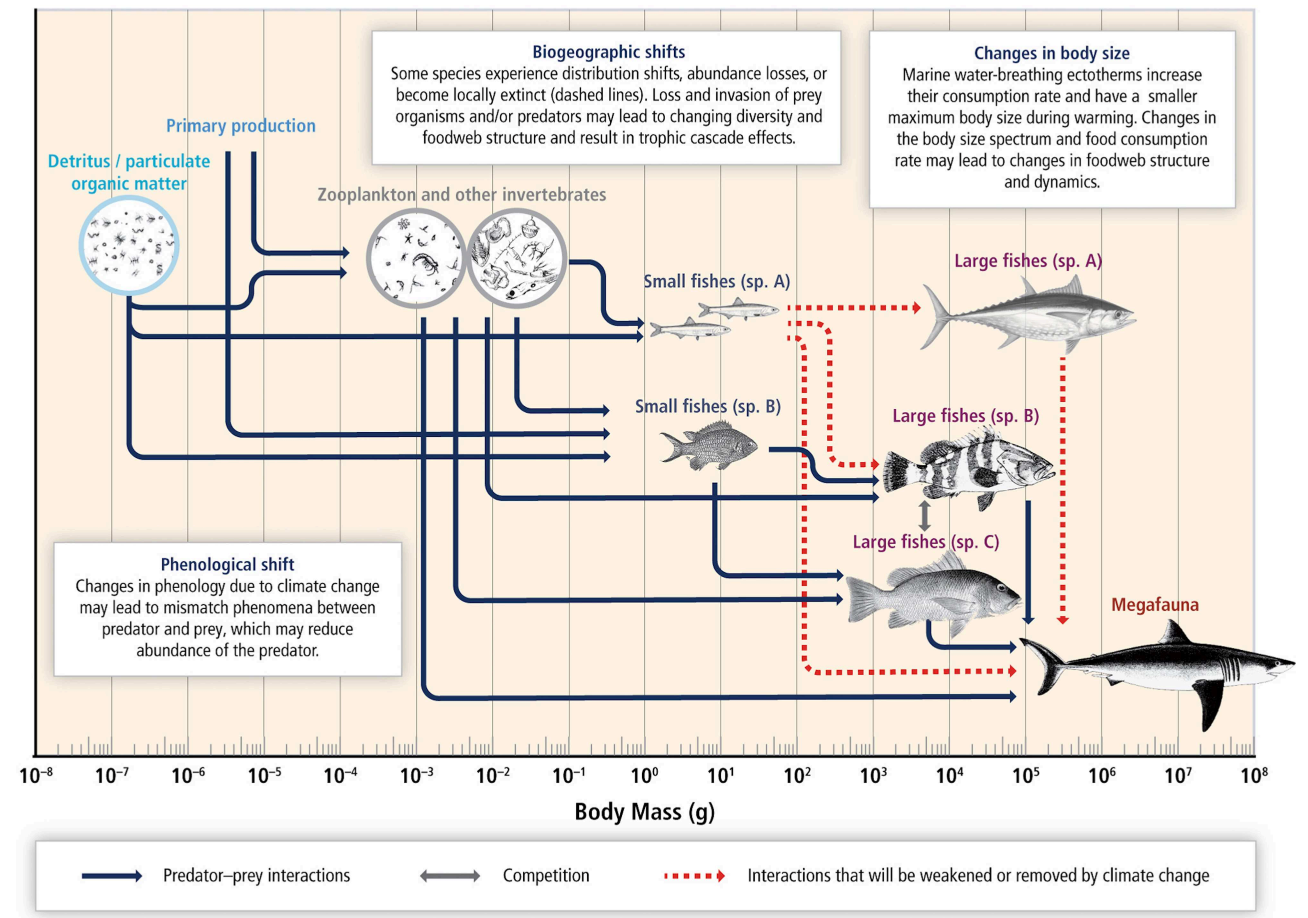
Possible expansion of OMZs will *likely* affect trophic interactions, species distribution, migration and composition. Small-bodied (<1 mm) hypoxia-tolerant animals and microbes will benefit at the cost of large bodied, active animals with high metabolic oxygen demands. There will be a loss of biodiversity as communities shift to specialists that are adapted to tolerate hypoxic conditions (Pörtner et al., 2014). Due to the specialized nature of animals living in hypoxic conditions, there is *high confidence* that expansion of OMZs will decrease biodiversity (Pörtner et al., 2014).

Microbes

New research from Storch et al. (2014) provide evidence that small, less complex eukarya, bacteria and archaea will benefit and proliferate under climate change as they evolve rapidly and can survive anaerobic conditions and higher temperatures (**Figure 8**).

There is *medium to low confidence* that the levels of ocean acidification projected under RCP8.5 will be beneficial for most non-calcifying phytoplankton and cyanobacteria (**Figure 8**; Pörtner et al., 2014). There is medium confidence that coccolithophores are vulnerable to projected end of century pH but new evidence from natural populations found in high CO_2 waters and long-term laboratory experiments lends *medium confidence* that they will be able to adapt to future conditions (Benner et al., 2013; Lohbeck et al., 2014; Pörtner et al., 2014).

Average global primary production is projected to decrease under RCP8.5 due to a lack of nutrients as the result of stratification (Pörtner et al., 2014); however, in high latitude spring blooms systems, photosynthesis is projected to increase.



Biogeographic shifts
Some species experience distribution shifts, abundance losses, or become locally extinct (dashed lines). Loss and invasion of prey organisms and/or predators may lead to changing diversity and foodweb structure and result in trophic cascade effects.

Changes in body size
Marine water-breathing ectotherms increase their consumption rate and have a smaller maximum body size during warming. Changes in the body size spectrum and food consumption rate may lead to changes in foodweb structure and dynamics.

Phenological shift
Changes in phenology due to climate change may lead to mismatch phenomena between predator and prey, which may reduce abundance of the predator.

FIGURE 7 | Schematic diagram of expected responses to climate change in a marine food web. A coupled pelagic and benthic food web is structured by the body size spectrum of species. Combined warming, hypoxia, and ocean acidification reduce body size, shift biogeographies, change species composition and abundance, and reconfigure trophic linkages and interaction dynamics. Fishing generally removes large-bodied species and truncates the body-size spectrum of the community. This confounds the detection and attribution of food web responses to climate change. Arrows represent species interactions (e.g., between predator and prey or competitors for food or space). Broken lines reflect the potential loss of populations and trophic linkages due to climate change. Source: Pörtner et al. (2014).

There is *high confidence* (with added weight from recent studies) that warming is also driving changes in phenology of plankton groups and will continue to do so under RCP8.5 (Behrenfeld, 2014; Hoegh-Guldberg et al., 2014; Poloczanska et al., 2014). From a global perspective, net primary productivity under RCP4.5 will show similar patterns to those projected under RCP8.5, decreasing moderately overall by 2100 but with increases in high latitude systems (Pörtner et al., 2014).

Macrophytes

There is *low confidence* that seagrasses and non-calcifying macroalgae will benefit under RCP8.5 conditions. As fleshy macroaglae are cool water adapted, it is predicted that under RCP8.5 warming, they will undergo significant changes in their distribution (**Figure 8**; Brodie et al., 2014). Seagrasses are thought to be more tolerant of increasing temperatures and may proliferate, particularly if they are able to colonize ecological niches provided by the decline of less tolerant groups such as crustose coralline algae (**Figure 8**; Brodie et al., 2014; Pörtner et al., 2014).

Animals

Temperature increase will lead to poleward migrations and phenological shifts with potential predator prey mismatches. Reduced ocean productivity will reduce the energy available to higher trophic levels and so fishery catches are projected to decrease in temperate and equatorial biomes by 38 and 15%, respectively under RCP8.5 (**Figure 8**; Pörtner et al., 2014).

Non-calcifying zooplankton are thought to be reasonably resilient to the effects of ocean acidification but sensitive to change in SST (Pörtner et al., 2014). The AR5 and more recent studies find it *likely* that zooplankton will continue to display large geographic and phenological shifts under increasing temperatures (**Figure 8**; Chambers et al., 2013; Poloczanska et al., 2014).

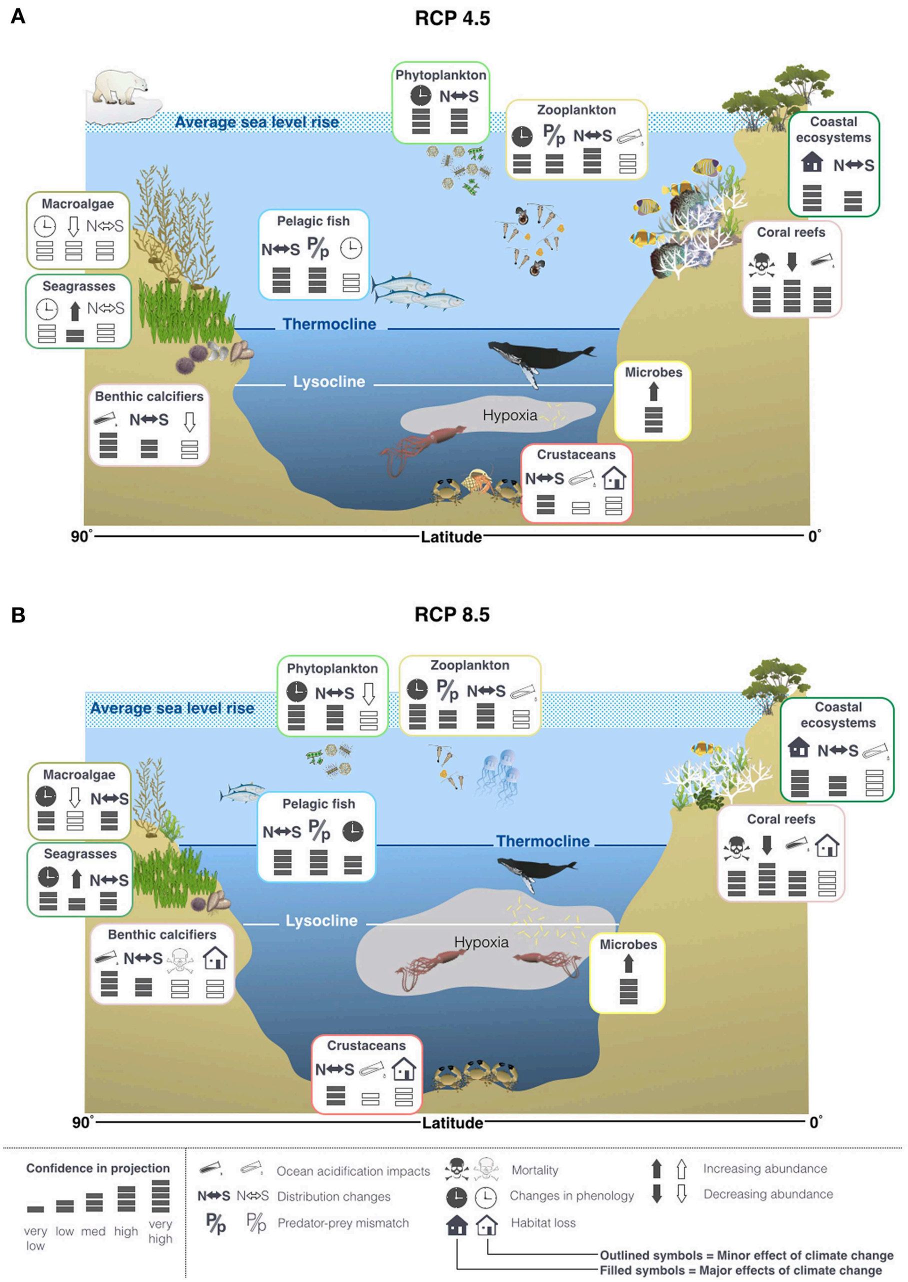


FIGURE 8 | Projected changes to physical features in the oceans and some of the potential impacts on life in the oceans under RCP4.5 (A) and 8.5 (B), based on the findings reported in the IPCC AR5 and literature published since the cut off dates (15/03/2013 for working group I and 31/08/2013 for working group II). It is projected that thermocline and lysocline will shoal to a greater extent and OMZs will expand more under RCP8.5 compared to 4.5. These changes will favor bacteria and hypoxic specialists (Pörtner et al., 2014; Storch et al., 2014) and limit the depth ranges of many species, causing habitat loss (Pörtner et al., 2014). In general, it is predicted that there will be a shift toward smaller body sizes and that many species will exhibit poleward migrations in response to increasing sea temperatures (Pörtner et al., 2014). Icons provided by http://ian.umces.edu/imagelibrary.html.

New research adds to the *high to medium confidence* that calcifying invertebrates, including commercially important species such as oysters, mussels and clams, will be vulnerable to end of century ocean acidification (Clements and Hunt, 2014; Scanes et al., 2014). There remains *low confidence* that crustaceans will be able to tolerate the projected pH decrease (**Figure 8**; Harms et al., 2014; Pörtner et al., 2014). These projections have profound implications for future trophic interactions and ecosystem function, as it is *likely* that many calcifiers will be out-competed by non-calcifying species. There is *high confidence* that elevated CO_2 will cause losses of diversity, biomass and trophic complexity in benthic marine communities

(Pörtner et al., 2014). The fossil record shows that ocean acidification events in geological history are marked by mass extinctions of calcifying taxa. It is *likely* that species extinctions will occur under RCP8.5.

Fish are also projected to be vulnerable under RCP8.5 conditions and there is *low confidence* from model predictions that ocean acidification will generally reduce fish biomass and catch (Pörtner et al., 2014). New projections support the AR5 statement that warming of Arctic waters under RCP8.5 will allow significant distributional shifts and potential interchange of fish species between the North Pacific and the North Atlantic, causing changes to fisheries, trophic dynamics and ecosystem functioning (Jones and Cheung, 2014; Wisz et al., 2015).

There remains *low confidence* that certain groups of calcifying invertebrates will be tolerant to RCP4.5 conditions, including foraminifers and some pelagic molluscs and *medium confidence* that crustaceans will also be able to tolerate these conditions (Pörtner et al., 2014). There is also *low confidence* that many fish species will be resistant under RCP4.5 (Pörtner et al., 2014).

Corals

There is *very high confidence* that, as warming progresses, coral bleaching and mortality will increase in frequency and magnitude over the next decade. Under A1B emission scenario (approximately RCP6.0), 99% of the reef locations will experience at least one severe bleaching event between 2090 and 2099 (Wong et al., 2014). New studies that take into account potential coral acclimation still predict that more than 50% will experience high frequency bleaching under RCP8.5 (Logan et al., 2014), causing long-term degradation by 2020 (**Figure 8**; Pörtner et al., 2014). There remains *limited evidence* and *low agreement* as to whether corals will be able to acclimate or adapt to increasing temperatures enough to limit bleaching events (Wong et al., 2014). There is *high confidence* that bleaching events will negatively impact coral community structure and diversity, with *medium confidence* of bleaching affecting the abundance and species composition of fish communities (Pörtner et al., 2014). New models that account for coral acclimation, predict that fewer than 50% of corals, globally, may experience high frequency bleaching under RCP4.5 throughout the 21st century (Logan et al., 2014), however, there is considerable question as to whether coral adaptive responses can truly keep pace with expected warming. Additionally, while some corals may find geographic refuge due to differential spatial patterns of 21st century warming (Van Hooidonk et al., 2013), opposing spatial gradients in ocean acidification may render them unable to keep pace with erosion as their calcification declines (Van Hooidonk et al., 2014).

There is *high confidence* that warm-water corals will be vulnerable to decreasing pH under RCP8.5 with widespread dissolution of reefs (*medium confidence*) and reduced larval dispersal and settlement (*low confidence*) occurring by 2100 (Wong et al., 2014). This is *very likely* to reduce habitat and refugia for associated fauna. There is *high confidence* that calcifying algae, which are associated with coral reefs are also vulnerable under RCP8.5 scenarios, many species are important for reef stability and function, therefore, losses may further impact coral reef health. There is *medium confidence* that an atmospheric CO_2 concentration expected under RCP4.5 (560 ppm) is the threshold at which global dissolution of reefs will occur (Wong et al., 2014). The habitat loss associated with reef dissolution under RCP4.5 will be less severe than for RCP8.5. There is *low confidence* as to whether RCP4.5 conditions will alter distribution of cold corals (Pörtner et al., 2014).

Ecosystems

It is *virtually certain* that climate change will cause major changes to ecosystems in high latitude spring bloom systems; warming is a primary driver of ecosystem changes in the North Atlantic (Goberville et al., 2014; Hoegh-Guldberg et al., 2014). There is *high confidence* that expansion and contraction of faunal ranges have been observed, with an associated increase in diversity as warmer water species colonize new areas (**Figure 8**; Hoegh-Guldberg et al., 2014; Poloczanska et al., 2014).

There is *medium confidence* that export of organic matter to the deep sea is controlled by temperature and that warming and changes to primary productivity in the upper ocean will reduce the export of organic matter to the deep sea. This has the potential to affect the distribution, abundance and composition of faunal communities in the deep sea (Hoegh-Guldberg et al., 2014).

The effects of warming will be less severe under the conditions predicted by the end of the century under emissions RCP4.5 than for RCP8.5. Nonetheless, many plants and animals will still be severely affected; however, species distributions and phenological shifts are likely to be less extreme with fewer negative implications on trophic interactions (Pörtner et al., 2014).

Discussion

Research published following AR5 endeavored to address many of the key uncertainties highlighted by the IPCC. Physical and biogeochemical advances include an improved understanding of variability and a growing observational coverage in key environmental drivers such as temperature, carbon and pH. New studies show that ocean heat content continues to increase and anthropogenic climate change continues at high speed. Ecological advances included studies assessing climate-related impacts to different developmental stages of various taxa, as well as an improved understanding of impacts arising from ocean acidification. In most cases the studies published since AR5 agree or add further weight to a growing body of evidence and, therefore, do not significantly alter the projections of future impacts.

The start of this review lists six key uncertainties, identified by the AR5, regarding potential climate-related impacts on biological and physical systems. In light of the new research detailed in this review, these points are revisited and reassessed.

(1) **The extent of warming in deep water masses (below 700 m) and limited observational coverage of the ocean, hampering more robust estimates of ocean heat and carbon content.**

New studies suggest that the warming hiatus in SST may be caused by heat sequestration in deep ocean basins and natural variability associated with Atlantic and Pacific multi-decadal oscillations. Improved estimates of warming in the deep ocean and southern hemisphere have been proposed (see section Warming).

(2) **The likelihood of climate-induced changes to major upwelling systems (i.e., increased or decreased upwelling) is still uncertain (Lluch-Cota et al., 2014).**

Models have improved assessment of changes to upwelling systems that have that have already occurred and added weight to the growing body of evidence that predicts regional intensification of upwelling (see section Upwelling).

(3) **Ways in which climate-induced changes in the physiology and biogeography of an individual species may alter ecosystem structures, species interactions, and food webs.**

Recent studies have identified additional evidence of changes in community size structure (Gibert and Delong, 2014) and food web composition (Chust et al., 2014; Verges et al., 2014), with observed examples of community phase shifts across polar, temperate and tropical marine ecosystems (Beaugrand et al., 2014; Engelhard et al., 2014; Potts et al., 2014; Verges et al., 2014).

(4) **An improved understanding of climate sensitivity at the ecosystem level that considers multiple drivers (e.g., ocean warming, acidification, and hypoxia) and synergistic impacts.**

Studies have recently begun to investigate ecosystem-level responses to climatic stressors (Chust et al., 2014; Comeau et al., 2014b; Guénette et al., 2014; Silverman et al., 2014; Hendriks et al., 2015), although there is still a paucity of ecosystem level studies that address the impacts of multiple drivers (see section Effects of Multiple Drivers).

(5) **The degrees to which species can track changes in climate as well as the influence of multiple stressors on their capacities to respond remained uncertain.**

Empirical and theoretical evidence continues to support the role of climate velocity in influencing species range shifts (Pinsky et al., 2013; Hiddink et al., 2014). Shifts in nutrient availability are a key driver for phytoplankton growth, possibly negating the positive growth effects of warming. Increasing numbers of studies examine the impact of multiple stressors on single species (see section Plants and Animals).

(6) **The capacity for phenotypic and evolutionary adaptation over generations to respond to long-term climate change.**

Increasing numbers of studies have begun to address this question. Trans-generational phenotypic plasticity is observed in response to warming and acidification (see sections Ocean Acidification and Impacts of Ocean Warming), suggesting the potential for genetic adaptation. Two recent studies find evidence of coccolithophores demonstrating evolutionary adaptation under ocean warming and acidification (Lohbeck et al., 2014; Schluter et al., 2014). Despite recent work, there is still a distinct paucity of studies addressing the long-term evolutionary response to climate change stressors, particularly in animals.

Conclusions

Anthropogenic emissions have caused measurable physical changes in the oceans. The oceans absorb 93% of the excess energy produced by global warming and approximately 28% anthropogenic CO_2, buffering the effects of climate change (Rhein et al., 2013). This buffering is not without cost and changes in ocean temperature, pH, and oxygen content have been observed over the second half of the 20th century (Rhein et al., 2013). Increasing atmospheric CO_2 will always lead to an increase in ocean carbon storage, all other things being held constant (Ciais et al., 2013), thus 21st century emissions will determine the condition of the world's oceans for centuries to come (Ciais et al., 2013). Under both RCP4.5 and 8.5, physical changes are projected to continue but with greater severity under RCP8.5 (Bopp et al., 2013; Ciais et al., 2013).

Impacts of warming on biological processes can already be observed (Poloczanska et al., 2014; Pörtner et al., 2014) as organisms shift their distributions polewards (Poloczanska et al., 2014), alter phenology (Pörtner et al., 2014) and instances of coral bleaching increase in frequency (Wong et al., 2014). Experimental evidence has shown many organisms to be sensitive to projected future levels of ocean acidification, with calcifiers showing the strongest responses. However, observations of the effects of ocean acidification on natural populations are scarce, except in areas with naturally high concentrations of dissolved CO_2 (Bednaršek et al., 2014). Changes in dissolved oxygen concentrations are highly variable among regions, but it is predicted that expanding OMZs will favor bacteria and hypoxic specialists whilst reducing habitat for organisms with higher oxygen demands (Pörtner et al., 2014).

The overarching findings of both the AR5, and much of the work published since, is that the effects of anthropogenically produced climate change on organisms are highly species specific. Impacts also varying regionally in response to local drivers and synchronously with other climate change drivers in unpredictable ways. As a result, there is limited ability to project the future for marine ecosystems.

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Chlorophyll variability in the oligotrophic gyres: mechanisms, seasonality and trends

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A 16-year (1998–2013) analysis of trends and seasonal patterns was conducted for the 5 subtropical ocean gyres using chlorophyll-a (Chl-a) retrievals from ocean color satellite data, sea surface temperature (SST) obtained from optimally interpolated Advanced Very High Resolution Radiometer (AVHRR) data, and sea-level anomaly (SLA) from Aviso multi-sensor altimetry data. Trend analysis was also performed on mixed-layer data derived from gridded temperature and salinity profiles (1998–2010) from the Simple Ocean Data Assimilation (SODA) model. The Chl-a monthly composites were constructed from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Moderate-resolution Imaging Spectroradiometer (MODIS) on Aqua using two different algorithms: the standard algorithm (STD) that has been in use since the start of the SeaWiFS mission in 1997, and a more recently developed Ocean Color Index (OCI) algorithm that is purported to provide improved accuracy in low chlorophyll waters such as the oligotrophic regions of the subtropical gyres. Trends were obtained for all gyres using both STD and OCI algorithms, which demonstrated generally consistent results. The North Pacific, Indian Ocean, North Atlantic and South Atlantic gyres showed significant downward trends in Chl-a, while the South Pacific gyre has a much weaker upward trend with no statistical significance. Time series of satellite-derived net primary production (NPP) showed downward trends for all the gyres, while all 5 gyres exhibited positive trends in SST and SLA. The seasonal variability of Chl-a in each gyre is tightly coupled to the variability in mixed layer depth (MLD) with peak values in winter in both hemispheres when vertical mixing is more vigorous, reaching depths approaching the nutricline (ZNO_3, here defined as the depth of the 0.2 μM nitrate concentration). On a seasonal basis, Chl-a concentrations increase when the MLD approaches or is deeper than the nutricline depth, in agreement with the concept that vertical mixing is the major driving mechanism for phytoplankton photosynthesis in the interior of the gyres. In addition, MLD and SST seasonal changes are well correlated indicating that SST is a reasonable index of vertical mixing in the gyres. The combination of surface warming trends and biomass reduction over the 16-year period has the potential to reduce atmospheric CO_2 uptake by the gyres and therefore influence the global carbon cycle.

Keywords: sub-topical gyres, ocean deserts, long-term trends, changes in productivity, driving mechanisms

INTRODUCTION

Subtropical gyre variability as seen from ocean color satellites has been analyzed in previous studies. McClain et al. (2004) showed that the oligotrophic waters of the North Pacific and North Atlantic gyres were observed to be expanding, while those of the South Pacific, South Atlantic and South Indian Ocean gyres show much weaker and less consistent tendencies. Their results were based on 8 months (November 1996–June 1997) of Ocean Color and Temperature Sensor (OCTS) and 6 years (September 1997–October 2003) of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) ocean color data. Polovina et al. (2008) used a 9-year (1998–2006) time series of SeaWiFS to examine temporal trends in the oligotrophic areas of the subtropical gyres. They concluded that in the 9-year period, in the North and South Pacific, North and South Atlantic, outside the equatorial zone, the areas of low-surface chlorophyll waters had expanded at average annual rates from 0.8% to 4.3%. In addition, mean SST in each of these 4 subtropical gyres increased over the 9-year period, with the expansion of the low-chlorophyll waters being consistent with global warming scenarios based on increased vertical stratification in the mid-latitudes.

An important biological characteristic of the subtropical gyres is the large variability in phytoplankton growth rates with minimal changes in biomass (Laws et al., 1987; Marra and Heinemann, 1987; Marañón et al., 2000, 2003). Therefore, understanding the interactions between physical and biological processes within the subtropical gyres is central for determining the magnitude and variability of the carbon exported from the surface to the deep ocean.

We used a satellite multi-sensor approach to analyze the biological response of all 5 subtropical gyres to changes in physical forcing. A major data source for our analysis was the chlorophyll-*a* (Chl-a) combined data from SeaWiFS and the Moderate-resolution Imaging Spectroradiometer (MODIS) on Aqua, which together provided 16 years of continuous high-quality global data. Satellite-based SST data were obtained from optimally interpolated (OI) Advanced Very High Resolution Radiometer (AVHRR) data (Reynolds et al., 2007) and dynamic height (*h*) from altimetry data. The results reported in this article are based on data records that are longer than the ones used in similar previous efforts (McClain et al., 2004; Polovina et al., 2008; Signorini and McClain, 2012). These previous studies reported significant changes in the sizes of most gyres. The seasonal cycle and long-term trends of the physical forcing and biological response are analyzed within the geographical domain of the subtropical gyres, based on the most recent reprocessing of the entire SeaWiFS data record (1998–2010) combined with MODIS data for the period of 2011–2013, the longest (16 years) ocean color record of adequate data quality for this analysis.

METHODOLOGY

The study domains for all 5 gyres, the North and South Pacific (NPAC and SPAC), the North and South Atlantic (NATL and SATL) and the South Indian Ocean (IOCE) gyres, are shown in **Figures 1–3** as polygons bounded by white lines. The choice for the gyre domain polygons follows the methodology of Signorini and McClain (2012). The oligotrophic regions (purple areas in **Figure 1A**) expand during summer and contract during winter following the seasonal strength of the winds and convective upper-ocean mixing. The rationale for choosing the size and shape of the study polygons is twofold: (1) they should contain the entire oligotrophic regions of the gyres during the maximum expansion in summer and (2) they should avoid peripheral regions where other dynamic processes prevail, such as coastal and equatorial upwelling, river discharge and western and eastern boundary current systems.

DATA SOURCES AND PROCESSING

Our analysis is based on five satellite data sources spanning the common period of 1998–2013. These include the combined time series of 9 km monthly Chl-a from the latest SeaWiFS and MODIS reprocessing (http://oceancolor.gsfc.nasa.gov/), 0.25° daily NOAA optimally interpolated (OI) SST, and Aviso 0.25° daily *h* from multi-sensor altimetry. Finally, we used global monthly net primary production from the updated Carbon-based Production Model-2 (CbPM2) to derive the combined SeaWiFS-MODIS (1998–2013) net primary production (NPP) time series for all gyres. The resolution of the NPP monthly grids is ∼18 km and a detailed description of the CbPM2, with vertically resolved photoacclimation, is given in Westberry et al. (2008). The SST and *h* products were averaged to monthly values after the daily SST and *h* time series of gyre domain averages were computed. Seasonal climatology and time series of averaged Chl-a, SST and *h* were produced within the limit domains of all 5 gyres. The anomalies of each parameter were then calculated by removing the seasonal climatology from the time series and long-term trends were derived for each parameter and gyre domain. The statistical analysis for the trends was done with MatLab using the regression diagnostics function "regstats" using a linear regression model.

In addition, mixed-layer time series data were derived from gridded temperature and salinity profiles (1998–2010) available from the Simple Ocean Data Assimilation (SODA) model (Carton et al., 2000) on a global 0.5 degree grid. The water density was calculated from the SODA temperature and salinity profiles and the monthly MLD were calculated using a critical density threshold of 0.03 kg m^{-3}.

MODIS AND SeaWiFS CHLOROPHYLL AND NPP

The global monthly Chl-a and NPP products used in this study were derived from NASA standard products of spectral water-leaving "remote sensing" reflectance over the visible spectral regime, Rrs(λ), associated with MODIS-Aqua version 2013.1 and SeaWiFS version 2010.0. The Rrs(λ) were produced by NASA using common algorithms and methods to maximize consistency across the two missions (Franz et al., 2012), with MODIS updated more recently to incorporate improved instrument temporal calibration knowledge (Meister and Franz, 2014).

For both SeaWiFS and MODIS, the STD Chl-a product uses a blue to green band ratio algorithm to relate Rrs (λ) to Chl-a that has been shown to perform well over a wide dynamic range of Chl-a (O'Reilly et al., 1998, with empirical coefficients updated via Werdell and Bailey, 2005). The recently developed OCI algorithm (Hu et al., 2012) is an alternative approach specifically developed to improve retrievals in low Chl-a waters. OCI uses a line-height approach wherein the Chl-a is related to the difference between Rrs (green) and a linear baseline from Rrs (blue) to Rrs (red). The advantage of this line-height approach is that it is robust to spectrally correlated biases, such as those associated with atmospheric correction error or residual sun glint contamination that can dominate the very low green reflectance in clear waters and thus drive-up uncertainty in the STD blue to green band ratio. OCI is therefore a logical choice for this study of ocean gyres, but the STD Chl-a time-series is also assessed, as that algorithm was used in all previous studies (McClain et al., 2004; Polovina et al., 2008; Signorini and McClain, 2012).

The SeaWiFS mission operated from late 1997 to late 2010, with some periods of sporadic operations in the latter 3 years, while MODIS-Aqua began operations in 2002 and continues to this day. This study thus makes use of a merged SeaWiFS-MODIS Chl-a and NPP time-series to span the period from 1998 to 2013, as derived from the consistently-processed monthly Rrs (λ). Specifically, the SeaWiFS monthly products were used exclusively from 1998 through 2007, MODIS was used exclusively from 2011–2013, and MODIS was used in the 2008–2010 period for those months where SeaWiFS data was incomplete or unavailable. Previous studies have demonstrated a high level of consistency between the STD Chl-a products of SeaWiFS and MODIS for global ocean regions (Franz et al., 2012, 2014), thus providing some confidence in the use of a merged time-series for trend

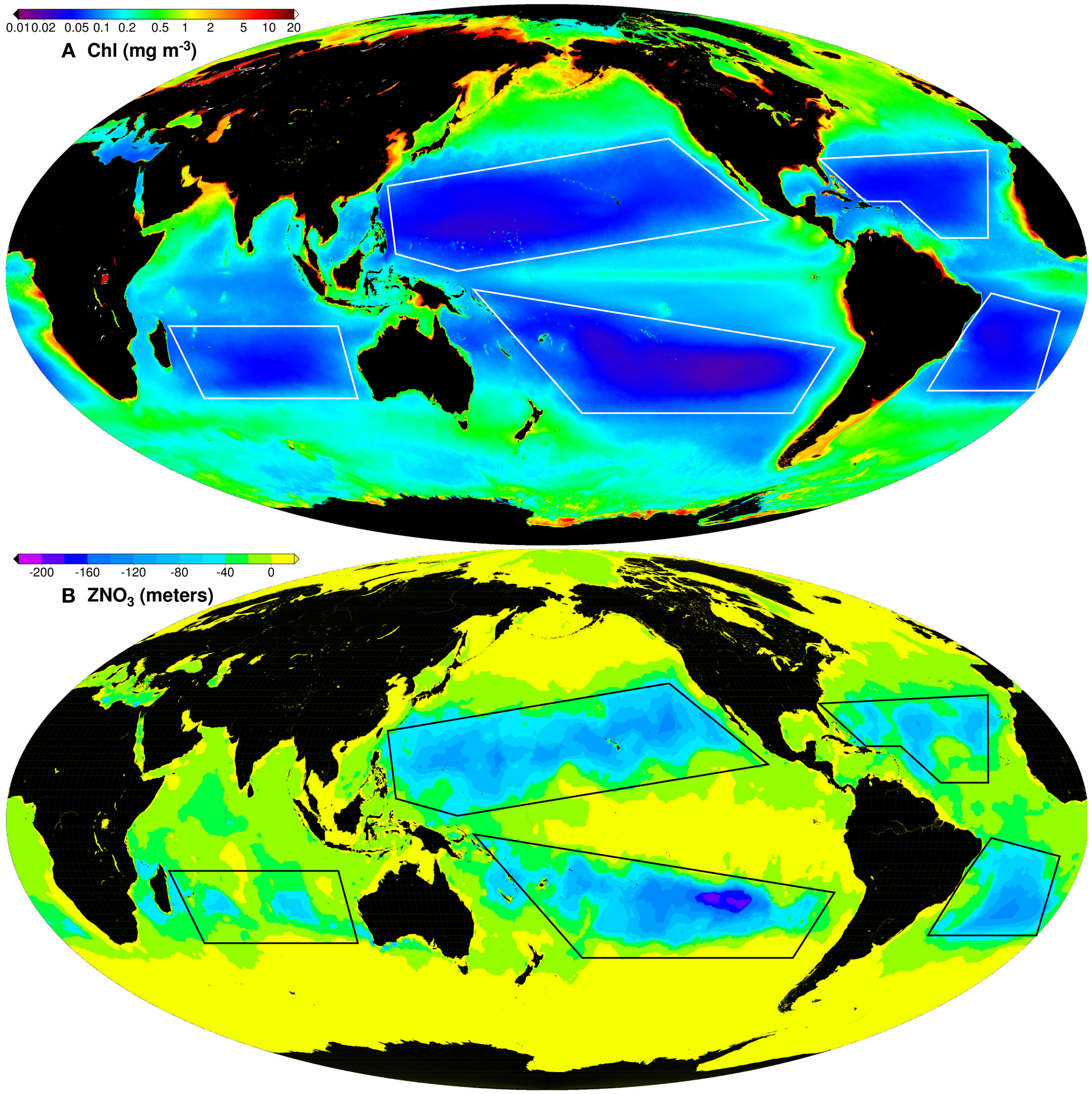

FIGURE 1 | Global maps of 9 km MODISA OCI Chl-a mission composite (A) and the depth of the 0.2 µM (ZNO_3) nitrate concentration (B) derived from the World Ocean Atlas monthly climatology. The transition to the yellow color in **(B)** indicates that the 0.2 µM nitrate horizon has reached the surface. The polygons represent the study areas of the 5 gyres.

analysis, but additional analyses were performed here to specifically assess the mission to mission consistency within the study domain.

DYNAMICS AND BIOGEOCHEMICAL CHARACTERISTICS OF THE SUBTROPICAL GYRES

Although the subtropical gyres are characterized by oligotrophic waters (low biomass and production), and are quite often referred to as the ocean deserts, their immense size (they occupy ∼40% of the surface of the earth) makes their contribution to the global carbon cycle very important. The upper kilometer of the subtropical gyres circulation is primarily wind driven (Huang and Russell, 1994). The horizontal and vertical motion in this layer plays a significant role in controlling the interaction between the atmosphere and ocean, which is of vital importance to our understanding of the oceanic general circulation and climate (Huang and Qiu, 1994). The gyres are characterized by a deep pycnocline at their centers and strong horizontal gradients of temperature and salinity at the fringes due to pycnocline outcropping. The flow in the western limbs (western boundary currents) is intensified by the latitudinal changes of the Coriolis acceleration (β effect), whereas the flow is relatively weak in the gyres' eastern parts. The broad region of relatively weak flow occupies most of the gyre and is called the Sverdrup regime (Pedlosky, 1990). The dynamic center of the gyres can be identified by a maximum sea-surface height (SSH). The pycnocline shoals in the mid-latitudes, where isopycnals outcrop at the subtropical front, and at the equator, where Ekman flow divergence promotes upwelling. The

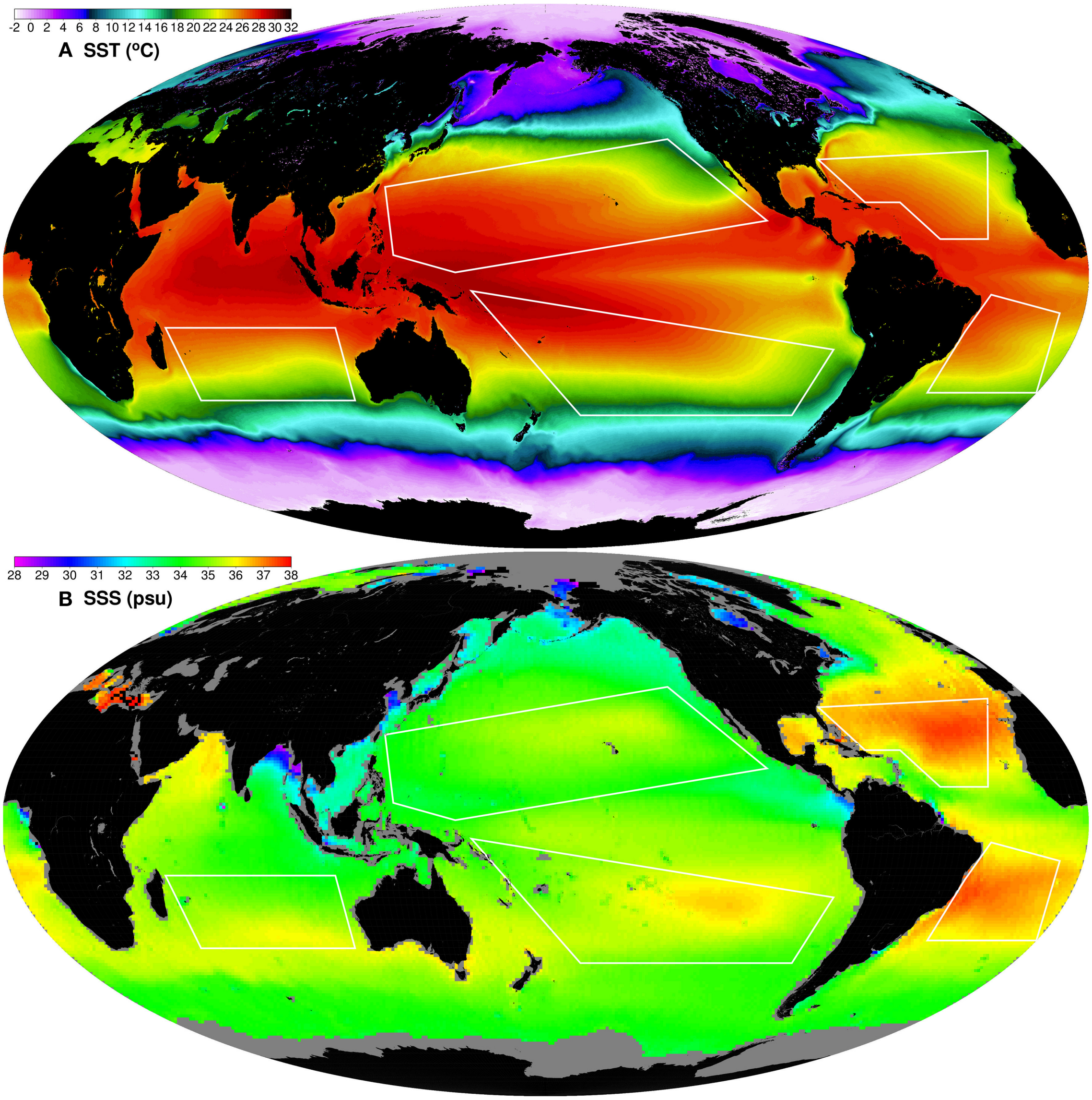

FIGURE 2 | Global maps of 9 km MODISA SST mission composite (A) and Aquarius 1-degree SSS based on the August 2011–July 2013 composite (B).

interior of the gyres are also characterized by Ekman downwelling. McClain and Firestone (1993) provide evidence of gyre downwelling in the North Atlantic.

The availability of light and nutrients is the driver for phytoplankton photosynthetic carbon production. In the interior of the gyres the depth of the nutricline is much deeper than in its fringes as a result of gyre dynamics. This limits the availability of nutrient renewal within the euphotic zone as the vertical mixing needs to penetrate much deeper to reach depths were nutrients are more concentrated, thus limiting phytoplankton growth. This is clearly illustrated in **Figure 1** which shows the MODIS mission composite global Chl-a map and the global nutricline horizon defined by the level at which the nitrate (NO3) concentration reaches 0.2 μM (ZNO_3). Areas inside the gyres have the clearest waters (low biomass) which are well correlated with the areas of deepest ZNO_3. The most distinctive feature of the phytoplankton size structure in these oligotrophic domains is the marked dominance of picoplankton (Marañón et al., 2001).

Previous studies indicate that the subtropical gyres undergo seasonal changes in the physical forcing and ecosystem response that alter the ratio of new vs. regenerated production. Brix et al. (2006) discussed the relationships between primary, net community, and export production in the subtropical gyres. They analyzed more than 10 years of data from two subtropical time-series stations (Hawaii Ocean Times-series (HOT) in the North Pacific, and Bermuda Atlantic Time-Series (BATS) in the North Atlantic) to investigate the regeneration loop vs. export pathway hypothesis, and in particular to test the idea that the switch between the two is controlled by enhanced input of nutrients. In

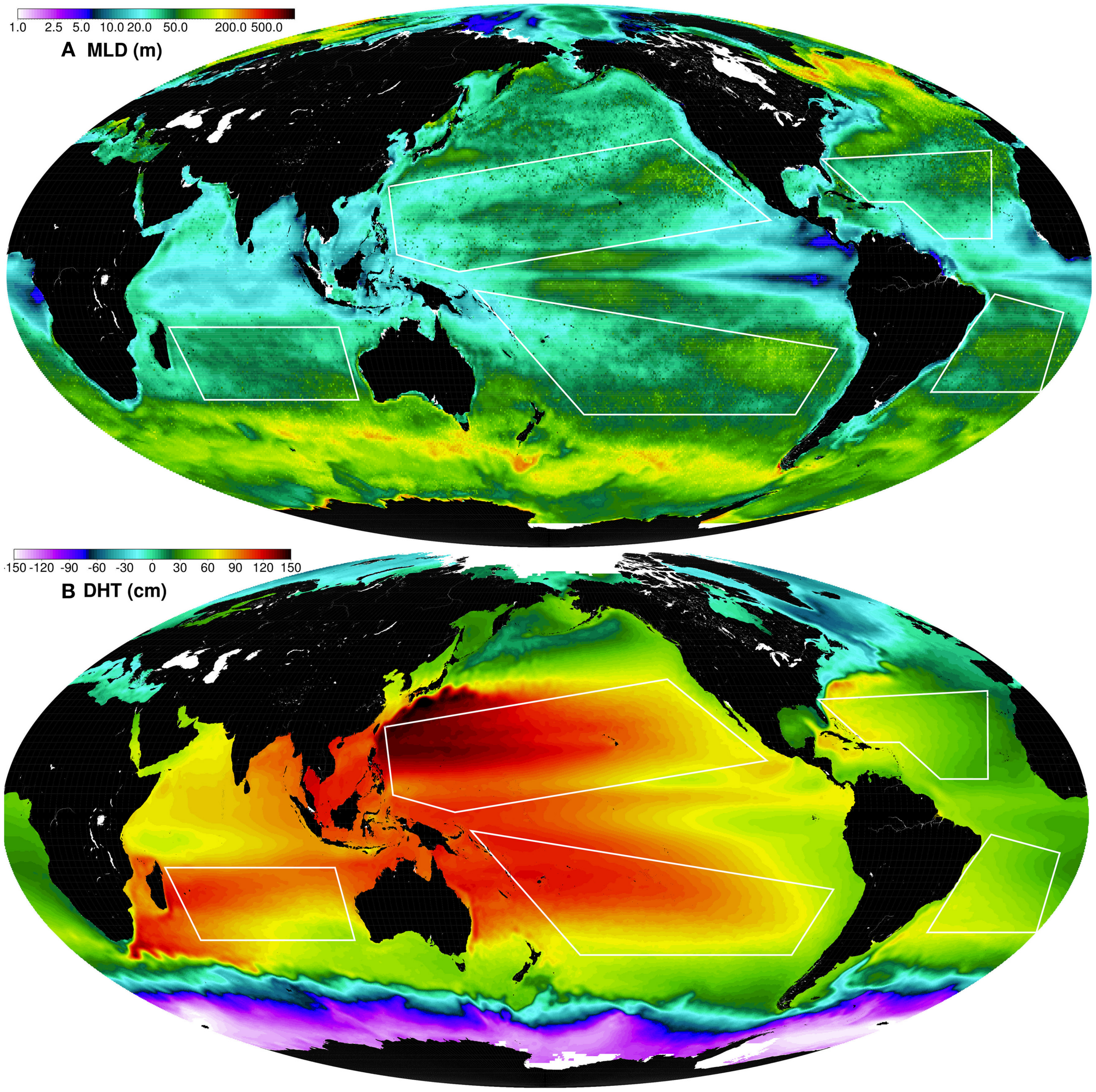

FIGURE 3 | Global maps of climatologic (1998–2010) SODA MLD (A) and Aviso dynamic height climatology (1998–2013) based on the sum of SLA and mean dynamic topography (B).

the decadal long-term mean, their study revealed export pathway characteristics at BATS, while at HOT production is dominated by the regeneration loop. This difference is consistent with stronger seasonal forcing at BATS leading to enhanced nutrient input. However, these characteristics are only valid for parts of the year. Especially at BATS, the export pathway exists only in spring and the system reverts to a regeneration loop in summer and fall. This is a consistent result given the strong summer-time stratification and the resulting low levels of nutrient input.

Heat and freshwater (precipitation-evaporation) fluxes, combined with the gyre circulation, are the dynamic drivers for SST and sea surface salinity (SSS) spatial and temporal variability that highly influence vertical mixing and thus the depth of the mixed layer. **Figure 2** shows global maps of MODIS SST and Aquarius SSS mission composites. There is large SST variability in the NPAC and SPAC gyres with warmest SSTs in the western equatorial region (Warm Pool) and significant decrease in SST toward the subtropical frontal regions. The Aquarius SSS global map shows that the surface salinity within the Atlantic gyres is greater than the salinity in the Pacific gyres. The mean Aquarius SSS for the NPAC, SPAC, IOCE, NATL and SATL are 34.620, 35.364, 35.125, 36.753, and 36.571, respectively. The mean SSS in the NATL gyre is about 2 psu higher than the mean SSS in the NPAC gyre. The mean SSS seasonal cycle of the NATL gyre has a range of ~0.3 psu, while the SATL and NPAC ranges are ~0.2 psu and the SPAC and IOCE have still smaller ranges (~0.1 psu or less). The minimum SSS occurs in summer-fall and the maximum in winter-spring for all gyres, except for the SATL gyre where the

SSS seasonal cycle is in phase opposition with the other 4 gyres. This may be due to a different seasonality pattern of precipitation-evaporation in the sub-tropical SATL. The variability in surface water density due to changes in SST and SSS, combined with wind stirring, are effective drivers of vertical mixing, which in turn control the renewal of nutrients within the euphotic zone.

A climatological global map of mixed layer depth (MLD) is shown in **Figure 3A**. There is a large spatial variability of MLD globally and within the gyres, a result of the interplay of the driving factors described above. The anti-cyclonic circulation patterns within the gyres are clearly shown in the climatological global map of Aviso dynamic height (**Figure 3B**), with the strongest western boundary currents being the Gulf Stream in the North Atlantic and the Kuroshio Current in the North Pacific, both originating from the western limbs of the gyres.

Gyre-averaged seasonal plots of MODIS Chl-a, MLD, and ZNO_3 (**Figure 4**) provide evidence of the biogeochemical forcing vs. response behavior within the gyres. Note that the time axes have been adjusted to provide synchronization of seasons between the northern and southern hemispheres, so winter, summer, spring and autumn appear in phase in all gyres. Summer and autumn, a period of relatively shallower MLDs, are the seasons with lowest biomass (Chl-a), while in the peak of winter strong vertical mixing drives the elevated biomass shown by the higher values of Chl-a. Also note that Chl-a increases as the MLD gets deeper than ZNO_3.

RESULTS

MODIS vs. SeaWiFS Chl TRENDS

Individual mission-long MODIS (July 2002—May 2014) and SeaWiFS (1998–2010) monthly time-series Chl-a anomaly trend analyses, as well as trend analyses for the combined MODIS and SeaWiFS (1998–2013) monthly time series record, were performed using both STD and OCI algorithms. The trends and corresponding statistical results are summarized in **Table 1**.

There is a general agreement of magnitude and sign of trends among the different sensors and algorithms, with some exceptions. The SPAC and SATL gyres are the only ones with positive trends, albeit with low statistical significance ($p > 0.05$). These 2 gyres show positive trends for the 13-year SeaWiFS record using both STD and OCI algorithms, while only the SPAC gyre shows consistent positive (weaker) trends for all other combinations of sensors and algorithms. The statistical significance for the trends is improved for some gyres when the longer MODIS-SeaWiFS 16-year combined record is used, except for the SPAC gyre which still shows a weaker positive trend with low statistical significance.

The trends for the 16-year record using the STD algorithm are −0.0057, +0.0008, −0.0080, −0.0093, and −0.0018 mg m^{-3} $decade^{-1}$ for the NPAC, SPAC, IOCE, NATL, and SATL gyres, respectively. The equivalent trends using the OCI algorithm are −0.0058, +0.0007, −0.0062, −0.0072, and −0.0018 mg m^{-3} $decade^{-1}$. The percent differences between the trends using the STD and OCI algorithms (based on 5 decimal places on the trends) are −1.2%, −12.7%, +28.8%, +29.0%, and +5.1% for the NPAC, SPAC, IOCE, NATL, and SATL gyres. The largest differences in trends between the IOCE and NATL gyres using the two different algorithms may be a result of stronger variability in the Chl-a anomalies in these 2 gyres (see **Figure 5**). There are several factors that contribute to the uncertainty associated with the estimation of the trends in the subtropical gyres, including sensor and algorithm accuracies and the length of available ocean color records.

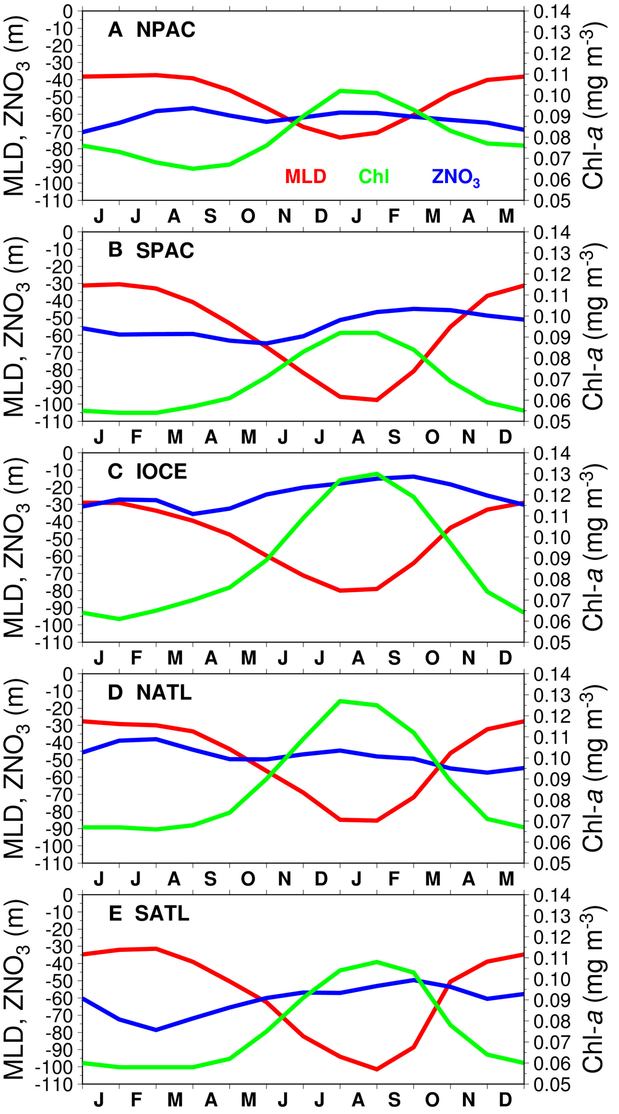

FIGURE 4 | Seasonal variability of MODISA OCI Chl-a (green), mixed layer depth (MLD, red), and depth of the 0.2 μM nitrate concentration (ZNO_3, blue) for the 5 gyres (A through E for the NPAC, SPAC, IOCE, NATL, and SATL, respectively). Values were averaged within the polygons shown in **Figure 1**.

Gregg and Rousseaux (2014) analyzed decadal trends in global pelagic chlorophyll by integrating multiple satellites, *in situ* data, and models. Although they did not present averaged trends for the subtropical gyres in their trend analysis, their North Central Pacific (NCP) and North Central Atlantic (NCA) regional domains contain the NPAC and NATL oligotrophic regions analyzed in this study. Their NCP and NCA regions showed Chl downward trends of −1.1 and −1.4% yr^{-1} for 1998–2012,

Table 1 | Mission-long trends (mg m^{-3} decade^{-1}) for SeaWiFS and MODIS using STD and OCI Chl-a.

Sensor STD/OCI	Gyre	Intercept	Slope (Trend) (mg m^{-3} dec^{-1})	r^2	*p*-value	Chl(yo) (mg m^{-3})	β (% yr^{-1})
SeaWiFS STD 1998–2010	NPAC	1.157	**−0.0058 ± 0.0007**	0.30	1.01e–13	0.065	**−0.89**
	SPAC	−0.194	+0.0010 ± 0.0001	0.01	1.51e–01	0.057	+0.17
	IOCE	1.565	**−0.0078 ± 0.0012**	0.21	1.88e–09	0.076	**−1.03**
	NATL	1.572	**−0.0078 ± 0.0014**	0.17	7.03e–08	0.073	**−1.07**
	SATL	−0.022	+0.0001 ± 0.0010	0.00	9.15e–01	0.062	+0.02
SeaWiFS OCI 1998–2010	NPAC	1.253	**−0.0062 ± 0.0007**	0.36	2.46e–16	0.081	**−0.97**
	SPAC	−0.049	+0.0002 ± 0.0007	0.00	7.29e–01	0.069	+0.04
	IOCE	1.451	**−0.0072 ± 0.0010**	0.24	8.94e–11	0.090	**−0.96**
	NATL	1.392	**−0.0069 ± 0.0012**	0.19	1.27e–08	0.089	**−0.95**
	SATL	−0.014	−0.0001 ± 0.0010	0.00	9.41e–01	0.077	+0.01
MODIS STD July 2002–May 2014	NPAC	0.286	−0.0014 ± 0.0008	0.03	6.13e–02	0.060	−0.24
	SPAC	−0.471	**+0.0023 ± 0.0007**	0.08	8.21e–04	0.055	**+0.42**
	IOCE	1.264	**−0.0063 ± 0.0012**	0.16	9.49e–07	0.071	**−0.89**
	NATL	0.107	−0.0005 ± 0.0012	0.00	6.58e–01	0.067	−0.08
	SATL	0.247	−0.0012 ± 0.0009	0.01	1.82e–01	0.060	−0.21
MODIS OCI July 2002–May 2014	NPAC	0.684	**−0.0034 ± 0.0008**	0.12	1.61e–05	0.078	**−0.44**
	SPAC	−0.577	**+0.0029 ± 0.0008**	0.09	3.86e–04	0.068	**+0.42**
	IOCE	0.853	**−0.0043 ± 0.0012**	0.08	6.92e–04	0.087	**−0.49**
	NATL	0.290	−0.0014 ± 0.0012	0.01	2.16e–01	0.085	−0.17
	SATL	0.152	−0.0008 ± 0.0011	0.00	5.06e–01	0.075	−0.10
SeaWiFS+ MODIS STD 1998–2013	NPAC	1.144	**−0.0057 ± 0.0005**	0.40	4.85e–23	0.065	**−0.88**
	SPAC	−0.159	+0.0008 ± 0.0005	0.01	1.01e–01	0.057	+0.14
	IOCE	1.604	**−0.0080 ± 0.0009**	0.29	6.56e–16	0.076	**−1.06**
	NATL	1.858	**−0.0093 ± 0.0010**	0.33	5.54e–18	0.073	**−1.26**
	SATL	0.368	**−0.0018 ± 0.0008**	0.03	1.75e–02	0.062	**−0.30**
SeaWiFS+ MODIS OCI 1998–2013	NPAC	1.159	**−0.0058 ± 0.0005**	0.43	1.07e–24	0.081	**−0.71**
	SPAC	−0.139	+0.0007 ± 0.0006	0.01	2.08e–01	0.069	+0.10
	IOCE	1.245	**−0.0062 ± 0.0008**	0.23	3.35e–12	0.090	**−0.69**
	NATL	1.440	**−0.0072 ± 0.0008**	0.29	9.76e–16	0.089	**−0.80**
	SATL	0.350	**−0.0018 ± 0.0008**	0.03	2.28e–02	0.077	**−0.23**

The variables Chl(yo) and β are mean Chl (mg m^{-3}) for the first year of the time series and percent change per year, respectively. The trends in bold indicate statistical significance at the 95% confidence level ($p < 0.05$). Values are also tabulated for the SeaWiFS-MODIS merged time series.

respectively. As shown in **Table 1**, the Chl trends derived in this study are very close to those reported by Gregg and Rousseaux (2014). The Chl downward trends from SeaWiFS for the 1998–2010 period are −0.9 (STD Chl) to −1.0% yr^{-1} (OCI Chl) for the NPAC, and −1.0 (OCI Chl) to −1.1% yr^{-1} (STD Chl) for the NATL. The trends for 1998–2013 derived from the merged SeaWiFS-MODIS data are −0.7 (OCI Chl) to −0.9% yr^{-1} (STD Chl) for the NPAC, and −0.8 (OCI Chl) to −1.3% yr^{-1} (STD Chl) for the NATL.

TREND ANALYSIS OF Chl, NPP, SST, SLA, AND MLD

The trends in Chl*, NPP*, SST*, SLA, and MLD* for all gyres, where the asterisk denotes anomalies, are presented in **Table 2**. The Chl* trends are tabulated for both the STD and OCI algorithms. The analysis was done using monthly data for the period of 1998–2013, except for the MLD which was limited by data availability (1998–2010). The units for the trends are chosen to enable uniform magnitude range and number of decimal places for all variables. The time series of monthly anomalies with superposed linear trends are shown in **Figure 5** for all variables analyzed.

As previously mentioned, the SPAC is the only gyre with a positive trend. It ranges from +0.069 to +0.079 μg m^{-3} yr^{-1}. All the other gyres have negative trends indicating an expansion of the oligotrophic areas. The SATL gyre has the weakest trend ranging from −0.175 to −0.184 μg m^{-3} yr^{-1}, while the NATL gyre has the strongest trend with values ranging from −0.718 to −0.926 μg m^{-3} yr^{-1}. The IOCE gyre has the second strongest negative trend ranging from −0.621 to −0.800 μg m^{-3} yr^{-1}. The warming trends in the gyres range from +0.123°C decade^{-1} in

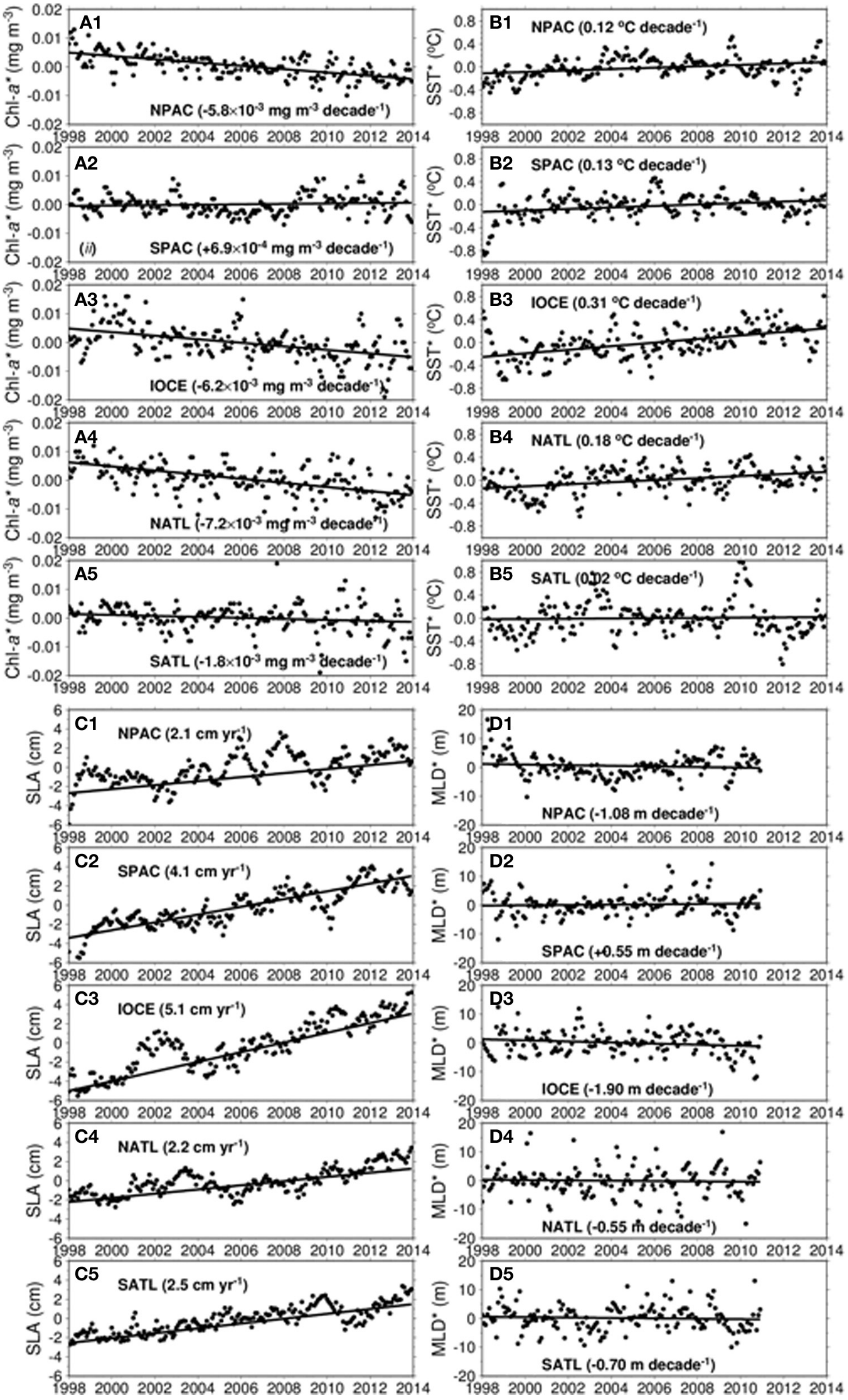

FIGURE 5 | Trends of gyre anomalies for chlorophyll (Chl*, A1–A5), sea-surface temperature (SST*, B1–B5), sea-level anomaly (SLA, C1–C5), and mixed layer depth (MLD*, D1–D5) for all 5 gyres.

Table 2 | Trends and statistics for Chl-a anomaly (Chl* in μg m^{-3} yr^{-1}) from SeaWiFS-MODIS combined data record using STD and OCI algorithms, CbPM net primary production anomaly (NPP* in mg C m^{-2} d^{-1} yr^{-1}), AVHRR optimally interpolated (OI) SST anomaly (SST* in °C decade^{-1}), Aviso sea level anomaly SLA (*cm* yr^{-1}), and mixed layer depth anomaly (MLD* in *m* decade^{-1}) derived from SODA temperature and salinity profiles.

Gyre Parameter	NPAC	SPAC	IOCE	NATL	SATL
Chl* STD	**−0.570 ± 0.050**	+0.079 ± 0.048	**−0.800 ± 0.090**	**−0.926 ± 0.097**	**−0.184 ± 0.077**
Chl* OCI	**−0.577 ± 0.049**	+0.069 ± 0.055	**−0.621 ± 0.083**	**−0.718 ± 0.082**	**−0.175 ± 0.076**
NPP*	**−7.354 ± 0.420**	**−3.608 ± 0.433**	**−5.345 ± 0.532**	**−7.318 ± 0.376**	**−5.135 ± 0.478**
SST*	**+0.123 ± 0.027**	**+0.129 ± 0.031**	**+0.313 ± 0.036**	**+0.179 ± 0.031**	+0.024 ± 0.046
SLA	**+0.209 ± 0.020**	**+0.406 ± 0.018**	**+0.506 ± 0.019**	**+0.219 ± 0.014**	**+0.254 ± 0.012**
MLD*	**−1.081 ± 0.316**	+0.552 ± 0.327	**−1.896 ± 0.327**	−0.546 ± 0.563	−0.700 ± 0.377

The trends in bold indicate statistical significance at the 95% confidence level ($p < 0.05$). The standard error is provided for each trend estimate. The analysis was done using monthly data for the period of 1998–2013, except for the MLD which was limited by data availability (1998–2010).

the NPAC gyre to +0.313°C decade^{-1} in the IOCE gyre, while the positive trend in the SATL gyre is relatively small and statistically insignificant. The SLA trends are also positive for all gyres, ranging from +0.209 cm yr^{-1} in the NPAC gyre to +0.506 cm yr^{-1} in the IOCE gyre. NPP trends are negative for all the gyres, −7.35, −3.61, −5.35, −7.32, and −5.14 mg C m^{-2} d^{-1} yr^{-1} for the NPAC, SPAC, IOCE, NATL and SPAC, respectively.

The MLD* gyre trends, which were derived from the SODA model density profiles, have signs that agree with the signs of the Chl* trends. A positive MLD* indicates a deepening of the mixed layer. Thus, as the MLD shallows (negative trend), the average Chl-a concentration in the gyres is expected to decrease (negative trend) following the dynamics of forcing vs. response described in section Dynamics and Biogeochemical Characteristics of the Subtropical Gyres. Therefore, a relatively small mixed layer deepening in a region of the gyres where the nutricline is much deeper (see **Figure 1B**) has a significant effect in phytoplankton production. The MLD* trends range from 0.546 m decade^{-1} in the NATL gyre to 1.896 m decade^{-1} in the IOCE gyre.

DISCUSSION

Our 16-year analyses of Chl trends in the oligotrophic regions of the subtropical gyres are consistent with the biogeochemical response to changes in the forcing factors affecting the gyre dynamics. The new (export) production in the gyres is controlled by inorganic nutrient inputs into the euphotic zone, which in turn result from seasonal vertical mixing driven by winter-spring convective overturning. During summer, the upper ocean waters re-stratify leading to shallow mixed layers and phytoplankton production is significantly reduced and primarily driven by ecosystem nutrient regeneration. This balance of nutrient supply/consumption can be altered by climatological changes in the physical forcing such as surface warming/cooling, surface freshening by changes in precipitation/evaporation, and sea level changes that potentially modify the dynamic characteristics of the gyres. In this study, we showed that these changes are indeed occurring and that the subtropical gyres are becoming more oligotrophic as a result of the forcing changes.

Our analyses revealed warming trends in all 5 gyres, as well as an increase in sea level height. Warming was more intense in the IOCE gyre with a 16-year trend of 0.31 °C decade^{-1}, concurrent with a sea level increase of 0.51 cm yr^{-1} and a decrease in MLD of 1.90 m decade^{-1}. As a result, the mean Chl-a concentration within the IOCE gyre decreased at a rate of 0.62–0.80 μg m^{-3} yr^{-1}. As shown in **Table 2**, trends with similar signs but with more gradual slopes are evident in the NPAC, NATL, and SATL gyres. The SPAC gyre is the only exception, with an increase in MLD of 0.55 m decade^{-1} and a relatively moderate Chl-a increase of 0.07 to 0.08 μg m^{-3} yr^{-1}, despite the warming of 0.13 °C decade^{-1} and a sea level rise of 0.41 cm yr^{-1}. Dynamic effects other than surface warming and increase in sea level are probably influencing the somewhat weak upward trend in Chl-a, but the upward trend in Chl-a associated with increasing MLD appears to be coherent with our original forcing vs. response hypothesis. The upward trends in SLA for all the gyres can be an indication that the thermocline, and thus the nutricline are getting deeper. Turk et al. (2001) showed that satellite SLA is strongly correlated with the depth of the thermocline in the tropical Pacific, and that measured new production also correlates well with thermocline depth, which in turn allowed them to estimate variation of new production in the region based on SLA satellite data. Our 16-year upward trends in SLA (**Table 2**) are potential indicators that new production is being reduced in all gyres.

There is a debate in the literature (Letelier et al., 1993; Winn et al., 1995; Morel et al., 2010) regarding the influence of photoacclimation on the phytoplankton Chl-a concentration in oligotrophic regions, especially during winter when the MLD becomes deepest and light availability is reduced. This effect has the potential to introduce uncertainties in the determination of biomass concentration from Chl-a. Mignot et al. (2014), based on BIO-Argo floats data in the interior of the NPAC and SPAC gyres, showed that the presence of a deep chlorophyll maximum (DCM) in oligotrophic regions is influenced by a photoacclimation process on a seasonal basis. In each of the regions investigated in their study, the Chl-a at the DCM increases from spring to summer and then decreases from summer to fall. They also measured particle backscattering (b_{bp}) and beam attenuation (cp) coefficients concurrent with the Chl-a measurements. The simultaneous seasonal variations of Chl-a, cp, and b_{bp} in the DCM, and the stability of cp/Chl and b_{bp}/Chl in the DCM over the seasons indicate that Chl-a variations in the lower euphotic zone result from biomass variations and not from photoacclimation processes (Mignot et al., 2014). Therefore, in summer, in addition to the photoacclimation effect on Chl-a, the DCM also results from a change in biomass.

To address these effects on the seasonal dynamics of phytoplankton biomass and DCM in the gyres, we used the carbon-based primary productivity model (CbPM) of Westberry et al. (2008) with vertically resolved photoacclimation to derive trends of NPP for all the gyres (see **Table 2**). The trend analysis shows that NPP is being reduced in all 5 gyres, with values ranging from -3.6 mg C m^{-2} d^{-1} yr^{-1} in the SPAC to -7.4 mg C m^{-2} d^{-1} yr^{-1} in the NPAC. The NPAC and NATL gyres have the strongest downward trends followed by the IOCE and SATL.

Our study also revealed the need for satellite multi-decadal records of physical and biological parameters, as well as well-calibrated ocean color sensors and algorithms, to enable accurate estimates of climate-induced trends in the subtropical gyres. These trends necessarily affect primary and export production in these large areas of the global oceans, and therefore influence the uptake of atmospheric carbon dioxide. Based on an estimate of the global ocean climatological net annual sea-air CO_2 flux given by Signorini and McClain (2009), we calculated the contributions of the sea-air CO_2 flux from each of the 5 gyres. The total global flux estimate is -1.126 PgC yr^{-1}, with the minus sign representing atmospheric uptake by the ocean. The individual fluxes for each gyre are -0.113, -0.098, -0.130, -0.073, and $+0.060$ PgC yr^{-1} for the NPAC, SPAC, IOCE, NATL, and SATL, respectively, with the IOCE being the largest uptake and the SATL being a weak source to the atmosphere. The combined sea-air flux from all gyres is -0.353 PgC yr^{-1}, or 31.4% of the global estimate. So the contribution to the global atmosphere CO_2 uptake by the gyres is substantial and therefore environmental changes that may alter the ability of the subtropical gyres to uptake CO_2, such as the reduction in efficiency of the solubility pump by SST warming and the biological pump efficiency by a reduction in inorganic nutrient renewal, will have a significant impact in the global carbon cycle.

SUMMARY AND CONCLUSIONS

We analyzed time series of satellite-derived biogeochemical (Chl, NPP, and ZNO_3) and physical (SST, SLA, model-derived MLD) parameters to investigate the seasonal and long-term (16 years) variability of biomass and phytoplankton productivity in the 5 subtropical gyres. Trends in the physical parameters are used to explain observed trends in Chl and NPP. Downward trends in Chl (except in the SPAC) and downward trends in NPP (response) are identified in all gyres and are in general agreement with the trends observed in the physical parameters (forcing).

For the NPAC, SPAC, IOCE, NATL, and SATL gyres the trends in Chl (mean of STD and OCI algorithms) are -0.574, $+0.074$, -0.711, -0.822 and -0.180 μg m^{-3} yr^{-1}, respectively. The equivalent trends for NPP are -7.354, -3.608, -5.345, -7.318 and -5.135 mg C m^{-2} d^{-1} yr^{-1}. For SST the trends are $+0.123$, $+0.129$, $+0.313$, $+0.179$ and $+0.024$°C decade^{-1}, for SLA $+0.209$, $+0.406$, $+0.506$, $+0.219$ and $+0.254$ cm yr^{-1}, and for MLD -1.081, $+0.552$, -1.896, -0.546 and -0.700 m decade^{-1}, respectively. The warming of the gyres, combined with the decline in NPP, have a potential impact on the efficiencies of the solubility and biological pumps and therefore potentially affecting the uptake of carbon from the atmosphere.

Our study also revealed the need for satellite multi-decadal records of physical and biological parameters, as well as well-calibrated ocean color sensors and algorithms, to enable accurate estimates of climate-induced trends in the subtropical gyres.

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Footprints of climate change on Mediterranean Sea biota

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The Mediterranean Sea ranks among the ocean regions warming fastest. There is evidence for impacts of climate change on marine Mediterranean organisms but a quantitative assessment is lacking. We compiled the impacts of warming reported in the literature to provide a quantitative assessment for the Mediterranean Sea. During the last three decades the summer surface temperature has increased 1.15°C. Strong heat wave events have occurred in years 1994, 2003, and 2009. Impacts of warming are evident on growth, survival, fertility, migration and phenology of pelagic and benthic organisms, from phytoplankton to marine vegetation, invertebrates and vertebrates. Overall, 50% of biological impacts in the Mediterranean Sea occur at summer surface temperature anomaly $\leq 4.5°C$ and at summer surface temperature of 27.5°C. The activation energy (geometric mean 1.58 ± 0.48 eV), the slope of the Arrhenius equation describing the temperature-dependence of biological processes, for the response of Mediterranean marine biota to warming reveals that these responses in the Mediterranean are far steepest than possibly explained by the direct effect of warming alone. The observations are biased toward the northern and western sectors of the basin, likely underestimating the impacts of warming in areas where warming is particularly intense.

Keywords: temperature, heat wave, species, biological traits, activation energy

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Introduction

The Mediterranean Sea is warming at two to three times the rate for the global ocean (Vargas-Yanez et al., 2008), showing an increase in the occurrence of hot extremes by 200–500% throughout the region (Diffenbaugh et al., 2007). This is due to a combination of its position in the boundary between two climatic regimes, the arid climate of North Africa and the temperate and rainy climate of central Europe, which renders Mediterranean climate vulnerable to even relatively minor modifications of the general circulation (Giorgi and Lionello, 2008), and its semi-enclosed nature (Diffenbaugh et al., 2007), leading to restricted hydrological exchange with the open ocean, resulting in a hydrological residence time of about 100 years and a capacity to store heat (Bethoux and Gentili, 1999). Indeed, climatic models predict rapid mean warming in the Mediterranean region along with a greater occurrence of extremely high temperature events (Giorgi and Lionello, 2008), also affecting the marine environment (Jordà et al., 2012). Moreover, as a result of its semi-enclosed nature, marine species endemic to the Mediterranean have a limited scope to adapt to ocean warming by shifting their biogeographical range poleward, tracking the migration of their isotherms to maintain their thermal niche (Burrows et al., 2011, 2014), as marine species do in general (Poloczanska et al., 2013).

As a consequence, there is concern on the impacts Mediterranean warming may have on marine biota. A recent review provided a narrative description of the evidence for impacts of climate change on marine biota (Lejeusne et al., 2010), concluding that it is already highly impacted. However, a quantitative assessment of these responses, allowing elucidation of the magnitude of responses, their relationship with warming and the thresholds of warming that are disruptive for various components of the life history and ecology of Mediterranean biota is still lacking. Such assessment would, however, provide a more precise description of the extent of impacts on Mediterranean marine biota already realized with warming and their vulnerability to further warming.

Here we provide a quantitative assessment of the impacts of climate change on Mediterranean biota. We do so by compiling the literature reporting evidence of such impacts, and extracting the conditions of warming relative to long-term mean values, and when these impacts occurred, thereby allowing the derivation of dose-response relationships as well as the identification of possible thresholds of warming beyond which Mediterranean marine biota experience disruptive impacts.

Materials and Methods

We searched for evidence of footprints of warming on biota in the Mediterranean Sea published in the literature until year 2014 using keywords "(Mediterranean) AND ((Bio* OR Eco*)) AND ((warming OR temperature)) AND ((Marine OR Ocean*)) NOT ((paleo*))" in ISI Web of Knowledge. We also searched for the term "cooling" in the Mediterranean, which retrieved mostly studies of paleo-events, and only one recent study, reporting impacts on zooplankton of a cooling event in 1987 in the Croatian Coast (Berline et al., 2012). From this search we only selected those articles directly attributing the changes observed in marine biota to warming. The type of data collected includes information about characteristics of the study conducted (i.e., year or period of years of the study, site name and coordinates, species name, taxonomic group, whether the species is sessile or mobile, native or introduced) and about the biological response (i.e., type of response, magnitude of response). We grouped the types of biological responses in large trait categories: abundance, survival, fertility, migration, phenology, and growth. The data set includes both qualitative and quantitative data. The data set compiled is publically available at http://digital.csic.es/handle/10261/116098 (Marbà et al., 2015).

We compiled a total of 464 evidence impacts of climate change on Mediterranean biota from 54 papers, 11 and 42 of them including narrative and quantitative evidence, respectively, and 1 both. Quantitative reports encompassed evidence of biological impacts after single warming events (276) and during longer-term monitoring assessments (72 time series; **Table 1**). The time series compiled have a median duration of 24 years (range 3–197 years) and a median central year at 1995.5 (range 1908.5–2004.5). Most impacts compiled are observed at local (43%) and regional (50%) scales while there are few evidence of footprints of warming at sub-basin (2%) and basin (5%) scales (**Table 1**).

TABLE 1 | Number of descriptive and quantitative reports compiled of footprints of climate change on Mediterranean biota at local, regional, sub-basin, and Mediterranean scales.

Type of evidence	Local	Regional	Sub-basin (Western, Central, Eastern)	Mediterranean	Total
Descriptive	16	109	0	1	126
Quantitative					
Event-based	156	110	7	3	276
Time-series	27	10	1	18	56
Shifts	2	2	1	1	6

The number of reports of impacts assessed from heat waves (event-based) and time-series and the number of reported thermal shifts in natural populations are indicated.

The information provided by the articles about the temperature associated to each reported impact was very heterogeneous. Different papers used different temperature diagnostics (e.g., monthly mean, instantaneous values), from different instruments and at different depths. Therefore, in order to use a homogenized temperature diagnostic, we have used the sea surface temperature (SST) at each specific location where an impact has been reported. In particular, we have computed the 99th percentile of the year of the impact (SST_{p99}) at the location where the impact has been reported [thus SST_{p99} is a function of space (x) and time (t)]. Then, we express it as anomaly with respect to the averaged august temperature computed for the period 1960–1985 for the same location [$\Delta SST_{p99}(x, t) = SST_{p99}(x, t) - SST_{Aug\ 1960-1985}(x)$]. August was chosen as the reference period because this is the month when the highest sea surface temperatures are reached in the Mediterranean. Hence, this is the time when warming impacts are most likely to be observed, as extreme temperature, when organisms may be exposed to temperature beyond their optima, are concentrated in August. Other diagnostics as the yearly maximum or the averaged summer temperature lead to similar conclusions.

The SST database used in this study spans the period 1960–2011 at daily frequency with a spatial resolution of 1/8° (∼10 km). For the period 1980–2011 we have used SST satellite observations. In particular, we have used the MyOcean reanalysis product which consists in a reprocessing of Pathfinder V5.2 (PFV52) AVHRR data (Casey et al., 2010) and provides daily gap-free maps (L4) of the foundation SST at the original PFV52 resolution at 1/24° (Nardelli et al., 2013). In order to reduce observational noise, the resolution of the satellite data has been degraded to 1/8° through cell averaging. For the period 1960–1980, we have used the outputs of an atmosphere-ocean regional climate model, the PROTHEUS system (Artale et al., 2010). The model is driven by ERA40 reanalysis fields at the lateral boundaries and provides daily means of SST for the period 1960–2000 with a spatial resolution of 1/8°. The period 1980–2000 has been used to calibrate the model outputs with satellite data in order to remove the model bias and to adjust the amplitude of the seasonal cycle. Then, the calibrated model outputs for the period 1960–1980 have been included in the database.

We used the temperature records (annual SST, SST for a particular season and occasionally *in situ* temperature) provided by the papers when changes in marine biota were assessed from long-term observations, except in two cases (Nincevic-Gladan et al., 2010; Mazzocchi et al., 2012) that we obtained SST time series for the study period as described above.

We quantified the effect of warming on biological parameters through the Activation Energy (E, in eV, Brown et al., 2004), which provides a metric of the relative temperature-dependence or sensitivity of a particular property or process. The activation energy has been shown to provide an adequate, predictable and robust description of the temperature-dependence of biological processes across a scales or organization ranging from molecular and evolutionary processes, to physiological, organismal and community and ecosystem levels (Brown et al., 2004; Dell et al., 2011). Whenever a time series describing interannual changes in biological properties was available, the Activation Energy (E, in eV) was derived as the slope of the Arrhenius equation,

$$\ln(V) = C + \left[E * \left(\frac{1}{kT}\right)\right]$$

where V is the value of the biological parameter or rate process, C is the intercept of the fitted regression equation, k is the Boltzmann constant and T is the temperature (in K).

Where impacts were reported as departures of values observed during a thermal anomaly (V_i) relative to a previous observation (V_0) observed for temperature T_i and T_0 (in K), respectively (where $T_o < T_i$), an effect size per unit temperature, equivalent to E, was calculated, assuming the differences to conform to an Arrhenius model, as:

$$E = \frac{\ln\frac{V_0}{V_i}}{\frac{1}{kT_i} - \frac{1}{kT_0}}$$

E calculated in this manner is equivalent to a ln effect size (Hedges et al., 1999) typically used to compare the magnitude of responses across multiple response variables in meta-analysis (e.g., Kroeker et al., 2013). When the trait decreased with temperature (e.g., net growth rates), the ratio was rearranged (i.e., $\ln\frac{V_i}{V_0}$) to provide all E estimates as positive values thereby facilitating comparison of effect size across biological traits.

Results

Warming Rates in the Mediterranean: Observations and Model Hindcast

The average summer SST ranges from 22 to 28°C with the highest values in the Levantine basin and the lowest in the north Aegean, the north western Mediterranean and the Alborán sea (**Figure 1A**). These local minima are caused by different factors. In particular, the minimum in the Alborán Sea is linked to the inflow of colder Atlantic waters through the Strait of Gibraltar. The minimum in the NW Mediterranean can be attributed to the strong winds acting in that area enhancing vertical mixing and therefore cooling the surface waters. Finally, the minimum in the north Aegean can be explained by a combination of the inflow of cold waters from the Black Sea through the Dardanelles strait and the action of local winds. Concerning the vertical structure of the summer temperature field, it is characterized by a strong stratification in the upper layer. Temperature decreases almost linearly by about 7–8°C over the top 50 m water layer (0.14–0.16°C m^{-1}) in both the eastern and western basins (**Figure 1B**), and it remains relatively uniform at deeper water.

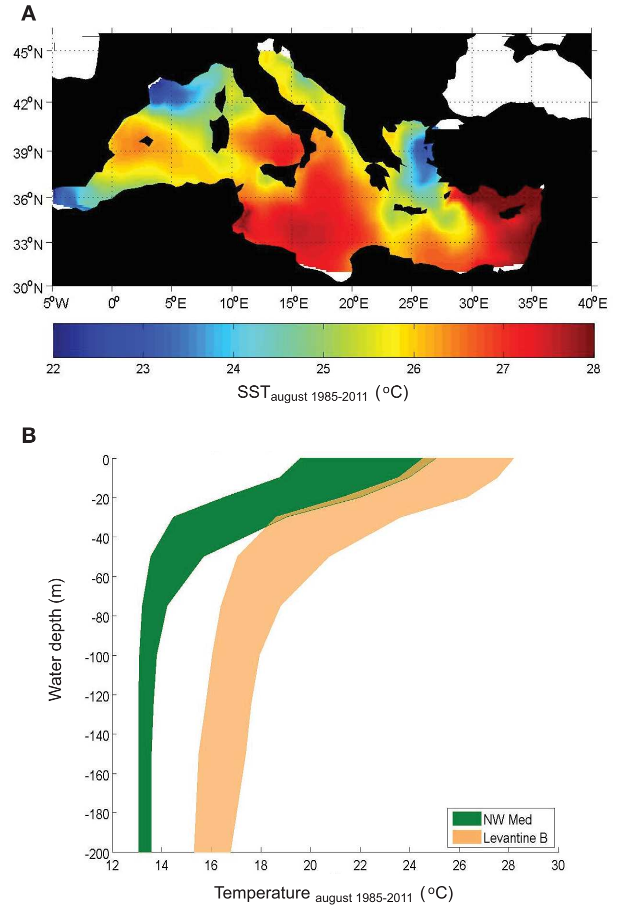

FIGURE 1 | Averaged Sea Surface Temperature for August during the period 1985–2011 (A) and averaged vertical profiles of temperature for August during the period 1985–2011 in the North Western Mediterranean (0–13°E, 40–45°N) and the Levantine basin (30–40°E, 31–37°N) (B).

Linear trends were fitted to the satellite SST for the period 1985–2011 in order to characterize multidecadal changes in summer SST (**Figure 2**). During the last three decades the summer surface temperature has increased, on average, 1.15°C. During this period, the warming trends range from 0.25°C decade^{-1} in the western basin to 0.65°C decade^{-1} in the eastern basin. The increase of the summer mean temperature, an important factor affecting biota is the occurrence of heat waves. We characterize heat waves as periods where SST at a particular location exceeded the 99th percentile of a reference

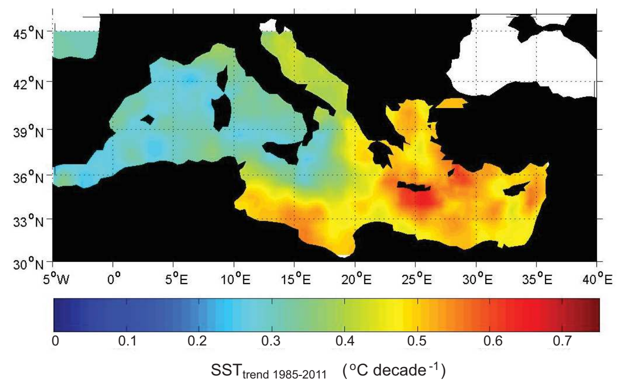

FIGURE 2 | Sea Surface Temperature Trend (in °C decade^{-1}) computed for the period 1985–2011 using satellite data.

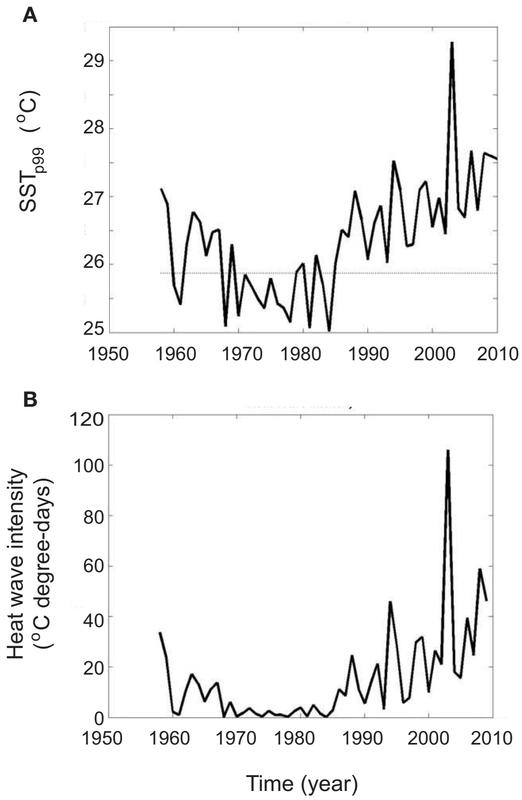

FIGURE 3 | Time series of basin average SST of 99th annual percentile (SST p99 in °C, A) and of basin average of heat wave intensity (in °C degree-days, B). The dotted line in plot A indicates the basin average of the reference value used to characterize the heat waves.

period (here 1960–1985) at the same location. The intensity of the heat wave at a given location is expressed in °C degree-days and is computed by integrating the excess temperature above the given threshold (in °C) during the time the threshold has been exceeded (in days). The annual 99th percentile shows a significant interannual variability with basin averaged values ranging from 25.1°C in 1984 to 29.3°C in 2003 (**Figure 3A**). Also, a multidecadal variability is also apparent with a minimum in the 70's and a significant increase since the mid 80's until present, in good agreement with the multidecadal change of the mean SST already reported by Mariotti and Dell'Aquila (2012). Concerning the heat wave intensity, there is also a strong interannual variability (standard deviation of 20°C degree-days) with strong heat wave events reaching up to 100, 60, and 50°C degree-days in 2003, 2009, and 1994, respectively (**Figure 3B**). The decadal variability in the heat wave intensity also follows the changes observed in the 99th percentile. During the 60's the averaged intensity was 15°C degree-days, during the 70's and until mid 80's the intensity was almost zero and since then the intensity has been rising. During the period 2000–2010 the averaged heat wave intensity was 40°C·degree-days.

Heat waves are not basin-wide processes and large differences can be found regionally. For instance, during 1998 a heat wave affected the Adriatic, the Ionian and parts of the Levantine basin (**Figure 4A**). In those regions the heat wave intensity was 60–75°C degree-days while in the rest of the basin it was hardly larger than 10°C degree-days. The 2003 heat wave affected a much larger area (**Figure 4B**). Almost the whole western Mediterranean, the Adriatic and central Mediterranean were affected by a long and intense heat wave that reached over 120°C degree-days in most of those areas. Conversely, the Alborán Sea, the Levantine basin and the Aegean Sea did not experience any heat wave that year.

Footprints of warming on Mediterranean Biota

A large number of impacts of warming on Mediterranean biota have been reported since year 1950, but 90% of them have been observed after 1987 (**Figure 5**). Most (61%) event-based biological impacts occurred in years 1994–1995, 1999, and 2003 (**Figure 5**). Despite most (90%) long term changes in marine biota attributed to warming follow linear trends, there are some evidence (6 out of 72) of abrupt shifts in Mediterranean biota attributed to shifts in SST in 1970, the end of the 80's and the end of the 90's (Supplementary Table 1).

Evidence of warming impacts on Mediterranean biota are largely (94%) concentrated in the North Western Mediterranean basin and the Adriatic Sea (**Figure 6**). No impacts are reported along the Southern Mediterranean coast, except Tunisia, and few impacts have been described in the central and eastern Mediterranean sub-basins (**Figure 6**). Mediterranean warming is already affecting the fitness of marine biota, as reflected by reports of changes in abundance, survival and fertility, their phenology and triggering species migration (**Figure 6**). Population abundance and survival are the biological traits accounting for most (68%) reported impacts of Mediterranean warming. Yet, migration of native and introduced (mostly Lessepian) species accounts for 15% of total biological footprints of Mediterranean warming (**Figure 6**). Footprints of Mediterranean warming have been observed in several marine phylum, including populations of invertebrates (porifera, cnidaria, polychaeta, mollusca, ascidians, bryozoa, echinodermata, crustaceans), vertebrates (fishes, reptiles, mammals), phytoplankton, and macrophytes (macroalgae and seagrasses). However, most (53%) evidence of

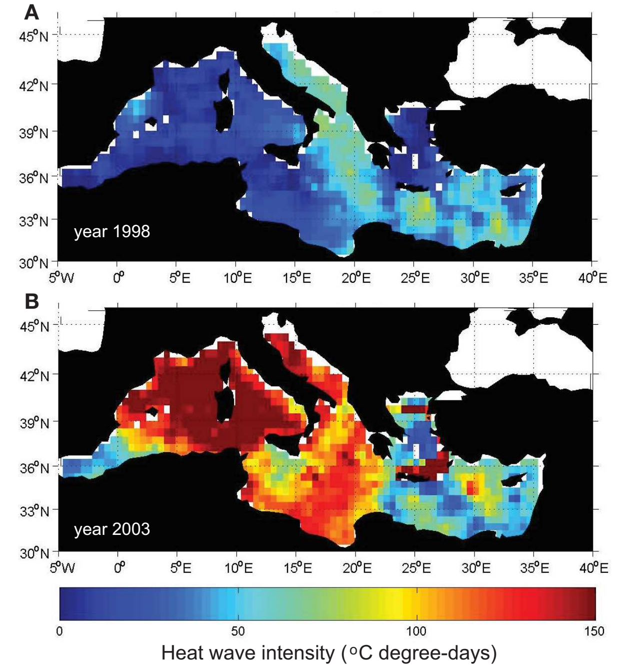

FIGURE 4 | Heat wave intensity for years 1998 (A) and 2003 (B) across the Mediterranean Sea.

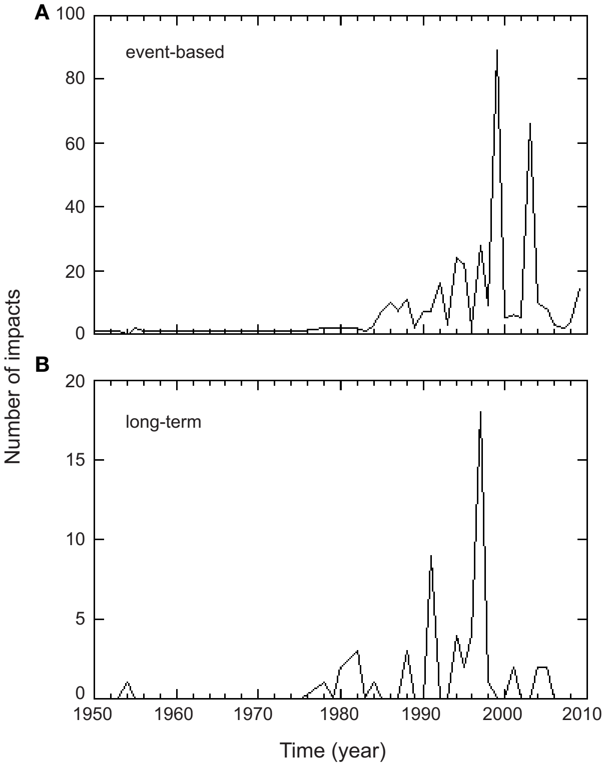

FIGURE 5 | Time series of the number of biological impacts attributed to Mediterranean warming assessed (A) from single warming events and (B) from long-term observations. The number of impacts assessed from long-term observations corresponds to the number of time-series exhibiting significant linear trends between biological parameters and temperature. Time in **(B)** corresponds to the central year of the observational period of each study (median duration 24 years).

impacts of warming on Mediterranean biota are reported for fish and cnidaria.

Impacts of warming on marine species living in the Mediterranean Sea have been observed at SST_{p99} anomalies up to 5.5°C (**Figure 7**). However, the frequency of anomalies decreases with anomaly strength. Thus, we corrected the thermal anomaly distribution of impacts for the frequency of occurrence of anomalies by dividing the number of impacts observed by the number of SST_{p99} anomalies within 0.5°C increments occurred since 1960. The magnitude of warming triggering impacts on Mediterranean marine biota varied across biological traits (**Figure 7**). Fertility is the biological trait that risks to be largely impacted by mild warming (50% probability of impact at SST_{p99} anomaly $\leq$ 1°C), followed by migration (50% probability of impact at SST_{p99} anomaly $\leq$ 2°C) and abundance (50% probability of impact at SST_{p99} anomaly $\leq$2.5°C, **Figure 7**). Conversely, 50% of impacts on phenology and survival occur at large SST_{p99} anomalies up to 3 and 4.5°C, respectively (**Figure 7**). Similarly, SST_{p99} exceeding 27.5, 25.5, 26, 28, and 28.5°C, respectively, triggers the probability of impact above of 50% on fertility, migration, abundance, phenology and survival of species living in the Mediterranean Sea, respectively (**Figure 8**). Overall, 50% of biological impacts in the Mediterranean Sea occur at SST_{p99} anomaly $\leq$ 4.5°C (**Figure 9A**) and at SST_{p99} of 27.5°C (**Figure 9B**).

The sensitivity of Mediterranean biota to warming varies across taxonomic groups. 50% of the impacts on ascidiacea, crustacea, echinodermata, fish, and phytoplankton occur at SST_{p99} anomaly up to 2 or 2.5°C, whereas those on cnidaria, mollusca and porifera, and seagrasses occur at SST_{p99} anomaly up to 5°C (**Figure 10**). The observed thermal anomalies impacting sessile marine organisms (76.6% affected survival and 1% phenology) on average are three-fold higher (1.51 ± 0.11°C, $N = 197$) than those (0.59 ± 0.09°C) impacting motile biota (4% affected survival and 4.1% phenology).

Because the attribution of reported impacts to warming at SST_{p99} anomalies smaller than 2°C (**Figure 9A**) involves considerable uncertainty, we defined a threshold at 2°C thermal difference, above which the attribution of estimated effect sizes to Mediterranean warming is likely robust, to assess the magnitude of the responses. Most (63%) of quantified changes in marine biological activity in the Mediterranean Sea, however, have been documented for thermal differences below 2°C. Calculation of the activation energy of biological activity could reach extremely large, abnormal values for thermal anomalies below 2°C (Supplementary Figure 1), thereby inflating the possible response of organisms to warming. When Mediterranean warming involves thermal differences exceeding 2°C, the median activation energy of marine biological activity is 2.25 eV (**Figure 11**), although when assessed from event-based observations (1.69 eV) is about half that estimated from time series (3.65 eV). However, the geometric mean of activation

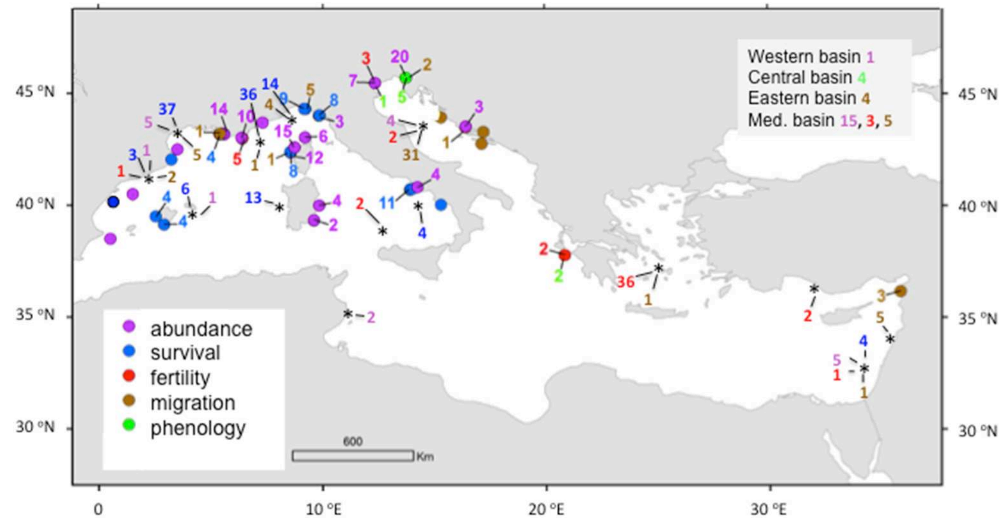

FIGURE 6 | Location of the reported impacts of temperature on biota in the Mediterranean Sea. The color of dots and numbers indicates the category of impact reported. The numbers next to the dots and quadrats show the number of impacts per impact category reported per site when it exceeds one. Impacts reported at local (color dots), regional (asterisks), sub-basin (Western, Central, Eastern Mediterranean), and Mediterranean basin scales are indicated.

energy of Mediterranean marine biological traits is comparable for event-based observations (1.24 ± 0.58 eV), and time-series observations (2.69 ± 0.78 eV), with an overall geometric mean activation energy of 1.58 ± 0.48 eV (**Figure 11**). Abundance and reproduction rates tend to be the traits displaying a steepest response to warming, followed my survival and phenology shifts, and migrations show, comparatively, a limited response (**Figure 11**).

Discussion

The warming trend of 0.25°C decade^{-1} in the western basin and 0.65°C decade^{-1} in the eastern basin can be partially explained by an increase of the Atlantic Multidecadal Oscillation (AMO) index. Mariotti and Dell'Aquila (2012) have shown that multidecadal variability of Mediterranean SST is highly correlated with AMO. AMO has been increasing during the last 40 years, which could explain an increase of about 0.10–0.15°C decade^{-1} in the Mediterranean SST during that period. The rest of the trend may be linked to global warming. Unfortunately up to our knowledge there are no dedicated studies on the attribution of recent Mediterranean warming to confirm this apportioning of warming trends.

The synthesis presented documents a large number (>450) of reported impacts of warming on the Mediterranean Sea, one of the rapid warming areas in the ocean (Hoegh-Guldberg et al., 2014). The geographical distribution of these reports reflects, to a large extent, the distribution of marine research institutions, with a high density of observations in the NW Mediterranean and a remarkable paucity of observations along the Northern African coast. This is unfortunate, as the NW Mediterranean is the area in the Mediterranean Sea with the most moderate long-term warming trend, whereas rates of warming were much higher in the Eastern basin and along the African coast from Algeria to Israel (**Figure 2**). Also, impacts driven by invasive behavior propelled by warming of lessepian migrants reaching the Mediterranean from the Red Sea are likely to be greatest in the Eastern basin. On the other hand, the intense research effort in the NW Mediterranean allowed for a thorough documentation of the impacts of the 2003 heat wave, the strongest recorded in the Mediterranean over at least the past 50 years and that is responsible for a high fraction (17%) of the reports of warming impacts on Mediterranean biota. Indeed, most reports were event-based rather than derived from time-series analyses, which weakens the attribution of these impacts to warming and, particularly, its anthropogenic component, which requires multi-decadal time series (Parmesan et al., 2013; O'Connor et al., 2014). An assessment of the robustness of studies assessing the impacts of climate change on Mediterranean biota shows these to be, on average, weaker than those available in the general field of climate change ecology (O'Connor et al., 2014). In particular, the studies for the Mediterranean suffer from insufficient data, particularly due to the prevalence of event-based observations, and inappropriate statistical analyses. In contrast, the expectations were formulated in a more explicit manner than usually encountered in the field.

There has been much discussion as to the role of anthropogenic climate change (very likely, confidence level >90%, that human influence was responsible, e.g., Stott et al., 2004) vs. other processes (e.g., aerosols from Saharan dust and forest fires, Lyamani et al., 2006) in causing the 2003 heat wave, upon which a significant fraction of the evidence rests. Regardless of whether the impacts associated with the 2003 heat in the NW Mediterranean can be attributed to anthropogenic climate change or not, this heat wave provides a proxy of

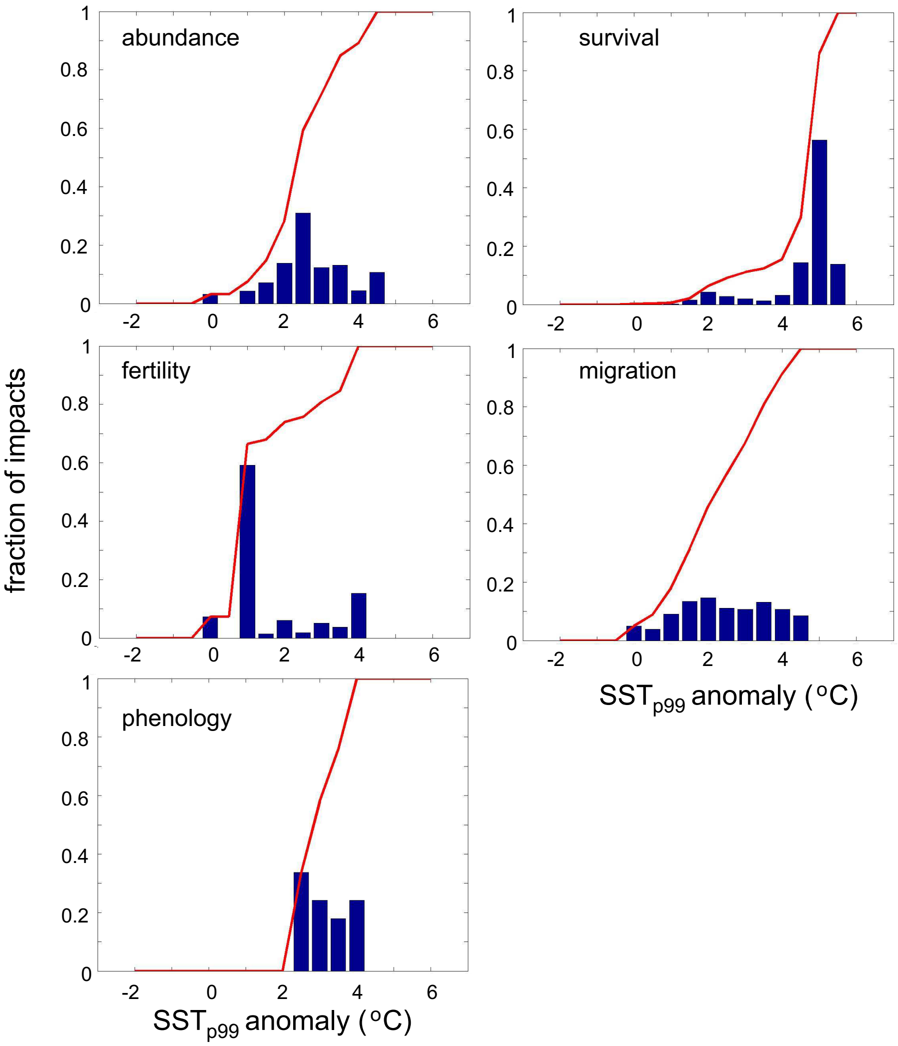

FIGURE 7 | Corrected histogram of the number of reported impacts as a function of SST$_{p99}$ anomaly (see text for details) for each trait: abundance, survival, fertility, migration, and phenology. The red line in each plot indicates the cumulative probability.

the impacts to be expected in the future when downscaled models predict that heat waves of this magnitude will become frequent (Jordà et al., 2012). The 2003 heat wave event was reported to result in mortality of benthic organisms, including gorgonians, sponges, molluscs, bryozoos (e.g., Garrabou et al., 2009; Bensoussan et al., 2010) and seagrass (*Posidonia oceanica*, Díaz-Almela et al., 2009; Marbà and Duarte, 2010) as well as mass flowering of *P. oceanica* (Díaz-Almela et al., 2007). These observations provide indications of the impacts that may be expected with future climate change in the Mediterranean, where the projected increased in the frequency and magnitude of heat waves will compromise the most vulnerable ecosystems, such as coral and *P. oceanica* meadows (e.g., Jordà et al., 2012).

The distribution of reports by taxa is dominated by reports on fish and cnidaria. This distribution of reports reflects a mixture of the vulnerability of the taxa and the availability of data. For instance, the existence of systematic and regular fishery surveys has provided a robust basis for the evaluation of the response of fishes to warming, not only in terms of the data available but the fact that these are usually available as time-series, which provide a stronger basis for detection and attribution (Parmesan et al., 2013; O'Connor et al., 2014). The availability of high quality-data for fish communities is likely responsible for the fact that impacts on fish were detected and reported at lower temperature anomalies (median 2.0°C) than reported for other taxa (overall median 5.0°C, **Figure 10**). In contrast, cnidaria, for which also a substantial (for not as high-quality) observational basis was available, seem to be more resistant to warming, as impacts were observed at relatively higher temperature anomalies (median 5.0°C, **Figure 10**).

Examination of the reports of impacts in relation to the weighted (by frequency of occurrence) thermal anomalies

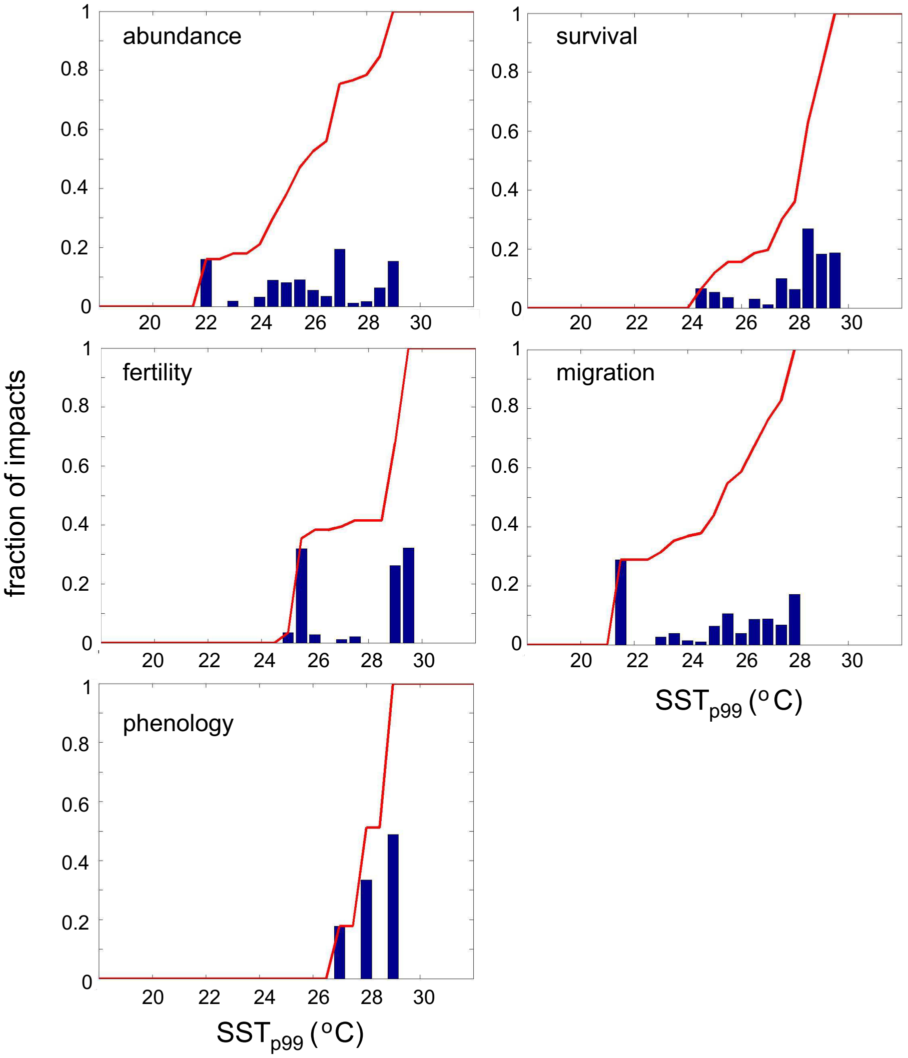

FIGURE 8 | Corrected histogram of the number of reported impacts as a function of SST_{p99} (see text for details) for each trait: abundance, survival, fertility, migration, and phenology. The red line in each plot indicates the cumulative probability.

showed that some impacts seem to respond continuously to warming, such as those on abundance, migration and phenology (**Figure 7**). It also showed that a number (2%) of reports of impacts which attribution to warming seem questionable, as impacts were reported with no, or negative, thermal anomalies (i.e., in the absence of evidence of warming or even in cooling periods, **Figure 9A**). In contrast, reports of enhanced mortality with warming showed a threshold behavior, where the likelihood of finding enhanced mortality increased abruptly at temperature anomalies in excess of 4°C.

The examination of activation energy for the response of Mediterranean marine biota to warming reveals a prevalence of high (>1 eV) activation energy values (geometric mean 1.58 ± 0.48 eV), which is about three-fold higher than the activation energy the metabolic theory of ecology assumes to govern biological processes (Brown et al., 2004). This implies that biological responses to warming in the Mediterranean are far steepest than possibly explained by the direct effect of warming alone. Indeed, warming affects a number of processes, in addition to its direct effect on biological processes. For instance, warming affects the strength of vertical stratification in the Mediterranean, which in turn affects turbulent nutrient supply to the photic layer, reducing primary production in the stratified season (e.g., Doney, 2006). Indeed, warming is leading to reduced primary production in the subtropical and tropical ocean (Boyce et al., 2010) and an expansion of the subtropical gyres (Polovina et al., 2008), largely through this mechanism. Moreover, warming does not occur in isolation but concurrently with other stresses, such as pollutant inputs (Duarte, 2014), where warming can amplify the sensitivity of organisms to other stresses. For instance, research in a Mediterranean Bay has shown that the probability of hypoxia increases with temperature

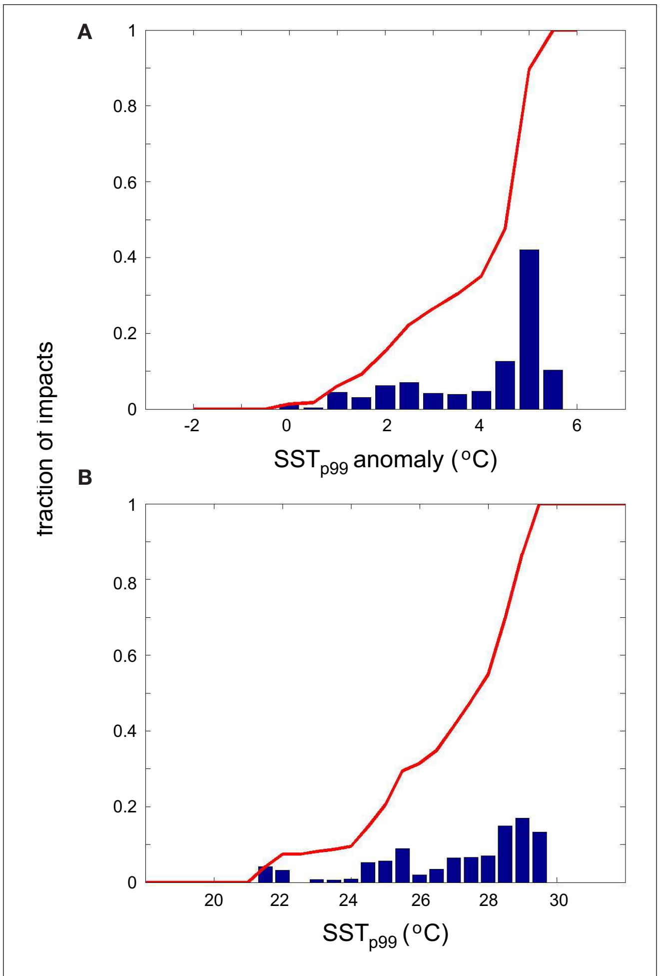

FIGURE 9 | Corrected histograms of the number of reported impacts as a function of SST$_{p99}$ anomaly (A) and as a function of SST$_{p99}$ (B) for all traits.

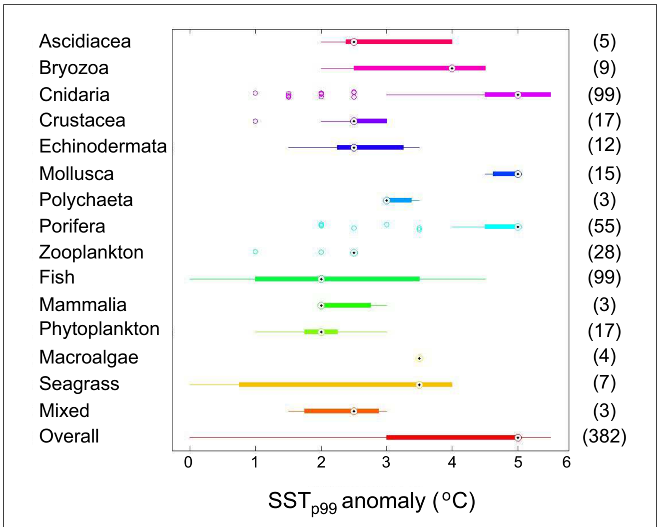

FIGURE 10 | Box plot of SST$_{p99}$ anomaly during reported warming impacts across taxonomic groups of Mediterranean biota. The number of single estimates is shown within brackets. Impact observations are corrected by the temperature anomaly distribution at the sites for the period 1950–2011.

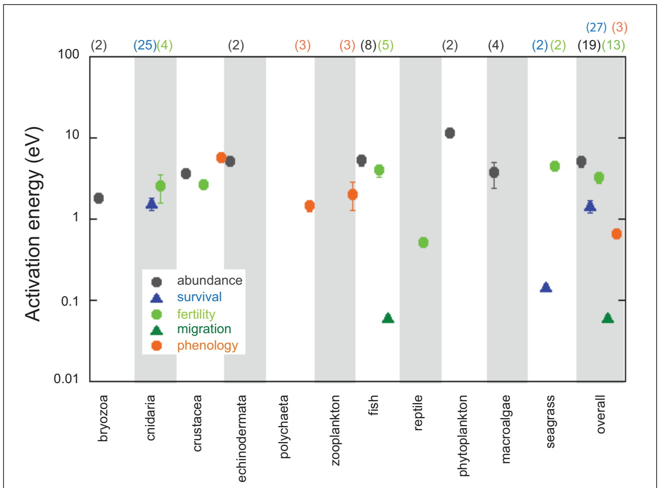

FIGURE 11 | Mean activation energy of biological traits (abundance, survival, fertility, migration, phenology) across taxonomic groups and overall calculated from event-based and long-term observations. Error bars are standard error of the mean value. The number of observations per taxon and trait category, when greater than one, is indicated within brackets. Only activation energy estimates for a temperature range exceeding 2°C are included.

(Vaquer-Sunyer et al., 2012), while warming also increases metabolic oxygen consumption (Regaudie-de-Gioux and Duarte, 2013) and raises the thresholds of oxygen concentration for hypoxia-induced stresses in marine organisms (Vaquer-Sunyer and Duarte, 2011). Hence, the geometric mean empirical activation energy of 1.58 ± 0.48 eV reported here for marine Mediterranean biota compounds the direct and indirect effects of warming and identifies a steeper response to warming than expected based on metabolic theory alone. The limited activation energy for migration compared to other traits likely reflects the confined nature of the Mediterranean basin, where organisms have limited scope for poleward migration (Burrows et al., 2011, 2014), thereby limited the role of migration as an adaptive strategy to cope with climate change (Poloczanska et al., 2013).

In summary, the synthesis presented here provides widespread evidence of severe impacts of warming on Mediterranean biota, mostly associated with the recent heat waves affecting this region, in particular the 2003 heat wave affecting the NW Mediterranean. The observations, however, are biased toward the northern and western sectors of the basin, where research institutions and, therefore, effort aggregate, likely underestimating the impacts of warming in areas, such as the African coast and Eastern basin where warming is particularly intense. The reported impacts of warming should be considered with caution when these are associated with thermal anomalies less than 2°C, as the reported warming derives largely, but not exclusively, from anthropogenic climate change. The analysis presented provides compelling evidence that Mediterranean biota is far more sensitive to warming than predicted by metabolic theory, as reflected in activation energy typically >1 eV across processes. We suggest that this reflects the multifaceted role of temperature in affecting biological processes directly, through its metabolic effect, and indirectly through effects on nutrient supply and physical processes and enhancing the vulnerability of biota to other stresses in the ecosystem.

Author Contributions

Conceived and designed the study: NM, GJ, SA, and CD. Acquired the data: NM, GJ, and CG. Analyzed the data: NM, GJ, and CD. Wrote the paper: NM, GJ, SA, CG, and CD. Final approval of the manuscript: NM, GJ, SA, CG, and CD.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2015.00056

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REVIEW
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The North Atlantic Spring-Bloom System—Where the Changing Climate Meets the Winter Dark

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The North Atlantic with its spring-bloom ecosystem has its particular responses to climate change, many of them different from the other parts of the world's oceans. The system is strongly influenced by anthropogenic climate change as well as to strong decadal to multidecadal natural climate variability. In particular, the northernmost part of the system and the Arctic is exposed to higher increase in temperature than any other ocean region. The most pronounced examples of poleward migration of marine species are found in the North Atlantic, and comprise the recent warming phase after the 1970s. The latitudinal asymmetric position of the Arctic Front and its nature of change result in a considerably larger migration distance and migration speed of species in the Northeast Atlantic part of the system. However, we here hypothesize that there is a limit to the future extent of poleward migration of species constrained by the latitudinal region adjacent the Polar Circle. We define this region the critical latitudes. This is because the seasonal light cycle at high latitudes sets particular demands on the life cycle of planktivorous species. Presently, boreal planktivorous species at high latitudes deposit lipids during the short spring bloom period and overwinter when phytoplankton production is insufficient for feeding. Unless invading temperate species from farther south are able to adapt by developing a similar life cycle future poleward migration of such species will be unlikely.

Keywords: future climate change impacts, multidecadal climate variability, seasonal light cycle, lipid accumulation, overwintering, climate-induced migration, critical latitude

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ECOSYSTEM ATTRIBUTES

The North Atlantic spring-bloom ecosystem extends from the northern rim of the North Atlantic subtropical gyre at about 30°N to the Arctic ecosystems of the Davis Strait between Canada and Greenland, across the Fram Strait between the Norwegian Sea and the Polar Basin and along the northernmost part of the Barents Sea at 80°N (Hoegh-Guldberg et al., 2014). The region is characterized by a predominant seasonal cycle in the primary production with the peak amplified and delayed with increasing latitudes (Racault et al., 2012) and with shortened bloom duration (Ellingsen et al., 2008). This is largely due to the extreme light cycle to the north of the Polar Circle where winter dark ceases primary production. This northernmost part of the North Atlantic is unique as it is the only part of the world oceans with ice-free, open-water conditions under the extreme light cycle of winter dark and summer midnight sun. In the northern North Pacific a similar light cycle only exists to the north of the Bering Strait within the Polar Ocean, and in the Southern Hemisphere the Antarctic continent occupies similar southern latitudes (**Figure 1**).

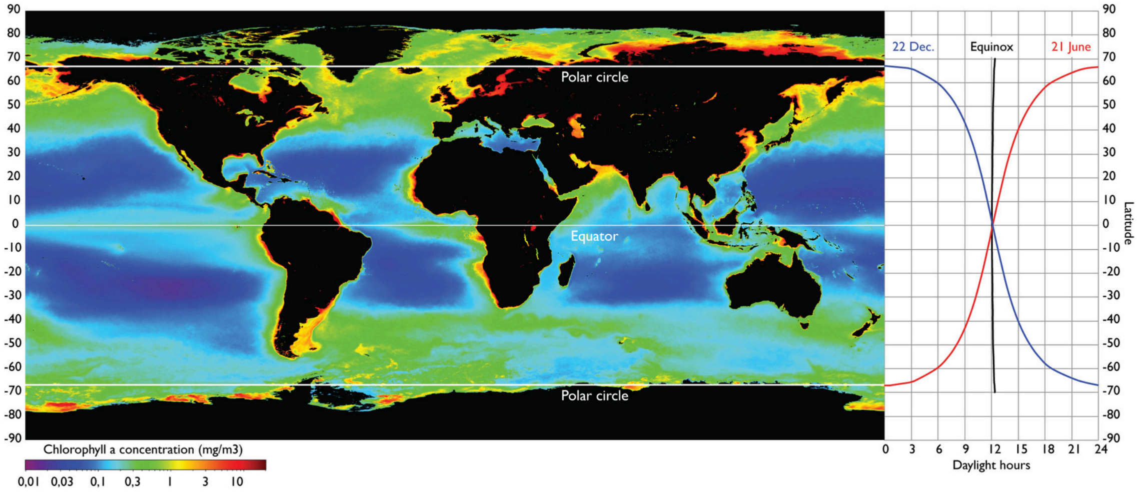

FIGURE 1 | The seasonal light cycle strongly structures the phytoplankton production at high latitudes, and this effect cascades to higher trophic levels. Right panel shows latitudinal variation in daylight length for the two solstices (about 21 June and 22 December) and for the two equinoxes (about 20 March and 22 September). The source of the global map of annual mean chlorophyll concentration is from SeaWIFS satellite sensor averaged over the interval 4 September 1997–30 November 2010 (**left panel**). http://oceancolor.gsfc.nasa.gov/cgi/l3/S19972472010334.L3m_CU_CHL_chlor_a_9km.png?sub=img.

Different from terrestrial ecosystems at high latitudes primary production at sea is asymmetric compared to the light cycle because of the extremely efficient nutrient uptake of the tiny and numerous phytoplankton with its high surface-to-volume ratio. This causes the nutrients that are mixed up from the depths into the photic zone during winter to be consumed very rapidly when light returns at spring time. After the collapse of the spring bloom, due to zooplankton predation and nutrient exhaustion, the summer production continues at much lower level primarily caused by regenerated production. Annual net primary production (NPP) ranges from about 500 g C year^{-1} in coastal regions to about 150 g C year^{-1} in the highest latitudes of the North Atlantic (Mueter et al., 2009). The southern and warmest part of the biome seems to have the highest primary production (Mueter et al., 2009). In the open-ocean, the system is dominated by diatoms in the initial phase of the spring bloom exhausting the silicate from the photic zone. It is followed by a flagellate-dominated phytoplankton community during moderate summer production (McQuatters-Gollop et al., 2007; Fox et al., 2009).

Organisms at higher trophic levels in Northeast Atlantic ecosystems are adapted to the seasonal cycle of the primary production with predominant seasonal activity in feeding and reproduction. Particularly egg production and the subsequent occurrence of the plankton-feeding offspring must be tuned to the seasonal cycle of the plankton production. Lack of synchrony in these processes has been hypothesized to cause recruitment failure to fish stocks (e.g., Hjort, 1914; Cushing, 1982). In the southern part of the biome winter primary production can be high enough to sustain autumn and winter spawning behavior, but at higher latitudes, particularly to the north of 60°N, marine organisms are increasingly forced into the spring-spawning cycle (e.g., Ellertsen et al., 1989) because of nearly complete absence of primary production during the dark winter time. This high-latitude seasonal light cycle has developed herbivore copepods with the particular attribute of very efficient feeding during the short phytoplankton production season and deposition of large stores of lipids for overwintering at deeper depths during winter (Falk-Petersen et al., 2009). The dominant zooplankton species with such attributes are the arcto-boreal *Calanus finmarchicus* and the Arctic *Calanus glacialis* and *Calanus hyperboreus* (Melle et al., 2004). The planktivorous Norwegian spring-spawning herring (*Clupea harengus*) is particularly adapted to the feeding on *C. finmarchicus* and has consequently developed a similar overwintering strategy (Holst et al., 2004) implying that the fish migrate out of the pelagic layer to larger depths where they reduce their activity. However, different from *C. finmarchicus* the herring is not dispersed in the deep layers, but maintains their schooling behavior during overwintering. Other planktivorous fish species have developed different adaptations. For example, the more temperate-adapted Atlantic mackerel (*Scomber scombrus*; Uriarte and Lucio, 2001) and the blue whiting (*Micromesistius poutassou*; Bailey, 1982) uses the high latitudes for summer feeding only, and migrate out of the high latitudes and southwards into regions where plankton concentrations are high enough to maintain winter feeding (e.g., Casini et al., 2004). Although bottom fishes and other piscivore species feed on larger organisms during winter and are independent of the plankton for food in the adult stages their planktivorous offspring must co-occur with the primary production cycle, and their spawning cycles must be tuned accordingly. Hence, the seasonal light cycle that is independent of climate change has a profound influence on organisms at all trophic levels in high-latitude marine ecosystems. Northward migration of lower-latitude temperate species induced by climate change may become constrained due to lack of adaptation to the needed lipid deposition and overwintering.

CLIMATE VARIABILITY OF THE NORTH ATLANTIC OCEAN

The North Atlantic Ocean has the most comprehensive time series of abundances of marine organisms from zooplankton to fish with which to examine climate impacts. Some of these time series extend back more than 100 years (e.g., Nakken, 1994; Toresen and Østvedt, 2000; Kjesbu et al., 2014). These allow a particular perspective on climate change in this region compared to other parts of the world's oceans. A range of spatio-temporal scales of variability has been identified, from interannual to multidecadal time scale. Generally, spatial and temporal scales are interlinked with climate phenomena of larger spatial extent having longer time scales (Drinkwater et al., 2014). Here, we will limit the description of climate variability to two specific phenomena, the interannual- to the decadal-scale North Atlantic Oscillation (NAO), and the Atlantic Multidecadal Oscillation (AMO). With a periodicity of approximately 60–80 years (Delworth and Mann, 2000; Alexander et al., 2014), it is difficult to distinguish between AMO-related increases in ocean temperatures and a climate change signal when analyzing relatively short time series. Likewise, attributing changes in short biological time series to responses to climate change may be misleading. The NAO, on the other hand, with its interannual to decadal-scale mode of variability and its limited spatial extent, compared to AMO, is trivial to distinguish from the anthropogenic global climate change. The two phenomena have been associated with a wide range of impacts on the marine ecosystems and their organisms. An overview of NAO impacts is presented by Hurrell et al. (2003); and overview of AMO is presented by Alheit et al. (2014).

The effects of decadal-scale climate variability has been well documented, particularly the impacts of NAO, an observed atmospheric pressure difference anomaly between the Icelandic Low (measured in western part of Iceland) and the Azores High (measured either on the Azores or at Lisbon, Portugal; e.g., Hurrell et al., 2003). The NAO is associated with opposite temperature and current flux manifestations in the Northeast and the Northwest Atlantic (Sundby and Drinkwater, 2007) and opposite storm tracks and precipitation in the northeastern and central-eastern/Mediterranean areas of the North Atlantic (López-Moreno et al., 2011). The impacts of the NAO on marine ecosystems are comprehensive and well documented (e.g., Drinkwater et al., 2003) although the mechanistic understanding is often unclear since the NAO results in changes in a number of climate variables such as sea temperature, wind forcing, volume flux changes, vertical mixing, precipitation and light conditions through its effects on cloudiness. In addition, due to the spatial differences in the NAO effects on the climate variables in the North Atlantic, the different regions of the North Atlantic display a large diversity of ecosystem responses. In the northeastern North Atlantic impacts on the marine ecosystems have been mainly associated with the combined effects on flux variability of Atlantic water into the region and temperature. In the Barents Sea high NAO index results in increased inflow of Atlantic water masses and higher temperature (Sundby and Drinkwater, 2007) resulting in higher production of plankton (Dalpadado et al., 2014). In turn, the higher temperatures are associated with increased fish production (e.g., Kjesbu et al., 2014). In the Mediterranean region positive NAO index is associated with lower than normal precipitation (Trigo, 2011). In the western Mediterranean catches of a number of coastal fish species increased with increased wind mixing and runoff from land associated with negative NAO index (Lloret et al., 2001). The responses to fisheries in the other parts of the Mediterranean are different from the western part as displayed through the fisheries of European hake (Maynou, 2011). A more comprehensive overview of the NAO-linked responses in the northeastern part of the North Atlantic and in the Mediterranean Sea are presented by Drinkwater et al. (2003) and Vicente-Serrano and Trigo (2011), respectively.

The other predominant climate mode, the AMO, is defined as the detrended sea surface temperature anomaly averaged over the North Atlantic from the equator to between 60° and 70°N, with the actual latitude chosen being author-dependent. An AMO-like periodicity has been detected from tree-ring data extending back to the sixteenth century (Gray et al., 2004) and to the fourteenth and fifteenth centuries in marine paleo records in the Caribbean (Kilbourne et al., 2014). The AMO has an opposite but weaker mode in the southern hemisphere (Sutton and Hodson, 2005).

The temperature increase in the North Atlantic since the late 1970s has occurred during a phase of increasing AMO implying that both the anthropogenic climate change and the positive phase of the AMO have contributed to increase the temperature in the North Atlantic sector during the recent 40 years. Because of the long time scale of the AMO and the switch to a positive phase since the late 1970s, it is challenging to interpret how large fraction of the recent temperature increase over the North Atlantic is related to the AMO and how much is caused by global anthropogenic climate change. In sum, the observed increase in sea surface temperature from 1970 to 2010 is higher in the northern North Atlantic than anywhere else in the world oceans (Rhein et al., 2013). For the same reason the Arctic sea-ice decrease since 1978 observed from satellite imagery (http://nsidc.org/arcticseaicenews/) should be interpreted with care as a global climate change signal since the AMO signal also extends into the Arctic (Drinkwater et al., 2014). In addition to the temperature signal the positive phase of AMO (high temperatures) is associated with anomalous low pressure between 20°S and 50°N causing reduced wind speed over the tropical Atlantic and increased precipitation in the eastern part of the tropical Atlantic (Alexander et al., 2014).

Impacts of the AMO variability on marine ecosystems have been documented for both planktivorous and piscivorous fishes, and as well as for zooplankton, although the latter is limited to the recent phase of temperature increase after the 1960s. The previous warming phase of AMO that occurred from the 1920s–1940s caused similar changes in the high-latitude marine ecosystems, as those during the recent warming. The warming in the early twentieth century was noticed by the marine science community, particularly the fish biologists, with a special ICES conference on climate change held in 1948 (Rollefsen and Vedel Tåning, 1949). Drinkwater (2006) presented a comprehensive review of the changes in the high-latitude part of the North Atlantic from Labrador to the Barents Sea during this first warming phase of the AMO in the twentieth century: Zooplankton abundance, although limited, appeared to have increased in most of the regions. Several herring stocks increased in biomass. Gadoid species such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) increased in biomass and shifted northwards with their northernmost fringes into the Arctic. Benthic species advanced toward Arctic regions. At the tail of the moving boreal distributions, warm-water species came into the region from the south. Alheit et al. (2014) showed that small pelagics, such as sardines and anchovies, became more abundant in the southern and central-eastern North Sea during both of the two AMO warm phases in the twentieth century. In the Mediterranean Sea, higher abundances of small pelagic fishes also seemed to be in phase with the warm mode of AMO (Alheit et al., 2014). Moreover, these authors pointed out that the earlier described Russell Cycle in the North Sea (Cushing, 1957; Russell et al., 1971) appears to be in phase with the AMO.

In the central western part of the North Atlantic (US east coast) a number fish species, particularly demersal species, moved poleward during the recent AMO warming period 1970–2008 by up to 8 km per year (Nye et al., 2009). These patterns of regional change resemble many of the AMO changes in the northeastern North Atlantic with increase in fish abundance in the north and decrease in the south (Nye et al., 2014).

The link between AMO and phytoplankton production is much less clear (Nye et al., 2014). This could be because changes in phytoplankton production are rather linked to other climate variables than ocean temperature itself, particularly to changes in vertical mixing that provides the nutrient flux from the deep layers to the photic zone where photosynthesis can occur (Boyd et al., 2014). For example, increased winter wind mixing during positive AMO modes increased phytoplankton production in the Mid-Atlantic Bight (Schofield et al., 2008). At higher latitudes of the North Atlantic, i.e., the Gulf of Maine, the Norwegian Sea, and the Barents Sea, increased temperature has been shown to increase the phytoplankton production (Mueter et al., 2009). It is, however, unclear to what extent such correlations are mechanistically caused by the temperature itself or by a combination with other climate variables.

The reported ecosystem responses to the AMO cited above cover limited phases of the AMO "cycle," either the warming phase from the 1920s to the 1940s (e.g., Rollefsen and Vedel Tåning, 1949; Drinkwater, 2006) or the recent warming phase from the 1970s. However, for two high-latitude fish species of the North Atlantic time series are available covering more than one full AMO cycle. Abundance estimates for the Norwegian spring-spawning herring (NSSH) inhabiting the Norwegian and Barents seas and for the Northeast Arctic cod (NEAC) inhabiting the Barents Sea are available from the beginning of the twentieth century. In addition, spatial spawning distributions are available for the NEAC from the beginning of twentieth century to 1975. Toresen and Østvedt (2000) showed that the spawning stock biomass (SSB) of the NSSH varied through the twentieth century in concert with the long-term averaged temperature variations similar to the AMO signal. During the cool period between 1900 and 1920 SSB ranged between 2 and 4 mill. tons. Thereafter, it increased abruptly with the temperature increase and ranged between 9 and 16 mill. tons during the warm phase between 1930s and 1950s. The collapse of the stock in the 1960s has been considered as the combined effect of cooler climate and overfishing (Toresen and Østvedt, 2000). The SSB fell to less than 100,000 tons in 1969 and it was uncertain during the 1970s whether the NSSH would ever recover. However, during the extraordinary spring of 1983 strong year classes of NSSH and NEAC, as well as the Northeast Arctic haddock, were produced, and this became the start of the recovery of Barents Sea fish stocks and, particularly, the new herring period that reached it new maximum SSB during the recent warm phase of AMO, peaking around 10 mill. tons in 2009.

The SSB of NEAC developed similarly to NSSH through the twentieth century although the NEAC did not collapse in the 1960s, but only reached a low level. Fishing yields of cod were relative low during the first decades of the twentieth century. The SSB reached a peak in 1947 of nearly 1.2 mill. tons. Thereafter, it decreased during the cooling phase in 1950s and 1960s. During the 1960s and 1970s the SSB varied between 100,000 and 300,000 tons, before the new increasing phase of the AMO from the early 1980s that contributed to the SSB reaching its all-time high in 2012 of about 1.9 mill. tons (Hollowed and Sundby, 2014). In concert with the increasing SSB, increasing sea temperature, and the retreating ice edge in the Barents Sea the NEAC is presently feeding farther north in the summer than previously recorded including along the shelf edge toward the Polar Basin north of Svalbard (Kjesbu et al., 2014). Also the spawning intensity of NEAC at the spawning sites along the Norwegian coast has varied in concert with the AMO (Sundby and Nakken, 2008). During cool phases the spawning site center of gravity is displaced southward toward the Møre coast of mid-Norway while during warm phases spawning sites along the Finnmark coast toward the Russian border are reoccupied.

The mean annual sea temperature of the Atlantic water masses (0–200 m depth) in the eastern Barents Sea [represented by the Kola Section (www.pinro.ru)] has ranged from 3.2 to 4.9°C since 1900. Presently, it seems that the recent positive AMO phase (for the entire North Atlantic) still has not reached the peak value (Alexander et al., 2014), although the data from the northernmost fringe of the AMO region (Kola Section of the Barents Sea) indicate that peak may have been reached between 2006 and 2010. As described above, NSSH and NEAC have responded linearly and reversibly in terms of both their spatial distribution and abundance within this temperature range, i.e., species displaced northwards during warming phases and southward again during cooling phases of AMO (e.g., Sundby and Nakken, 2008) It is however, unclear whether these boreal species will continue to respond linearly and reversible to future temperature changes predicted throughout the present century. According to all of the climate scenarios (IPCC, 2013) these changes are expected to result in considerable higher ocean temperatures than those observed through the past century, particularly at high latitudes of the northern hemisphere where the regional temperature increase is expected to be twice as large as the global average (Collins et al., 2013). This is higher than anywhere else on the globe. The Atlantic cod stocks are presently distributed around the North Atlantic in waters with ambient annual mean temperatures ranging from 2 to 11°C. For the present largest Atlantic cod stock, the NEAC, ambient annual mean temperature is about 5°C. Planque and Frédou (1999) analyzed how past and present natural temperature variability impact recruitment in Atlantic cod stocks. They found that those cod stocks with ambient temperature below about 7°C benefited from increased temperature while those cod stocks inhabiting ambient temperatures above 7°C had reduced recruitment under increasing temperature. Based on these results Drinkwater (2005) estimated the anticipated changes in abundance of Atlantic cod stocks under temperature increases of 1, 2, 3, and 4°C assuming that the existing thermal envelope of the Atlantic cod stocks would not change. While the cod stocks at their southern limit (i.e., Georges Bank, Celtic Sea and North Sea cod stock) were anticipated to decrease or possibly collapse at only a 1°C temperature increase, only the those at the northernmost fringe would initially increase and remain high for the highest (4°C) temperature rise. However, the recent RCP8.5 scenario (IPCC, 2013) indicates a considerably higher regional temperature increase by the end of twenty first century in the Arctic regions. Under such a scenario distribution of Atlantic cod stocks would probably collapse to the coast of Greenland.

The observed temperature preferences for Atlantic cod stocks as described above is assumed to be associated with the direct effects on basic physiological processes (Pörtner et al., 2008). However, in addition, temperature could also be a proxy for the abundance and transport of key zooplankton prey upon which the early life stages of cod depend (Sundby, 2000). This is particularly true for *Calanus finmarchicus* that has similar temperature preferences to many boreal fish species but their distributional responses to climate change are different from fish species along the continental shelves as *C. finmarchicus* depend on overwintering at large ocean depths off the shelves (Heath et al., 2000). Hence, responses of fish to climate change are more complex than under the assumption of only direct temperature responses. Particularly, a successful migration and displacement of spawning areas of Atlantic cod to the high-latitude shelf edges toward the Polar Ocean would depend on *C. finmarchicus* successfully establishing themselves in the Polar Basin or an increase in other potential key prey species such as *C. glacialis* and *C. hyperboreus*.

PHYTOPLANKTON PRODUCTION

The fundamental and generic processes influencing the new primary production are (1) the vertical flux of nutrients from the depth into the photic zone and (2) photosynthetic light from above (Boyd et al., 2014). Temperature itself has a minor role influencing these two processes except indirectly through its effect on the thermal stratification that contributes to controlling the vertical flux of nutrients. Other important factors controlling the vertical flux of the nutrients (Chavez et al., 2011) are wind-induced turbulent mixing and fresh water run-off from land in coastal regions, while cloud cover influences light levels. It should be emphasized that all these climate processes may show a diversity of correlations to temperature disguising the responsible mechanism(s). Caron and Hutchins (2013) pointed out that the link between temperature and other important physical processes for primary production vary strongly across ecosystems and biomes of the world oceans, including the wind-induced transport of iron-containing dust to the ocean regions. In addition, primary production is influenced by microzooplankton and bacteria. This might be of particular importance in cold-water environments (Rose and Caron, 2007; Rose et al., 2009). Recently, Wernand et al. (2013) reported that old observations of ocean color from 1889 compared with the present data on ocean color from satellite observations indicate that the changes have developed differently in the various parts of the world oceans, increasing biomass in the North Atlantic and the northwestern Pacific, and decreasing in the other parts of the Pacific Ocean and in the Indian Ocean. These results support the scenarios on primary production modeling that increase in temperature causes increased primary production at high latitudes (Bopp et al., 2013).

Although temperature itself is only an indirect factor for the primary production it appears to be positively correlated with primary production at high latitudes. Higher (lower) temperatures in the northernmost latitudes of the North Atlantic have been observed to lead to increased (decreased) primary production (Mueter et al., 2009). This has been observed under natural climate variability phenomena such as the NAO based on continuous plankton recorder (CPR) data (Edwards et al., 2001) and the AMO as observed from satellites (Martinez et al., 2009). In addition, global modeling in this part of the world's oceans (Steinacher et al., 2010; Bopp et al., 2013), as well as regional modeling in the Barents Sea (Ellingsen et al., 2008) show that increased temperature under future global climate change will likely increase primary production at high latitudes, particularly above the Arctic Circle.

There are multiple causes linking temperature and primary production at these latitudes. Here, the direct effects of increasing temperature have been hypothesized to result in an earlier onset of the spring bloom (e.g., Sverdrup, 1953; Lewandowska and Sommer, 2010) and hence a longer production season (Kahru et al., 2010; Dalpadado et al., 2014). In regions with seasonal variations in sea-ice cover, higher temperatures reduce sea-ice extent which also results in earlier blooms, a longer growing season and increased area available for production, thus resulting in higher productivity (Mueter et al., 2009; Kahru et al., 2011; Dalpadado et al., 2014). Satellite-derived chlorophyll estimates and observations from the *in-situ* SAHFOS plankton recorders confirm that the growing season increased in the Northeast Atlantic and the North Sea between 45 and 60°N during warm periods (Raitsos et al., 2014). On the other hand, in the tropics and subtropics of the North Atlantic increased temperature has been observed to shorten the growing season (Racault et al., 2012) and to reduce the phytoplankton abundance in the temperate region of the northeastern Atlantic (Richardson and Shoeman, 2004). This is primarily due to decreased nutrient availability caused by increased thermal stratification. In northern regions, high summer temperatures may also increase remineralization causing increased regenerated production subsequent to the spring bloom.

The issue of how grazing from zooplankton might interact with climate change to impact primary production was addressed by Chust et al. (2014) for a wide range of different marine ecosystems using a hydrodynamic climate model coupled with a biogeochemical, phytoplankton and zooplankton model system. Model results from the 1980–2000 were compared with 2080–2100. An increase in net primary production occurred in the Barents, Baltic, Celtic, Black and Adriatic seas, while in the Atlantic margin, North Sea, Bay of Biscay, Aegean Sea and the Benguela upwelling region net primary production decreased. For some of the ecosystems an amplification of the change occurred from phytoplankton to zooplankton. In the Barents Sea and in the northern Baltic Sea the positive amplification was particularly large, apparently because of reduced sea ice extent.

Alvarez-Fernandez et al. (2012), who analyzed the North Sea phytoplankton during the shifting climate from the cold 1970s to the present warm phase, found that wind speed, humidity and air temperature, in addition to the inflow of Atlantic water between the Orkneys and Norway, were the major abiotic driving forces for the plankton biomass seasonal dynamics through most of the period studied.

A comprehensive literature exists for marine zoogeography, their temperature habitats, and how the recent warming since the 1980s has displaced species polewards in the North Atlantic. However, literature on species-wise geographic distribution of phytoplankton and marine microbes are sparse, and consequently little is known about how climate change impacts the distribution of the various species. Mesocosm studies indicate that temperature-induced changes in zooplankton grazing might influence phytoplankton diversity subsequent to the spring bloom (Lewandowska et al., 2014). Phenology of the succession of the spring bloom of the North Atlantic is well described with the initiation of diatom bloom succeeded by flagellates and coccolithophorids (Margalef, 1978) and linked to the changes in turbulent mixing, stratification and light. With respect to temperature changes, however, phytoplankton might have considerably higher phenotypic plasticity than organisms at higher trophic levels (Rubao et al., 2010). This in turn supports our review above that other climate processes and variables than sea temperature (e.g., turbulent mixing, stratification and light) are more important ambient factors for phytoplankton. In addition, bacterial activity and the grazing from zooplankton might structure the phytoplankton community.

ZOOPLANKTON DISTRIBUTION

The arcto-boreal copepod *Calanus finmarchicus* and the boreal-temperate copepod *Calanus helgolandicus* are the most studied zooplankton species of the northern North Atlantic. Largely, they have separate habitats. *C. finmarchicus* is distributed to the north and west of the North Atlantic Current with two core production regions located in the two gyres of the Nordic Seas and the Subarctic Gyre, respectively (Sundby, 2000). The *C. helgolandicus* is generally distributed to the south and east of the North Atlantic Current. However, the habitats of *C. helgolandicus* and *C. finmarchicus* are to a certain extent overlapping, particularly in the eastern part of the distribution. For example, in the North Sea the two species co-occur (Helaouët and Beaugrand, 2007) with *C. finmarchicus* dominating in the north and *C. helgolandicus* in the south, but with overlapping distributions in the thermal range 9–11°C (Hinder et al., 2014). During the recent warming, i.e., after the 1980s, there has even been observed adults (copepodite stage V) of *C. helgolandicus* as far north as the in coastal water masses of the southwestern Barents Sea (Dalpadado et al., 2012). However, they observed no clear increasing trends with the increasing temperature, and they termed the presence of *C. helgolandicus* "episodic immigrants."

Boreal and Arctic herbivore copepod species like *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* are all adapted to the extreme short and hectic spring-bloom dynamics at high latitudes, i.e., north of about 64°N. They accumulate lipids during the intense bloom season and overwinter at depth during the dark winter when no phytoplankton is produced. Scott et al. (2000) found that the lipids comprised between 31 and 70% of the dry mass of these three hibernating species by the end of the growth season (August-September) in Kongsfjorden, northern Svalbard (∼79°N). Jónasdóttir (1999) found that the lipid dry mass fraction of *C. finmarchicus* at the start of overwintering in October within the Faroe-Shetland Channel (i.e., at 60°N) ranged between 40 and 64%. Johnson et al. (2008) reported similar lipid contents, 40–70%, in *C. finmarchicus* prior to overwintering in the northwestern North Atlantic in the lower Gulf of St. Lawrence at ∼48°N. Hence, lipid accumulation in *C. finmarchicus* seems to be largely invariant within its habitat range of the western and eastern part of the North Atlantic and across a considerable latitudinal range from 48 to 79°N. This is in spite of the fact that the phytoplankton bloom dynamics varies considerable across these latitudes. Kristiansen et al. (2011), who studied the seasonal survival potential for larval cod at four selected spawning areas, found that seasonal feeding conditions for herbivores varied substantially across latitudes. At Georges Bank (∼42°N) phytoplankton production occurs year around, although with a spring peak. In the North Sea (∼54°N) the seasonal phytoplankton production is amplified compared to Georges Bank with a secondary autumn peak. At Iceland (∼64°N) and Lofoten, northern Norway (∼67°N) the seasonal cycle of the phytoplankton production is so large with complete lack of production during winter so that lipid accumulation and overwintering becomes mandatory for herbivore copepods like *C. finmarchicus*. Interestingly, lipid accumulation and overwintering of *C. finmarchicus* also occur in the southern part of the habitat as far south as the Gulf of Maine (∼43°N) where, in principle, it could feed on the winter phytoplankton production (Runge et al., 2015). However, their regular seasonal life cycle known from the highest latitudes seems to become distorted and irregular limiting their overwintering to a shorter part of early winter.

A key question arises from the above reasoning: What happens when temperate herbivore zooplankton species, like *C. helgolandicus*, encounter thermal conditions in which they can thrive at the high latitudes of the North Atlantic and where the winter dark prevents winter phytoplankton production? Are the required processes for herbivore organisms established at high latitudes with lipid accumulation during spring/summer, overwintering and fasting something that a lower-latitude marine organism just can turn on when climate change makes the high latitudes available for temperate species? The finding by Runge et al. (2015) cited above indicates that the opposite processes, namely turning off the lipid accumulation and the overwintering when high-latitude organisms migrate southwards of the latitude where winter feeding is possible, do not seem to occur. As observed by Dalpadado et al. (2012) there have been episodic presence of the temperate *C. helgolandicus* in coastal region at the southwestern entrance of the Barents Sea (∼71°N) during the recent warm phase of AMO, but no established population. Broms (2015) reported that zooplankton species typically endemic in the North Sea have been observed in increasing abundances in the southern Norwegian Sea (i.e., south of ∼64°N) over the recent decades. However, after 2011 these species have been less abundant. For example, the temperate copepod *Mesocalanus tenuicornis* that was observed frequently in the southern Norwegian Sea earlier in the recent warm phase was not present in 2014. Similarly, *C. helgolandicus* does not show any clear increasing trend in the southern Norwegian Sea. *We hypothesize that the latitudinal change in bloom dynamics determined by the destined and stable latitudinal-dependent seasonal light cycle represents a fundamental barrier at high latitudes to the onward climate change-induced migration of temperate-adapted planktivorous from lower latitudes, unless they are able to adapt by depositing lipids and undertake overwintering.* *C. helgolandicus* with its core production area to the south of the North Atlantic Current is a copepod species that is known to deposit only limited amounts of lipids and with no clear evidence of overwintering response (Wilson et al., 2015). There is no need since this temperate species can feed during winter, although less so than during spring/summer/autumn. We, therefore, conclude that it is not possible to extrapolate the present observed northward migration of temperate species beyond the latitude where spring-spawning species alone dominate the ecosystem, again implying that it would be impossible to maintain sustainable temperate species in the region to the north of about 63–68°N. We define this as the range of *critical latitudes*. Poleward of the *critical latitude* planktivorous organisms must adapt by depositing lipids during the limited feeding season and overwintering behavior with reduction in energy consumption at depth during the winter dark when the energy demand for feeding activity and metabolism exceeds net energy uptake from the food. The exact latitude where this shift occurs is likely to vary between species, since the planktivorous food and feeding strategy of the various planktivorous predators differ. Hence, we define a latitudinal transition range as indicated in **Figure 2**.

Wilson et al. (2015) reviewed the literature on the two congeneric calanoid copepods *C. finmarchicus* and *C. helgolandicus*. They concluded that there were surprisingly small differences between the two species. However, while there is a comprehensive amount of literature on the lipid deposition and overwintering dynamics of the arcto-boreal *C. finmarchicus*, the spares literature on the similar issues for the temperate *C. helgolandicus* indicates that lipid deposition is much less (Rey-Rassat et al., 2002) and too low for bringing the latest copepodite stages through the winter dark with a positive energy balance. Moreover, Wilson et al. (2015) found "no direct evidence that *C. helgolandicus* undergoes a period of diapause." We do not know whether future life cycle adaptation (i.e., large lipid deposition and overwintering) would be possible for temperate species like *C. helgolandicus*. If so, such adaptation would need to take place within the present century when temperate climate conditions are expected to be reached in high-latitude regions like the Barents Sea under the business-as-usual emission scenarios (RCP 8.5).

The next key question is whether the boreal lipid-accumulating and overwintering species, such as *C. finmarchicus*, would be able to adapt to the projected future higher temperatures in the boreal region in the central parts of the Nordic seas and in the Subarctic Gyre to the east of Newfoundland and south of Greenland. The present thermal habitat of *C. finmarchicus* is typically in the range between 0 and 12°C (Sundby, 2000; Hinder et al., 2014) and with the highest abundances between 2 and 6°C. In the Gulf of Maine, at the upper bound of thermal habitat, Preziosi and Runge (2014) found stable high hatching success of *C. finmarchicus* eggs up to 19°C but it dropped to less than 25% at 22°C. This is a surprisingly high thermal tolerance for a boreal copepod that is seldom found at temperatures beyond 14°C. It suggests that adaptations to higher temperatures could be possible for arcto-boreal species, although it is not clear whether the Gulf of Maine *C. finmarchicus* is a subpopulation of the species with genetic attributes different from that of the Norwegian Sea and Barents Sea.

If temperate zooplankton species would not adapt to the high-latitude light cycle by developing lipid deposition and overwintering, nor that the boreal lipid-depositing zooplankton species adapt to the higher temperatures under future climate change, the high latitude northeast Atlantic region between the North Atlantic Current and the Arctic could become a region with low and decreasing ecosystem productivity. This is different from the present predominating scientific view (e.g., Cheung et al., 2011; Hoegh-Guldberg et al., 2014) that high-latitude marine ecosystems would become a region with increasing ecosystem and fish production under future climate change.

DISTRIBUTIONAL CHANGES INDUCED BY CLIMATE CHANGE

The most prominent feature of change in marine species in the northern North Atlantic during the recent 40 years is their tendency for poleward migration. Poloczanska et al. (2013) synthesized marine ecological studies world-wide on longer-term (i.e., up to interdecadal) changes in phenology and distribution of species. Altogether, they considered 1735 reported marine biological responses. The major part of the study was from the Northeast Atlantic. However, very few were from the high latitudes to the north of 62°N. The global average propagation for the leading edge of marine species was 72 km per decade which is one order of magnitude larger than for terrestrial species. The variability in propagation between taxa and functional groups

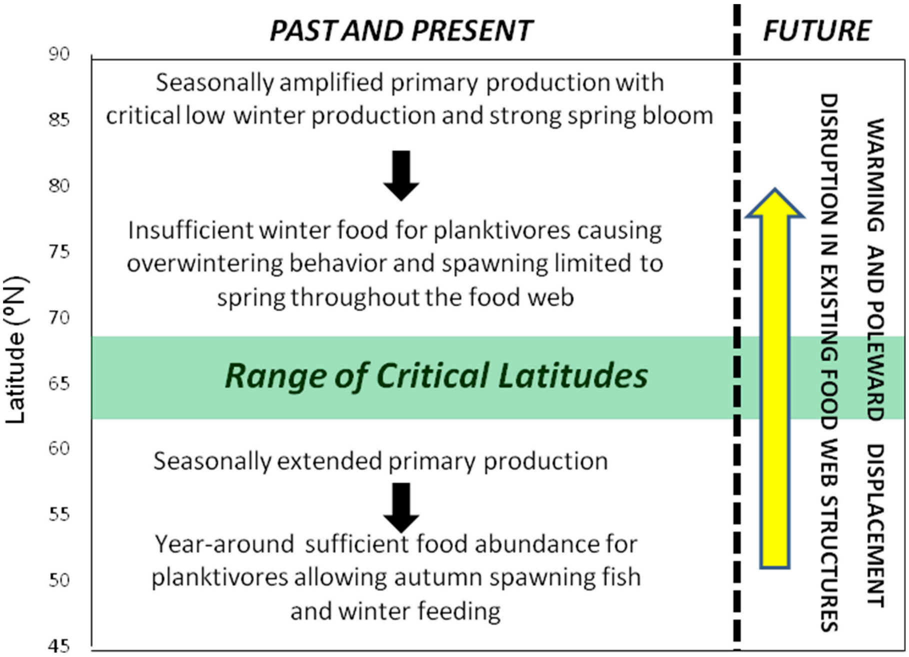

FIGURE 2 | The attributes of the marine ecosystems north and south of the range *of Critical Latitudes*. North of critical latitudes planktivorous organisms need to develop a specific life cycle strategy to survive the lack of planktonic food during the winter dark. This implies building up lipid storage during the short feeding season during spring to summer and overwintering with reduced metabolism during autumn, winter and early spring to survive the dark season without sufficient plankton production. At higher trophic levels piscivorous organisms that can feed during winter dark are also influenced by overwintering planktivorous, since they have to limit their spawning to the spring time in order to provide planktonic food for their pelagic offspring.

was large, however, with the main distinction between benthic species with low propagation speeds (~20 km per decade) and species confined to the free water masses with an average propagation speed one order of magnitude larger than benthic species. Among the taxa in free water masses, variability in speed was large but with no apparent pattern. For example, studies on phytoplankton showed a propagation speed of 470 km per decade, zooplankton 142 km per decade and bony fish 277 km per decade. It is, however, reasonable to expect that pelagic organisms should have much more dynamical distributions than demersal species that are generally constrained by shelf topography and even more for benthic species that can only change distribution during the early life pelagic stages.

A major constraint for shifts in species distribution is their spawning location. If spawning areas remain unchanged, the area for juvenile settlement will also remain largely unchanged since the distance of free pelagic drift for the offspring are limited by the currents. Under such conditions, only changes/and or expansion in adult feeding migrations, which at high latitude typically occurs poleward, could displace populations as temperature increases. This implies that bottom spawning fish like capelin (*Mallotus villosus*) and herring with very specific demands for bottom substrates and current conditions have less potential for gradual changes in spawning areas than pelagic spawners. For example, Atlantic mackerel has wide spawning distribution west of the British Isles and in the North Sea. In the North Sea, spawning initiates at temperatures in the surface layers of 10–12°C (Jansen and Gislason, 2011). During the recent warming period from 1994 to 2013, mackerel in the Northeast Atlantic shifted its northernmost distribution from the Shetland-Western Norway region in 1994 (Uriarte and Lucio, 2001) to occupy the major parts of the Norwegian Sea northward to Spitsbergen and westwards in the northern Irminger Sea to the East Greenland Current (Nøttestad et al., 2013). The large migration of northeastern Atlantic mackerel over a 19-year period compares to a migration speed of nearly 1200 km per decade that exceeds by far any reporting up to the present as synthesized by Poloczanska et al. (2013). Such migration speed would probably only be possible by the two factors acting together: (1) the large feeding migration potential of the adult stock and (2) a displacement of the spawning areas into the Norwegian Sea as optimal spawning temperatures now also can be found in the southern Norwegian Sea.

Another remarkable feature of the present advancement of the leading edge distribution of Atlantic mackerel in the northern Northeast Atlantic is that this northern fringe of the population is found at lower temperatures in the present warm phase than during the previous colder climate. The stock is now distributed during summer feeding westwards toward the edge of the East Greenland Current in the Irminger Sea and the Iceland Sea and northwards in the west coast fjords of Spitsbergen. This particular feature of populations migrating into colder temperature habitats as part of warming climate was pointed out by Landa et al. (2014) who studied the northeastward migration of Northeast Arctic haddock in the Barents Sea during the recent 30-year period from the 1980s. The average temperature of the ecosystem of the Barents Sea increased by about 0.8°C during this period while the haddock increased in abundance and occupied more of the northeast Barents Sea. However, the average ambient temperature of haddock decreased during the same period implying that the stock over-compensated for the temperature increase by advancing into colder waters. The authors suggested that this could be caused by the two factors (1) the increasing stock abundance would need to occupy a larger habitat, and (2) the increased temperature could have increased the plankton production that in turn would cascade to higher trophic levels generating improved food conditions. A support for the latter factor is that Beaugrand et al. (2009) also found that the average speed of shifts in distributions for calanoid copepods in the Northeast Atlantic during the period 1958–2005 was somewhat higher than the northwards movement of the isotherms of SST.

Different from the distributional shifts of actively migrating fish stocks, the displacement speeds of zooplankton species are constrained by the speed of the ocean currents. On the other hand, they seem to be less constrained than fish in shifts of spawning areas. The shifts in spawning areas seem to be limited by the shifts in optimal ambient conditions for zooplankton spawning and of the generation time for the zooplankton. The distribution shift speed of calanoid copepods in the Northeast Atlantic during the second half of the twentieth century was on the average 231 km per decade (Beaugrand et al., 2009), and hence, quite large compared to many fish species.

Finally, it should be emphasized that the speed of shifts in distribution, independent of taxa and functional groups, are very different in the Northeast Atlantic and in the Northwest Atlantic. This is because of the spatial structure in ocean climate (as well as in the terrestrial climate) in the northern North Atlantic region. In the Northwest Atlantic the frontal system between the Arctic and the temperate regions are much more compressed and geographically locked. From Georges Bank to Newfoundland the annual mean SST shift from about 15–5°C over a distance of about 1600 km. In the Northeast Atlantic a similar change in temperature is from the Bay of Biscay to southern Spitsbergen, a distance of 3700 km. Over geological time scales it has been shown for shifts between ice ages that the thermal structure in the Northwest Atlantic have largely remained unchanged while large thermal shifts have occurred in the Northeast Atlantic (Zahn, 1992).

CONCLUDING REMARKS

The North Atlantic spring-bloom ecosystem has its specific structure and functioning differently from other marine ecosystems of the world's oceans. In addition, the anthropogenic change in temperature, as well as the modes of natural temperature variability, is larger than in other ocean regions. The region contains the most comprehensive biological and hydrographic time series of the world oceans, some of them extending back to the beginning of the twentieth century. This implies that it is possible to distinguish between twentieth century anthropogenic temperature change and multidecadal climate signals like the AMO. Marine species of the Northeast Atlantic has been subjected to the largest poleward displacements in the world oceans in response to the change in temperature because of the latitudinal asymmetric shape of the Arctic front. This can explain differences in displacement speeds depending on functional groups. Benthic species display the lowest displacement speeds, while pelagic species with a large feeding migration potential seems to have the largest displacement speeds, particularly those species that more easily shift their spawning areas as well. A remarkable feature in displacement speeds is that many species over the recent decades of warming, from zooplankton species to pelagic and demersal species, have shifted poleward more than the shift in the thermal structure. This implies that the leading edge of the species is found at colder ambient temperatures during the present warm phase of the ecosystems than during the cold phase 40 years ago, possibly linked to the fact that these species also have increased in biomass and consequently would need larger habitats. Finally, we hypothesize that there is a limit to the poleward migration of species under future climate change. This is linked to the extreme seasonal light cycle at high latitudes with midnight sun during summer and day dark during winter that strongly influence the seasonal cycle of phytoplankton production. In response to this particular primary production cycle the present boreal planktivorous species at high latitudes deposit lipids during the short spring bloom and overwinter at depth during winter dark when phytoplankton production is insufficient for feeding. Unless invading temperate species from south are able to adapt by developing similar life cycle future poleward migration of such species will not be possible.

AUTHOR CONTRIBUTIONS

All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication. SS was responsible formulating and developing the hypothesis and for synthesizing the major part of the literature. KD contributed to the synthesis of the literature. OK contributed on the further development the hypothesis and to the revisions of the paper.

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frontiers in Marine Science

REVIEW
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Under Pressure: Climate Change, Upwelling, and Eastern Boundary Upwelling Ecosystems

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The IPCC AR5 provided an overview of the likely effects of climate change on Eastern Boundary Upwelling Systems (EBUS), stimulating increased interest in research examining the issue. We use these recent studies to develop a new synthesis describing climate change impacts on EBUS. We find that model and observational data suggest coastal upwelling-favorable winds in poleward portions of EBUS have intensified and will continue to do so in the future. Although evidence is weak in data that are presently available, future projections show that this pattern might be driven by changes in the positioning of the oceanic high-pressure systems rather than by deepening of the continental low-pressure systems, as previously proposed. There is low confidence regarding the future effects of climate change on coastal temperatures and biogeochemistry due to uncertainty in the countervailing responses to increasing upwelling and coastal warming, the latter of which could increase thermal stratification and render upwelling less effective in lifting nutrient-rich deep waters into the photic zone. Although predictions of ecosystem responses are uncertain, EBUS experience considerable natural variability and may be inherently resilient. However, multi-trophic level, end-to-end (i.e., "winds to whales") studies are needed to resolve the resilience of EBUS to climate change, especially their response to long-term trends or extremes that exceed pre-industrial ranges.

Keywords: upwelling intensification, stratification, upwelling drivers, climate change impacts, general circulation model projections

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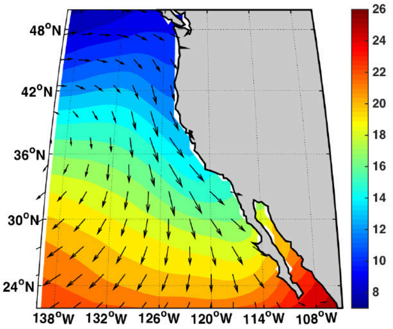
INTRODUCTION

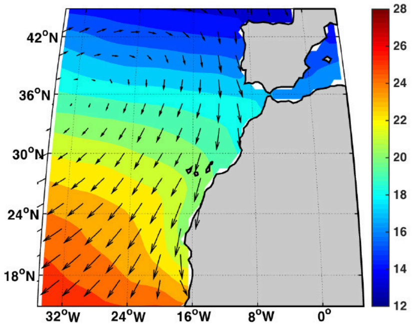
Eastern Boundary Upwelling Systems (EBUS) are biologically productive marine regions covering <1% of the ocean area, but providing up to 20% of the world's capture fisheries (Pauly and Christensen, 1995). These systems, embedded in the California, Humboldt, Canary/Iberian, and Benguela Currents (**Table 1**), provide ecosystem, economic, and recreational services to about 80 million people living along their coasts and in their immediate hinterlands. The high levels of productivity in the EBUS result from large-scale atmospheric pressure systems that favor alongshore, equatorward winds, which in combination with the Coriolis effect, advect surface water

TABLE 1 | Eastern Boundary Upwelling Systems (EBUS).



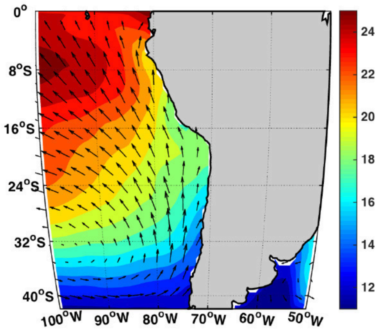
California

The California Current spans from central Baja California, Mexico, to central British Columbia, Canada. Upwelling is more intense in central/northern California and highly seasonal off Oregon and Washington. This system experiences significant natural variability from such sources as the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation with important ecosystem consequences.



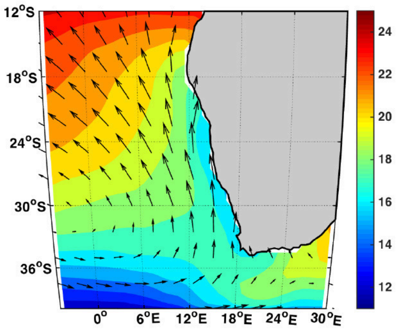
Iberian/Canary

The Iberian/Canary Current extends from the Iberian peninsula to West Africa, and is divided by the Gulf of Cadiz at the entrance to the Mediterranean Sea. The most intense and persistent upwelling is found off Northwest Africa. The Iberian section is heavily influenced by the North Atlantic Oscillation.



Humboldt

The Humboldt Current is the largest of the four EBUS, extending from the tip of the South American continent to the equator, where it connects with the equatorial current. Environmental and biological variability are heavily influenced by ENSO.



Benguela

The Benguela Current extends from the southeast tip of Africa to Angola. Upwelling is strongest and most persistent off Namibia in the Lüderitz region. Interannual variability in the physical and biological conditions relate to Benguela Niños and Pacific ENSO. In the south it is largely influenced by the variability in the Agulhas Current.

Maps show long-term means (1960–2014) of sea surface temperature (SST, °C) and wind speed (m/s) and direction for summer months (June (December) in the northern (southern) hemisphere) around EBUS. SST is from the HadISST1 dataset (Rayner et al., 2003), and wind data are from the NCEP/NCAR reanalysis (Kalnay et al., 1996), which is generally congruent in mean wind velocity patterns with those from other sources (Kent et al., 2013).

offshore (**Figure 1**). Due to mass conservation, this advection causes deeper, cold, nutrient-rich waters with high CO_2 concentrations, low pH, and low oxygen concentrations to be upwelled from depth into the coastal photic zone (Huyer, 1983) where they fuel primary production in the form of phytoplankton blooms.

In embayments and other wind-protected inshore areas and in places where local circulation patterns may favor retention

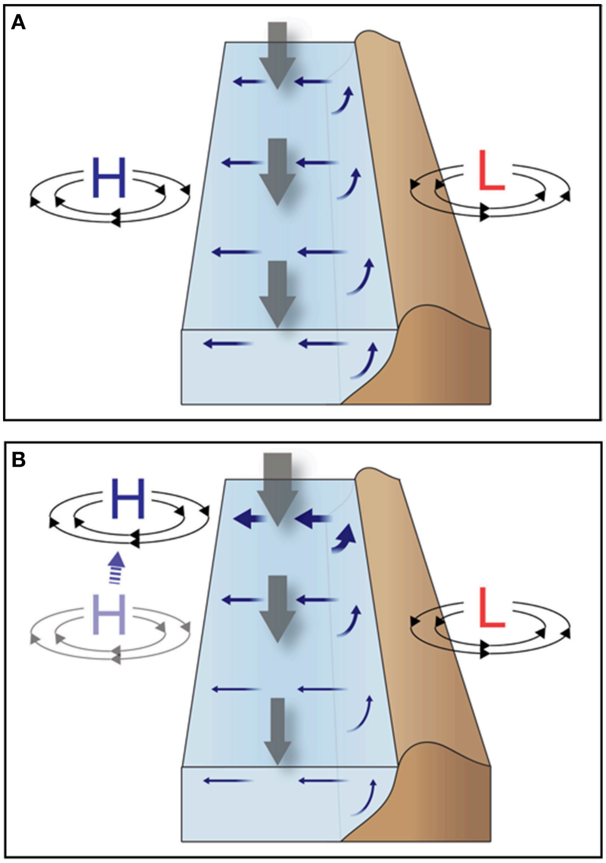


FIGURE 1 | Expected changes under climate change, from a Northern Hemisphere perspective. (A) Present: Pressure between ocean high- and land low-pressure systems drive upwelling-favorable winds (gray arrows) and thus upwelling (blue arrows). **(B)** Future: Poleward migration of ocean high-pressure systems, leading to enhanced (weakened) winds and upwelling in poleward (equatorward) regions of eastern boundary upwelling systems.

of local water masses, primary production can be intense and sustained (Graham and Largier, 1997). These "upwelling shadows" are sites of the highest chlorophyll concentrations in EBUS (Vander Woude et al., 2006), contrasting with lower productivity in areas with strong advection; this variability may influence zooplankton and higher trophic levels (Santora et al., 2011). Overall, the "bottom-up" drivers of nutrient enrichment, advection and retention, coupled with the transfer of carbon and energy up the food web make EBUS "hotspots" of productivity and upper-trophic-level biodiversity (Arístegui et al., 2009; Block et al., 2011), providing substantial economic value to coastal communities.

Because the mechanisms underpinning upwelling originate from large-scale atmospheric-oceanographic coupling, the amplitude and timing of upwelling-favorable winds are sensitive to climate variability (Montecinos et al., 2003; Macias et al., 2012), and are *highly likely* to be affected by global warming (Barros et al., 2014; Bakun et al., 2015). In particular, it is predicted that global warming will impact atmospheric pressure gradients and hence the coastal winds that cause upwelling (Bakun, 1990; Bakun et al., 2015). Recent observations (Sydeman et al., 2014a) generally support this notion, and global model projections suggest intensification of regional coastal winds during the twenty-first century (Rykaczewski et al., 2015; Wang et al., 2015).

Understanding how these winds will change is of vital importance. For example, weaker upwelling may limit nutrient enrichment of the photic zone with potentially negative impacts on primary production (Chhak and Di Lorenzo, 2007). By contrast, stronger upwelling may increase nutrient input, but at the same time increase offshore transport (Cury and Roy, 1989; Botsford et al., 2006; Bakun et al., 2010, 2015). Other impacts include increased turbulence with increased winds (Cury and Roy, 1989; Yáñez et al., 2001) and changes in chemical mechanisms, e.g., ocean acidification and deoxygenation (Gruber, 2011; Doney et al., 2012), that may affect productivity.

Management of fisheries and other marine resources in EBUS could be improved by better understanding how nutrient enrichment and primary production are related to upwelling processes, and how they are likely to change in the future. While there have been a number of studies on this topic (Diffenbaugh et al., 2004; Di Lorenzo et al., 2005; Auad et al., 2006; Bakun et al., 2015), the Intergovernmental Panel on Climate Change 5th Assessment Report (IPCC AR5) has concluded that there is low confidence in projections regarding upwelling (Stocker et al., 2013; Barros et al., 2014). In part, this is a result of the substantial spatial heterogeneity in physical characteristics within EBUS, which emphasizes the role of local processes and resultant local biotic effects (Nelson and Hutchings, 1983; Dorman and Winant, 1995; Barton et al., 2013; Bakun et al., 2015). However, the low confidence in predictions regarding the ecological future of EBUS is driven more heavily by uncertainty surrounding the potentially counteracting effects of intensifying winds on the one hand, and increasing thermal stratification on the other. The former might lead to enhanced nutrient influx, while the latter could limit it (Di Lorenzo et al., 2005).

Even though the underlying complexity of upwelling-ecosystem relationships presents a challenge to forecasting, knowledge of EBUS is deep, as these systems have been extensively studied for nearly a century (Peña and Bograd, 2007), and there is a vast body of literature examining climatic impacts on upwelling as well as upwelling impacts on ecosystems. Given this context, and a spate of studies published while the IPCC AR5 was being prepared, we provide here a new synthesis of current research focused on the present and future impacts of climate change on coastal upwelling. We emphasize here the drivers of upwelling-favorable winds, the factors influencing nutrient enrichment, and potential changes in biogeochemistry.

PRESSURE, WIND, AND UPWELLING IN A WARMING WORLD

In EBUS, cross-shore atmospheric pressure gradients lead to alongshore, equatorward winds that drive coastal upwelling. Recognizing this, A. Bakun proposed that increasing global concentrations of greenhouse gasses would enhance warm-season upwelling (Bakun, 1990). The proposed mechanism was simple: air over land would warm more rapidly than air over the ocean, and resultant deepening of the continental thermal low-pressure systems (CTLPS) should increase the cross-shore pressure gradients that drive upwelling-favorable winds.

Trends in Upwelling-Favorable Winds

Several studies have focused on assessing trends in upwelling-favorable winds, and they found mixed results. The failure to reach consensus revolves largely around two related phenomena: (1) the small amplitude of unidirectional wind trends relative to amplitudes of seasonal, interannual, and decadal wind variability, and (2) the short duration of most observational time series relative to decadal variability. Further complications include (i) disparate data sets examined, (ii) inconsistencies in data treatment, including analyses of warm season vs. annual means as well as variable observation periods or quality and density of data, and (iii) changes in measurement techniques or models used to interpolate or reanalyze data (Cardone et al., 1990; Josey et al., 2002). Based on these differences, the IPCC AR5 (Stocker et al., 2013) concluded *low confidence* in common trends in upwelling-favorable winds.

A recent meta-analysis of published studies (Sydeman et al., 2014a), each with more than 20 years of observational or model-derived data, however, finds a more coherent pattern of intensifying upwelling-favorable winds in the Humboldt and the California Systems during the warm season. In the Benguela System, only annual data are available, but there, too, alongshore winds are intensifying. By contrast, in the Canary System, wind trends are equivocal, and even appear to be weakening in the Iberian region. Importantly, there is stronger agreement that significant trends of upwelling intensification are evident at higher latitude for all EBUS. Among studies excluded from the meta-analysis, either because they did not meet the strict selection criteria or because they were published after the analysis was completed, most (Di Lorenzo et al., 2005; Alves and Miranda, 2013; Barton et al., 2013; Bylhouwer et al., 2013; Stocker et al., 2013; Cropper et al., 2014; deCastro et al., 2014; Jacox et al., 2014; Sydeman et al., 2014b; Varela et al., 2015) show results consistent with the findings of Sydeman et al. (2014a). Those containing seemingly contradictory results (Demarcq, 2009; Dewitte et al., 2012) add uncertainty, but do not refute the findings of the meta-analysis, as they focus on local regions, use short time series and do not add uncertainty. Despite the fact that the meta-analysis by Sydeman et al. generally supports Bakun's proposition, we still cannot attribute coastal wind intensification in EBUS to global warming because we cannot discount the role of multi-decadal climate variability in the observed trends (Chhak and Di Lorenzo, 2007; Narayan et al., 2010; Pérez et al., 2010; Macias et al., 2012; Santos et al., 2012; Cropper et al., 2014; Jacox et al., 2014), nor is it a test of the Bakun hypothesis mechanism.

A gap in our understanding arises because the vast majority of studies focus on measures of central tendency (means or medians) in wind magnitude. Even though ecologically consequential changes in variance and phenology (timing of upwelling) have been observed in EBUS, studies examining trends in variance and timing remain rare. Such work is hindered by the complexities of the systems; the only generality that can be made is that upwelling-favorable winds tend to be most intense during the warm months of the year (Huyer, 1983; Nelson and Hutchings, 1983). Beyond this, however, the timing, intensity, and persistence of upwelling-favorable winds are remarkably variable within and among EBUS (Chavez and Messié, 2009). Of all EBUS, the most information on this subject is available from the California Current. In the central-northern portion of this system, upwelling winds primarily occur during the warm months of the year, while the seasonal range of pressure gradients in the southern portion of the system is reduced, and upwelling can occur there year-round. This pattern, however, is not static. Over recent decades, the timing of upwelling has trended toward later and shorter upwelling seasons in the northern portion of the California System and longer upwelling seasons in the southern portion (Bograd et al., 2009; García-Reyes and Largier, 2010). In contrast, a modeling study on wind stress curl (Diffenbaugh et al., 2004) found increased (decreased) upwelling in the late season in the northern (southern) California System.

Resolving these issues is important because variation in the timing of upwelling strongly influences ecosystem productivity. Years with early upwelling tend to be more productive at the upper trophic levels than those with later onset of upwelling (Black et al., 2011; García-Reyes et al., 2013b). Adding complexity to the picture, increases in the variability (extremes) of upwelling-favorable winds in the California Current have been observed since the late 1940s (Macias et al., 2012; García-Reyes et al., 2014), a finding consistent with increased upwelling-favorable winds during the warm months (Sydeman et al., 2014a). Less variability has been observed in the strength of upwelling winds through the year in the central Benguela and Canary Currents (Shannon and Nelson, 1996; Varela et al., 2015), though this conclusion might be influenced by a lack of studies. Clearly, further research is needed in all EBUS on changes in the timing and variability of upwelling given the influence these phenomena have on their ecosystems (Black et al., 2011; García-Reyes et al., 2014).

Wind projections from coupled atmosphere-ocean general circulation models (AOGCM) assembled for the IPCC AR5 have limited agreement that upwelling-favorable winds will intensify in response to climate change. Projections for the Humboldt (Garreaud and Falvey, 2009; Goubanova et al., 2011; Echevin et al., 2012; Belmadani et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015), Benguela (Jury and Courtney, 1995; Rykaczewski et al., 2015; Wang et al., 2015), and Iberian Systems suggest future intensification of upwelling winds (Miranda et al., 2013; Casabella et al., 2014; Lopes et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015). In contrast, the California System projections show non-significant or decreasing trends (Mote and Salathé, 2010; Rykaczewski et al., 2015; Wang et al., 2015). Furthermore, recent publications on wind trends based on global models reveal consistency in the spatial heterogeneity found by the meta-analysis, with increasing (decreasing) upwelling-favorable winds for poleward (equatorward) regions of EBUS (Rykaczewski et al., 2015; Wang et al., 2015). Note that these projections agree with observational records only in the Humboldt and Benguela Systems, though observational records corroborate that intensification trends are most likely in poleward regions of EBUS (Sydeman et al., 2014a).

The variability in trends derived from global-scale models may be due either to their relatively coarse resolution, which precludes adequate representation of smaller-scale coastal processes, including upwelling (Miranda et al., 2013; Casabella et al., 2014), or to their failure to adequately incorporate processes relevant to upwelling, e.g., cloud cover, inversion-layer height (Winant et al., 1988), or land-ocean pressure gradients. Downscaling global models to the coastal domain of EBUS is required to address some of these issues. Promising results from this type of approach have been obtained in the Humboldt System (Garreaud and Falvey, 2009; Belmadani et al., 2014).

Drivers of Wind Intensification

While Bakun's proposition of wind enhancement with global warming appears to be generally supported, the mechanism of change [intensification of CTLPS relative to the Ocean High-Pressure System (OHPS)] may require revision. Wang et al. (2015) suggest support for this mechanism in their analyses of AOGCM outputs, but they did not examine the intensification of the CTLPS and consequent steepening of the cross-shore pressure gradient, key elements of the Bakun hypothesis. A more comprehensive analysis (Rykaczewski et al., 2015) of AOGCM output demonstrates that Bakun's mechanism breaks down at this crucial step: no deepening of the CTLPS occurs with increasing temperatures, except in the Canary Current System.

Changes in the structure of CTLPS seem intuitive under climate change. Nevertheless, the latitudinal differences in upwelling-favorable wind trends found in models (Rykaczewski et al., 2015; Wang et al., 2015) and in observations from recent decades (Sydeman et al., 2014a), in conjunction with evidence that winds in the EBUS are driven mainly by the magnitude and position of the OHPS (García-Reyes et al., 2013a; Schroeder et al., 2013), suggest that wind trends might be more sensitive to the poleward migration of the OHPS rather than changes in the CTLPS (**Figure 1**; Falvey and Garreaud, 2009; Belmadani et al., 2014; Bakun et al., 2015; Rykaczewski et al., 2015). Indeed, Rykaczewski et al. show that, in an ensemble of AOGCMs, the location of maximum upwelling along the EBUS coasts is correlated with the central latitude of the OHPS. Moreover, most AOGCMs show poleward expansion of the OHPS in the future (Diffenbaugh, 2005; Lu et al., 2007; Garreaud and Falvey, 2009; Echevin et al., 2012; Belmadani et al., 2014) caused by poleward expansion of the Hadley Cells in both hemispheres (Lu et al., 2007; Seager et al., 2010), and intensification of the OHPS in the northern hemisphere (Li et al., 2012). While one study using reanalysis data shows no evidence of trends in the position of mid-latitude atmospheric pressure centers over the past decades (Stocker et al., 2013), the prominent natural variability in the position of these systems over decadal time scales might mask potential trends (Bograd et al., 2009; Gutiérrez et al., 2011; Santos et al., 2012; Stocker et al., 2013). Understanding and predicting the intensity and position of OHPS is of great importance to the ecology of EBUS (Schroeder et al., 2013, 2014), making this area ripe for future analyses.

WATER TEMPERATURES AND THE COUNTERACTING ROLES OF UPWELLING AND STRATIFICATION

Global ocean temperatures have increased during the twentieth century and are expected to continue rising (probably at an accelerating rate) with climate change (Stocker et al., 2013). It is well known that coastal sea surface temperatures (SST) in EBUS are distinctively cooler than offshore regions at similar latitudes due to the nearshore upwelling of cold, nutrient-rich water. Moreover, global trends in SST may be counteracted by upwelling intensification in the poleward domains of the EBUS. Therefore, trends in coastal temperature in EBUS are expected to differ substantially from regional and global patterns of temperature change; indeed upwelling systems are viewed more generally as a source of significant bias in the global patterns of temperature change.

There is substantial but conflicting evidence on SST trends in EBUS (Mendelssohn and Schwing, 2002; Arístegui et al., 2009; Belkin, 2009; Demarcq, 2009; Lebassi et al., 2009; García-Reyes and Largier, 2010; Rouault et al., 2010; Gutiérrez et al., 2011; Seo et al., 2012; Barton et al., 2013; Barros et al., 2014; Sydeman et al., 2014b; Salvanes et al., 2015). Agreement among studies is low for two reasons: (1) the varying spatio-temporal resolutions of SST data capture different aspects of upwelling processes, and (2) trends are obscured by the interannual to multi-decadal variability that result from regional/local ocean and atmospheric processes. Different SST datasets also suggest different trends within and among EBUS, depending on resolution and other intrinsic factors (Belkin, 2009; Demarcq, 2009). In general, the coarse resolution of most SST datasets makes it difficult to separate nearshore upwelling-related temperatures (which could be decreasing due to upwelling intensification) from regional and eastern boundary current temperatures (which are likely to be increasing). Also, these data cannot resolve smaller-scale advection or retention areas within EBUS, which could potentially have contrasting trends. Where high-resolution data have been analyzed, for example Lima and Wethey's (2012) analysis of daily AVHRR data at 0.25° resolution, recent cooling trends are obvious for coastal areas in all but the Canary EBUS, especially at high latitudes and in summer months. There is, however, agreement among studies that coastal and offshore temperature trends differ. These studies exhibit decreasing or slowly increasing trends in nearshore SST, compared with increasing trends offshore in the Benguela (Rouault et al., 2010; Santos et al., 2012; Salvanes et al., 2015) and California systems (Mote and Salathé, 2010), a pattern consistent with observed increased upwelling-favorable winds (Sydeman et al., 2014a). When studying EBUS as units, given their spatial complexity, climate-change associated trends may be obscured by the counteracting effects of offshore warming and inshore cooling.

In general, regional ocean climate oscillations like the El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) for the California and Humboldt Current Systems, the Northern Atlantic Oscillation for the Canary/Iberian Current System, and Benguela Niño for the Benguela Current System

(Minobe and Mantua, 1999; Lluch-Cota et al., 2001; Mendelssohn et al., 2003; Montecinos et al., 2003; Richter et al., 2010; Seo et al., 2012), impose considerable variability on temperatures and complicate attempts to assess long-term trends (Demarcq, 2009). Indeed, many of the observed trends in recent decades might be associated with these oscillations (Santos et al., 2012; Barton et al., 2013). Though predictions are controversial, some of these climate oscillations are expected to increase in amplitude or variance with climate change (Timmermann et al., 1999; Kuzmina et al., 2005; Sydeman et al., 2013; Cai et al., 2015), which would further mask monotonic trends.

AOGCM ensembles (Hoegh-Guldberg et al., 2014) show that modest rates of warming (0.22–0.93°C between 2010 and 2039) are expected within the four EBUS in the near-term, but the reliability of such projections is questionable, as AOGCMs do not represent upwelling adequately. In simulations of historical periods, large discrepancies between observed and predicted EBUS coast SST fields are found (Stock et al., 2011; Cambon et al., 2013), which could translate into biases in projected changes. However, coastal upwelling generally occurs within 50 km of the shore and these projected temperature changes might be more representative of the offshore portions of EBUS less influenced by upwelling. As with studies on wind fields, dynamic downscaling of AOGCMs might help in the resolution of these questions regarding future trends in coastal temperatures.

Warming of the ocean surface will, in time, propagate down through the water column and increase thermal stratification (Gruber, 2011). In upwelling systems, strong stratification limits the depth from which water is upwelled, and therefore the amount of nutrients brought to the euphotic zone (Chhak and Di Lorenzo, 2007; Jacox and Edwards, 2011; Jacox et al., 2015). Without alternative inputs from sources like rivers, the interplay between the intensity of upwelling winds and stratification determines the amount of nutrients entrained in the systems and thus strongly mediate biological productivity (McGowan et al., 1998; Di Lorenzo et al., 2005). On a global scale, stratification of the water-column between 0 and 200 m has increased by an estimated 4% during the period 1971 to 2010 as a result of climate change (Stocker et al., 2013). In the EBUS, however, stratification studies are sparse, as are associated observational data. In the central California Current EBUS, Palacios et al. (2004) estimated that stratification has increased since the 1950s in coastal and offshore areas. However, this change may reflect interdecadal variability (Bograd and Lynn, 2003; Chhak and Di Lorenzo, 2007), and its impacts on the nutrient input and consequent biological productivity have not been assessed except by theoretical modeling (Brochier et al., 2013; Schroeder et al., 2014). In other systems, similar studies are lacking due to the paucity of observational data on water-column temperature. At resolutions that capture the upwelling process, negative trends in nearshore SST seem to be consistent with increasing trends in upwelling-favorable winds (García-Reyes and Largier, 2010; Rouault et al., 2010; Lima and Wethey, 2012; Santos et al., 2012; Seo et al., 2012; deCastro et al., 2014). While not a measure of stratification, negative temperature trends suggest that the threshold at which stratification limits the nutrient content of upwelled water has not yet been reached, at least in some regions of the EBUS.

There is limited research on the future of stratification in EBUS under climate change, once again because AOGCMs fail to resolve upwelling adequately. Nevertheless, a modeling study by Brochier et al. (2013), based on downscaling of an AOGCM (Echevin et al., 2012), found that stratification might increase in the Humboldt Current under global climate change. In conjunction with negligible change in winds, their models showed limited nutrient input into the euphotic zone, which would negatively affect biological productivity. Ultimately, the ecological impacts of ocean warming and stratification might be ameliorated by increased upwelling-favorable winds combined with the innate resiliency of systems adapted to considerable intraseasonal to decadal temperature variability (Hare and Mantua, 2000; Santos et al., 2005). However, climate change impacts could still be important (Gruber, 2011), especially in regions where rising temperatures and decreasing upwelling co-occur.

UPWELLING, STRATIFICATION AND BIOGEOCHEMISTRY

Variability in the biogeochemical properties of upwelled waters will influence the ecology and productivity of EBUS. The deep waters brought toward the surface by upwelling are typically rich in nutrients and dissolved CO_2, a consequence of the relatively long period where they have been isolated at depth from the euphotic zone and air-sea gas exchange (Feely et al., 2008). Below the euphotic zone, heterotrophic processes remineralize organic matter, consuming oxygen, and releasing CO_2 in the process (Capone and Hutchins, 2013). Variability in the rate of upwelling associated with changes in local wind forcing, ventilation processes, or the source-water pathways that supply the EBUS have the potential to influence oxygen, nutrient, and CO_2 concentrations in upwelled waters at the surface (Rykaczewski and Dunne, 2010).

Efforts to explore variability in source-water properties have been more intense in the California Current System than in any other EBUS. Here, decreased pH of shelf waters has been associated with strong upwelling at interannual scales (Feely et al., 2008), though longer-term data are generally not available. Over longer periods, decadal-scale changes in ventilation and source-water properties have likely resulted in decreased oxygen concentrations and shoaling of the oxygen minimum layer in the California (Bograd et al., 2008; McClatchie et al., 2010) and Benguela Systems (Monteiro et al., 2008; Salvanes et al., 2015). Such changes, however, have also been associated with known modes of decadal variability in ocean-atmosphere processes (Deutsch et al., 2005; Chhak and Di Lorenzo, 2007).

Over centennial time scales, increased ocean stratification associated with surface warming may further reduce the ventilation of deep-water masses. As these water masses continue to be forced to the surface by the upwelling process, future decreases in oxygen concentration and pH and increases in nutrient concentration are expected (Rykaczewski and Dunne, 2010). While EBUS biotic systems might be resilient to changes in acidity and oxygen given their adaptations to naturally variable conditions (Capone and Hutchins, 2013), persistent changes in pH or oxygen may have important repercussions, such as displacement of suitable habitat (Hamukuaya et al., 1998; Grantham et al., 2004).

SYNTHESIS

There is robust observational evidence that upwelling-favorable winds have intensified in recent decades in some EBUS. Climate models also demonstrate, with high confidence, increasing (decreasing) trends in upwelling-favorable winds in the poleward (equatorward) regions of the EBUS. Recent decadal-scale trends in winds are consistent with predictions of the Bakun hypothesis of increasing upwelling with climate change. However, the mechanisms responsible for changes in winds are likely to be different. An alternative mechanism is that OHPS have migrated poleward and will continue to do so (**Figure 1**), as supported by a high level of agreement among different generations of global models. Reconciliation of this mechanism with a general lack of trends in strength and position of mid-latitude pressure systems in previous decades, which is almost certainly due to large degree of decadal-scale variability, will require further investigation.

There is low confidence regarding the future effects of climate change on coastal temperatures and biogeochemistry in the EBUS. This is partially due to the complexity of integrating global (climate change) and local (coastal upwelling) processes, but also due to the resolution, availability, and period of available data combined with the large degree of interannual to decadal variability in temperatures and biogeochemical properties. Most global climate models do not have the resolution to represent the upwelling process adequately; therefore the changes in physical and biogeochemical properties projected for the EBUS by the current generation of models are unlikely to be as accurate as those for other portions of the world's oceans. Downscaling of climate models shows promise in correcting this bias by including higher-resolution representation of winds and more accurately modeling relevant atmospheric and oceanic processes such as land- and ocean-air interactions, cloud formation, and oceanic mesoscale processes.

Owing to their inherent natural variability, it might be expected that EBUS will prove more resilient to climate change than other ocean ecosystems, but evidence of this resiliency is based more on these systems' abilities to recover from short-term climate extremes. Much of our understanding of ecosystem responses to extremes stems from observations associated with ENSO (as well as PDO) in the California Current (Peterson and Schwing, 2003; Blamey et al., 2012; Sydeman et al., 2013; Black et al., 2014). How EBUS will respond to long-term changes in the mean magnitude of upwelling winds, stratification, and the biogeochemistry of source waters remains uncertain, as do interactive effects with natural interannual extremes, which could also change in behavior under climate change.

This lack of clear expectations for EBUS ecosystem properties is worrying because these regions are biologically rich, and thus highly relevant to society in terms of economics, conservation, and biodiversity. Given the uncertainties in present and future trends in the intensity and seasonality of upwelling, the paucity of studies on stratification, and the resultant effects on source-water characteristics, confidence in predicting biological

TABLE 2 | Observed and projected climate-change impacts on Eastern Boundary Upwelling Systems (EBUS).

	Observed	Expected	Uncertainty
Upwelling-favorable winds *High confidence*	Intensification of upwelling-favorable winds (except Canary/Iberian System) during warm months. Increased variability and trends in phenology.	Increasing (decreasing) trends in upwelling winds in poleward (equatorward) regions of the EBUS.	The influence of large-scale decadal variability.
Large-scale drivers of upwelling-favorable winds *Medium confidence*	No evidence of multi-decadal trends in strength or position of pressure systems.	Models suggest poleward migration of ocean high-pressure systems, but little to no change in intensity of the thermal continental low-pressure cells.	
Coastal temperature and stratification *Low confidence*	Complex integration of global (climate change) and local (coastal upwelling) processes. Differences in global and EBUS SST trends are observed.	Complex integration of global (climate change) and local (coastal upwelling) processes. Ocean warming and stratification might be ameliorated by increased upwelling.	Trends are sensitive to location (nearshore vs. offshore), resolution, period and dataset considered, as well as to decadal variability.
Biogeochemistry *Low confidence*	Decreased pH and oxygen concentration.	Decreased pH and oxygen concentration, and increased nutrient concentration.	Uncertainty due to short period of data availability.

These assessments are based on variable periods and datasets (see text and references). Confidence, based on amount of evidence and agreement among evidence, is noted in italics.

impacts remains low. This synthesis (**Table 2**) highlights the need for comprehensive "winds to whales" studies that investigate consequences of present and future changes on various components of the upwelling process as well as the need to improve coupling between ecological and physical models.

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Synergistic effects of hypoxia and increasing CO_2 on benthic invertebrates of the central Chilean coast

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Ocean acidification (OA) and hypoxic events are an increasing worldwide problem, but the synergetic effects of these factors are seldom explored. However, this synergetic occurrence of stressors is prevalent. The coastline of Chile not only suffers from coastal hypoxia but the cold, oxygen-poor waters in upwelling events are also supersaturated in CO_2, a study site to explore the combined effect of OA and hypoxia. We experimentally evaluated the metabolic response of different invertebrate species (2 anthozoans, 9 molluscs, 4 crustaceans, 2 echinoderms) of the coastline of central Chile (33°30′S, 71°37′W) to hypoxia and OA within predicted levels and in a full factorial design. Organisms were exposed to 4 different treatments (ambient, low oxygen, high CO_2, and the combination of low oxygen and high CO_2) and metabolism was measured after 3 and 6 days. We show that the combination of hypoxia and increased pCO_2 reduces the respiration significantly, compared to a single stressor. The evaluation of synergistic pressures, a more realistic scenario than single stressors, is crucial to evaluate the effect of future changes for coastal species and our results provide the first insight on what might happen in the next 100 years.

Keywords: hypoxia, ocean acidification, Chile, invertebrates, respiration rate

Introduction

The term Ocean Acidification (OA) is used to describe the decline in seawater pH due to the invasion of ocean waters by anthropogenic CO_2 (Caldeira and Wickett, 2003; Caldeira, 2005; Orr et al., 2005; Raven, 2005). About 1/3 of the CO_2 released by human activity since the industrial revolution has entered the ocean, leading to a decline in surface pH values by ~0.12 units, with a further decrease of 0.3–0.4 units predicted for a doubling of atmospheric CO_2 by the end of the century (Orr et al., 2005; Doney et al., 2009). These decreases in pH are expected to have negative but variable effects specifically on calcifying organisms as altered carbonate chemistry directly affects the deposition and dissolution rates of the $CaCO_3$ used for structures (Gattuso and Buddemeier, 2000; Orr et al., 2005; Raven, 2005; Kleypas et al., 2006; Gazeau et al., 2007;

Fabry et al., 2008; Range et al., 2011; Andersson and Gledhill, 2013; Kroeker et al., 2013). Calcifying organisms, such as corals (Marubini and Davies, 1996; Gattuso et al., 1998; Marubini and Atkinson, 1999; Langdon et al., 2000), coral reef communities (Langdon et al., 2000, 2003; Leclercq et al., 2000), and planktonic organisms (Bijma, 1991; Riebesell et al., 2000), are known to be among the most vulnerable. Nevertheless, it has been shown in several studies, that some corals and molluscs were able to calcify and grow even faster when transplanted along carbonate saturation gradients (Rodolfo-Metalpa et al., 2011). Even under low pH some species are able to maintain, or even increase, their net calcification, indicating that the use of carbonate saturation state is inconsistent to predict marine calcification (Wood et al., 2008; Cohen et al., 2009; Ries et al., 2009; Rodolfo-Metalpa et al., 2010). As reviewed by Hendriks et al. (2015), these organisms have different mechanism to cope with OA. Close to the organism's surface the pH can be higher through metabolic activity since rate limiting transport in the Diffusive Boundary Layer (DBL) prevents a direct equilibration with the water column (Hendriks et al., 2015). In foraminifera and diatoms the pH in the DBL ranges from 8.0 to 9.1 (Köhler-Rink and Kühl, 2005; Kühn and Raven, 2008), which allows them to create a microenvironment with increased pH (by 0.5 units) compared to ambient seawater. Moreover, calcifying organisms are able to control the pH in extracellular fluids, or control the deposition in a regulated, intracellular environment. Tissues and external organic layers play a major role in protecting shells and skeletons from corrosive sea water, limiting dissolution, and allowing organisms to calcify (Ries, 2011; Trotter et al., 2011). Some organisms can benefit from symbiotic relationships, e.g., coral symbionts remove CO_2 and increase pH due to photosynthesis, enhance conditions for calcification and growth (Gattuso and Jaubert, 1990; Muscatine, 1990).

Whereas increasing atmospheric CO_2 clearly drives OA in the open ocean, drivers of changes in pH and the carbonate system in coastal systems are far more complex (Duarte et al., 2013; Waldbusser and Salisbury, 2014). Coastal ecosystems, unlike the surface waters of the open ocean, may display a diversity of pH trajectories, affected by emissions from volcanic vents, watershed processes, eutrophication, upwelling, and changes in ecosystem structure and metabolism (Duarte et al., 2013). Therefore, the carbon system of the coastal ocean is more dynamic and complex than that of the open ocean (Borges and Gypens, 2010; Cai, 2011), and thereby, a general prediction of the trajectories of pH for coastal systems is difficult to make, as regional differences will be important (Duarte et al., 2013). In these shallow environments benthic engineering species, such as corals, seagrass, macroalgae, salt marshes, mangroves, sponges, and oyster reefs, have the capacity to affect the chemical and physical conditions of the ecosystem (Gutierrez et al., 2011), and exert metabolic control on coastal seawater pH values and variability (Duarte et al., 2013).

Coastal ecosystems are also progressively affected by hypoxia, with a current rate of increase of $5.5 \pm 0.2\%$ year^{-1} in coastal areas (Vaquer-Sunyer and Duarte, 2008), and predicted of faster increase in the future (Conley et al., 2009). Hypoxia, is a condition characterized by oxygen levels below a threshold where marine organisms show atypical behavior (Riedel et al., 2013) and eventually leads to mass mortality (Diaz and Rosenberg, 1995; Vaquer-Sunyer and Duarte, 2008). It is typically triggered by respiratory consumption of oxygen to remineralize the excess of organic matter produced in eutrophic coastal systems (Gray et al., 2002). Accordingly, hypoxic coastal waters are characterized by low O_2 concentrations and elevated CO_2, and, therefore, low pH (Pörtner et al., 2005). This is also the case of coastal areas affecting by upwelling of oxygen-poor, corrosive waters, such as the Oregon and Washington coasts (Feely et al., 2008; Gruber et al., 2012) and much of the Chilean coast (Mayol et al., 2012). Yet, the bulk of the literature on the impacts of hypoxia on marine invertebrates focuses on the role of low oxygen, and the impact of concurrent reduced pH has been generally ignored.

The Respiration Index (*RI*) was proposed by Brewer and Peltzer (2009) to capture the combined effects of hypoxia and high CO_2 on the efficiency of aerobic respiration, by using the basic oxic respiration equation and the free-energy relation. The *RI* is a simple numeric constraint linearly related to the available energy to support respiration:

$$RI = log10\,(pO2/pCO2) \tag{1}$$

where $RI \leq 0$ corresponds to the thermodynamic aerobic limit, a formal dead zone; at $RI = 0$ to 0.4, aerobic respiration does not occur; the range $RI = 0.4$–0.7 represents the practical limit for aerobic respiration, and the range $RI = 0.7$–1.0 delimits the aerobic stress zone (Brewer and Peltzer, 2009). The *RI* links hypoxia and CO_2, implying that the thermodynamic constraints for aerobic organisms do not depend on O_2 alone, but also on CO_2. The implication is that high CO_2, by lowering *RI*, affects the vulnerability of marine organisms to hypoxia.

Considering the impact of CO_2 on respiration suggests that the distribution and spatial extent of ocean dead zones will rise, even if the oxygen levels as such do not decline, as a result of rising CO_2 concentrations (Brewer and Peltzer, 2009), which will increase the stress to aerobic organisms and raise the O_2 thresholds for hypoxia. Rising CO_2 concentrations will induce metabolic depression in invertebrate species, reduce the rate of gas exchange across respiratory epithelia, deplete the internal oxygen stores, and accumulate respiratory CO_2 (Pörtner et al., 2005) and, thereby, decrease the buffering capacity in hypoxic bottom water (Hagens et al., 2015).

However, the *RI* index has not been experimentally tested and the underlying expectations have been criticized. Seibel and Childress (2013) argue that CO_2 could never reach concentrations that would limit the thermodynamics of this reaction, because of the large standard free energy change for organic carbon oxidation ($\Delta G^\circ = -686$ kcal mol^{-1}), and that a PCO_2:PO_2 ratio of 10503 would be required to reach equilibrium (equilibrium constant, $K_{eq} = 10503$; where $\Delta G = 0$). Thus, they argued that a *RI* of −503 would be the real thermodynamic limit to aerobic life. Although it has been shown that in crabs and catfish the pCO_2 in plasma dropped to 45 and 56 mm Hg, respectively, when exposed to elevated CO_2, Pörtner et al. (2005), Seibel and Childress (2013), and Cameron and Iwama (1989) argue that cellular respiration and oxygen provision are kinetically controlled and environmental oxygen and CO_2

concentrations exert little control on intracellular concentrations. Yet, evidence for synergistic effects of low O_2 and high CO_2 includes increased bacterial infections in the pacific white shrimp *Litopenaeus vannamei* (Burgents et al., 2005), inhibition of growth and metamorphosis in the early life stage of bivalves (bay scallops, *Argopecten irradians*, and hard clams, *Mercenaria mercenaria*, Gobler et al., 2014), depressed growth rates for juvenile red abalone (*Haliotis rufescens*, Kim et al., 2013) and synergistic metabolic depression via the effect of adenosine on central nervous functions of the marine invertebrate *Sipunculus nudus* (Reipschläger et al., 1997; Pörtner et al., 2005). In field studies hypoxia and OA seasonally may occur simultaneously in shallow water tidal creeks and lead to sub-lethal effects on organismal and populational levels and reduce oxygen uptake in blue crabs *Callinectes sapidus* (Hypes, 1999). Regardless of the accuracy of the thresholds of *RI* proposed by Brewer and Peltzer (2009), it is clear that the efficiency of aerobic respiratory processes is dependent on the ratio of the partial pressures of both O_2 and CO_2, suggesting that threats from hypoxia will also be aggravated by increasing CO_2 (Brewer and Peltzer, 2009). This is particularly important, as hypoxic and high CO_2 stresses are likely to co-occur (Mayol et al., 2012), with both stresses forecasted to increase in the future (Orr et al., 2005; Vaquer-Sunyer and Duarte, 2008).

Here we evaluate the combined effects of hypoxia and OA on the survival and metabolic rates of benthic invertebrate populations in Central Chile. The invertebrates of the coastline along Chile may be regularly exposed to both stressors, as the Humboldt Current System (HCS) is one of the largest naturally hypoxic areas of the word's oceans (Levin et al., 2002; Thiel et al., 2007; Ulloa and Pantoja, 2009). The HCS is a quite complex dynamic region, characterized by the presence of a system of along-slope currents that brings waters of both tropical and subpolar origin, and by upwelling of cold, oxygen-poor waters supersaturated in CO_2 (Torres et al., 2002; Mayol et al., 2012). Hence, invertebrates in the HCS coastal region may regularly experience high CO_2 and low O_2 and are expected to be adapted to these stressors. All except anthozoans are calcifying species, believed to be particularly vulnerable to OA (Kroeker et al., 2013). We experimentally tested the effect of these stressors on invertebrate species by exposing them to 4 different treatments (high O_2 and low CO_2, low O_2 and low CO_2, high O_2 and high CO_2, and both low O_2 and high CO_2) and measuring survival and respiration rate after 3 and 6 days.

Materials and Methods

The experiments were conducted between October 17 and December 13, 2012 at the ECIM marine station in Las Cruces, Chile. Organisms were collected during low tide from two sites, the surrounding coastal area of the ECIM marine reserve at Las Cruces and El Tabo, both located on the coastline of central Chile (33°30′S, 71°37′W).

A total of 17 species out of 4 taxonomic groups were tested at control and 3 treatment conditions (**Table 1**). The selected invertebrate species included 2 anthozoa, 9 molluscs, 4 crustaceans, and 2 echinoderms (**Table 2**) collected along the coastline of Las Cruces and El Tabo during low tide. These species were selected because of their abundance and significance along the coast, often including a commercial use (e.g., *Tegula atra*, *Prisogaster niger*, and *Concholepas concholepas*). Individuals were acclimated in 25L-tanks with aeration and running seawater, allowing conditions to follow the natural fluctuations occurring in the sea (average ± SD; pH ∼ 7.596 ± 0.040, oxygen ∼ 8.60 ± 1.10 mg L^{-1}, temperature ∼ 15.44 ± 0.07 °C, salinity = 34.26 ± 0.089, see Ramajo et al., 2013; Lardies et al., 2014) for at least 2 days, before being placed into experimental aquaria. Previous to experiments, predators were fed every 1–2 days with bivalves and gastropods, which were collected at the same sites.

Four experimental conditions were used, involving two different levels of pH and oxygen: (1) $H_{O2}L_{CO2}$—involving pH corresponding to atmospheric equilibrium (380 ppm) and saturated oxygen (20% oxygen in the gas mixture); (2) $L_{O2}L_{CO2}$—pCO_2 corresponding to atmospheric equilibrium (380 ppm) and low oxygen (4% oxygen in the gas mixture); (3) $H_{O2}H_{CO2}$—a treatment with elevated CO_2 (low pH), corresponding to

TABLE 1 | Mean (±SE) of the seawater parameters in the aquaria per treatment.

	$H_{O2}L_{CO2}$		$L_{O2}L_{CO2}$		$H_{O2}H_{CO2}$		$L_{O2}H_{CO2}$	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Temperature (°C)	16.2	0.1	16.4	0.1	16.3	0.1	16.3	0.1
Oxygen (mg L^{-1})	9.71	0.18	3.11	0.13	9.84	0.17	2.61	0.06
pH (16°C)	8.06	0.01	8.01	0.02	7.72	0.01	7.80	0.01
Alkalinity (μmol kg^{-1})	2189.8	46.1	2230.8	27.0	2238.7	43.9	2216.7	32.7
CO_2 (ppm)	519.2	17.9	604.5	26.8	1239.0	32.2	1011.4	24.3
HCO_{3-} (μmol kg^{-1})	1879.3	7.1	1941.9	8.6	2080.9	3.5	2032.7	4.6
CO_{32-} (μmol kg^{-1})	124.7	2.9	116.5	3.4	63.7	1.4	74.1	1.9
Ω Aragonite	1.92	0.04	1.80	0.05	0.98	0.02	1.14	0.03
Ω Calcite	2.99	0.07	2.80	0.08	1.53	0.03	1.78	0.04
RI	1.69	0.02	1.12	0.03	1.31	0.01	0.81	0.01

The treatments are: $H_{O2}L_{CO2}$ (ambient O_2 and ambient pH), $L_{O2}L_{CO2}$ (low O_2 and ambient pH), $H_{O2}H_{CO2}$ (ambient O_2 and low pH), and $L_{O2}H_{CO2}$ (low O_2 and low pH).

TABLE 2 | Respiration rate (± SE) and results of the General Linear Model off all tested species after 6 days.

Species	Taxa	Day	Prob. > F		Average respiration rate (± SE)				General linear model (GLM)
					$H_{O2}L_{CO2}$	$L_{O2}L_{CO2}$	$H_{O2}H_{CO2}$	$L_{O2}H_{CO}$	$pH^{*}O_2$
Anemonia alicemartinae n = 12	Anthozoa	6	0.0009	Average	0.00091	0.00047	0.00132	0.00008	0.0001
				(± SE)	0.00004	0.00003	0.00016	0.00005	
				Students' T*	B	C	A	D	
				Tukey HSD*	AB	BC	A	C	
				Mortality	0	0	0	0	
Phymactis papillosa n = 24	Anthozoa	6	0.0001	Average	1.38461	0.15462	1.64402	0.53504	−0.1210
				(± SE)	0.10966	0.01999	0.09036	0.13040	
				Students' T*	A	C	A	B	
				Tukey HSD*	A	B	A	B	
				Mortality	0	0	0	0	
Concholepas concholepas n = 12	Gastropoda	6	0.0107	Average	0.08198	0.03974	0.07502	0.03050	0.0023
				(±SE)	0.00521	0.00700	0.01151	0.01178	
				Students' T*	A	B	A	B	
				Tukey HSD*	A	B	AB	B	
				Mortality	0	0	0	0	
Tetrapigus niger (big) *n* = 12	Echinoidea	6	0.0066	Average	0.00079	0.00056	0.00060	0.00030	0.0001
				(±SE)	0.00008	0.00007	0.00006	0.00005	
				Students' T*	A	B	AB	C	
				Tukey HSD*	A	AB	AB	B	
				Mortality	0	0	0	0	
Tetrapigus niger (small) *n* = 12	Echinoidea	6	0.0375	Average	0.00094	0.00076	0.00101	0.00045	0.0004
				(±SE)	0.00010	0.00014	0.00015	0.00005	
				Students' T*	A	AB	A	B	
				Tukey HSD*	AB	AB	A	B	
				Mortality	0	0	0	0	
Petrolisthes violaceus (medium) *n* = 12	Crustacea	6	0.0154	Average	0.04138	0.02853	0.03472	0.02345	−0.0016
				(±SE)	0.00346	0.00261	0.00387	0.00180	
				Students' T*	A	BC	AB	C	
				Tukey HSD*	A	AB	AB	B	
				Mortality	0	0	0	0	
Petrolisthes tuberculatus n = 12	Crustacea	6	0.0446	Average	2.45355	1.81667	1.42996	1.21440	−0.4213
				(±SE)	0.15931	0.02476	0.44057	0.07371	
				Students' T*	A	AB	B	B	
				Tukey HSD*	A	AB	AB	B	
				Mortality	0	−0.07	0	0	
Allopetrolisthes angulosus n = 24	Crustacea	6	0.0015	Average	2.23465	1.12140	2.00113	0.55751	0.2974
				(±SE)	0.40062	0.10822	0.23791	0.08258	
				Students' T*	A	B	A	B	
				Tukey HSD*	A	BC	AB	C	
				Mortality	0	0	−0.07	0	
Pagurus edwardsi n = 24	Crustacea	6	0.1109	Average	2.66199	2.71286	2.63324	1.64802	1.0361
				(±SE)	0.25803	0.73458	0.15050	0.35126	
				Students' T*	A	A	AB	B	
				Tukey HSD*	A	A	A	A	
				Mortality	0	0	0	0	

*Levels not connected by the same letter are significantly different (after Student's T and Tukey HSD tests). Mortality Rate was calculated as ln(Nt/N0)/days. Numbers marked red show significant difference. *Letters mark the significance groups.*

atmospheric levels expected by the end of the century (1000 ppm, Orr et al., 2005) and saturated oxygen; and (4) $L_{O2}H_{CO2}$—treatment with low O_2 (4% oxygen in the gas mixture) and high CO_2 (1000 ppm) and low pH. These four experimental conditions conform to an *RI* gradient, ranging from 0.81 ± 0.01 *RI*, indicative of aerobic stress ($L_{O2}H_{CO2}$treatment) to an *RI* of 1.69 ± 0.02, without limits for aerobic respiration ($H_{O2}L_{CO2}$ conditions). The respiration index was calculated after Equation (1) following Brewer and Peltzer (2009) from the average of the daily pO_2 and pCO_2 measurements of the four treatments.

To reach the treatment conditions the aquaria were bubbled with a mixture of nitrogen and air to lower the oxygen content, and with pre-determined pCO_2 levels. To set the CO_2 content of the air, ambient air was collected via pumps and passed through soda-lime columns to strip the air of CO_2. Precise volumes of CO_2-stripped air and pure CO_2 gas from a commercial 50 L-bottle were administrated using mass-flow controllers (MFCs; Aalborg GFC-17) and mixed in a container filled with marbles to increase mixing efficiency by increasing surface area to achieve pCO_2 concentrations of 380 ppm ($H_{O2}L_{CO2}$, $L_{O2}L_{CO2}$) and 1000 ppm ($H_{O2}H_{CO2}$ and $L_{O2}H_{CO2}$). To reach hypoxic conditions, nitrogen was added to the air-CO_2 mixture to reduce the oxygen in the water, maintaining the DO between 2.0 and 3.5 mg L^{-1}, corresponding to sublethal hypoxic levels as defined by (Vaquer-Sunyer and Duarte, 2008; Steckbauer et al., 2011).

Aquaria were filled water filtered over 20 μm filters, equilibrated to the treatment conditions, and placed in temperature-controlled tanks set to ambient temperature. Three replicas were used per treatment, resulting in a total of 12 experimental aquaria per species. We used an optic fiber oxygen-meter (Microx TX3, PreSens, Germany), with diameter tips of 20–50 um. Zero calibration was performed using a sodium sulfite (Na_2SO_3) solution (0% saturation) and 100% was calibrated using vigorously air-bubbled seawater. Experimental pH was measured at 5 min intervals with pH_{NBS} sensors (Metrohm and Hanna Instruments), connected to a Consort D130 datalogger. At least once per week, pH in total scale was measured using a pH–meter (pH mobile 826, Metrohm), connected to a combined electrode (double juncture), calibrated using buffers Tris (pH = 8.089) y 2–Aminopiridine (pH = 6.786) at 25°C in a temperature controlled water bath (Torres et al., 2011). Water samples for alkalinity analyses were taken at least once per week, fixed with 20 μL $HgCl_2$ and analyzed within 3 months, using a Metrohm Titrando 808 after Dickson et al. (2007). pH_{NBS}, temperature, alkalinity and salinity values were used to calculate pCO_2, the saturation state of aragonite (Ω_{Ar}) and calcite (Ω_{Ca}) in each treatment using CO2SYS (Pierrot et al., 2006), with K1 and K2 constants from Mehrbach et al. (1973), as revised by Dickson and Millero (1987), and the K_{HSO4} constant from Dickson (1990).

After 3 and 6 days, individuals were transferred to 300 or 1000 mL air-tight vessels and incubated in treatment water for 1–5 h, depending on the size of the animal and vessel, to measure oxygen consumption at 14°C. Temperature was stabilized using a temperature-controlled water bath (JioTech, Co). Oxygen was measured using calibrated PreSens micro-optodes at the beginning and the end of the incubation and the difference was used to calculate the consumption rate using dry weight (DW) and size (in mm) as mg $O_2 g^{-1}$ DW min^{-1} and mg O_2 mm^{-1} min^{-1}. After the experiment, the body size (maximum length, mm) and wet weight (g) of the animals were measured, and the organisms were kept frozen until further processing. To evaluate the dry weight, organisms were dried for at least 24 h at 60°C and weighted. For gastropods, shell and soft parts were treated separately.

Statistical Analysis

To compare the results of the 3 treatments to the $H_{O2}L_{CO2}$ data across species ranging broadly in size and other traits, we calculated the log "effect size" after Hedges et al. (1999) and Gurevitch and Hedges (1999). Response ratios quantify the proportional change resulting from experimental manipulations and ln-transformed response ratios are commonly used because of their robust statistical properties and ease of biological interpretation (Hedges et al., 1999; Kroeker et al., 2010). The effect of the different water conditions on the oxygen consumption was measured for each treatment as the ln-transformed response ratio,

$$\text{LnRR} = \ln(\text{XE}) - \ln(\text{XC}), \quad (2)$$

where X_E and X_C are the mean values of the response variable in the experimental and $H_{O2}L_{CO2}$ treatments, respectively. As our goal is to test the effects of low O_2 and high CO_2 as stressors we designated high O_2 and low CO_2 as the control treatment, even though ambient values in the ecosystem where the organisms grow are closer to the high O_2 low CO_2 treatment (see below).

Three-Way ANOVA's were conducted to test the effect of species, treatment and time (i.e., difference in the responses measured between day 3 and 6) on the respiration rate. A One-Way ANOVA was used to test for differences in respiration rate between treatments for each species. Where the respiration showed significant differences, a Student's *t*-test and post-hoc Tukey HSD test were conducted to resolve which treatments resulted in different respiration rates. Moreover, a General Linear Model (GLM) was used to quantify response to changes in pH, oxygen and their interaction. If the interaction term was significant and positive, then there were synergistic effects between the stressors, and if the interaction term was significant and negative the effects were antagonistic. All analyses were done using RStudio (version 0.97.336) and JMP (version 10.0) with the level for significance set at 0.05.

Results

Seawater temperature averaged (±SE) 16.31 ± 0.06°C during the experimental period and did not differ among treatments (**Table 1**). Mean dissolved oxygen concentration varied from 9.77 ± 0.12 mg O_2 L^{-1} in the normoxic treatment to 2.86 ± 0.08 mg O_2 L^{-1} in the hypoxic treatments, respectively (**Table 1**), and were significant different from each other ($p < 0.001$, ANOVA). Mean pH was 8.03 ± 0.01 in the ambient and 7.75 ± 0.01 in the high CO_2 treatments ($p < 0.001$, ANOVA), respectively. The average alkalinity was 2219.0 ± 18.7 μmol kg^{-1} throughout the treatments and experimental duration. The mean pCO_2 in the water was 562 ± 17 µatm in the normal and 1142 ± 25 µatm in the high CO_2 treatments, respectively. Ω_{Ar} and Ω_{Ca} averaged 1.86 ± 0.04 and 2.89 ± 0.05 in the normal and 1.05 ± 0.02 and 1.63 ± 0.03 in the high CO_2 treatments, respectively (**Table 1**). The *RI* averaged 1.69 ± 0.02 for the $H_{O2}L_{CO2}$, 1.12 ± 0.03 for the $L_{O2}L_{CO2}$, 1.31 ± 0.01 for the high CO_2 and 0.81 ± 0.01 for the $L_{O2}H_{CO2}$ treatment (**Table 1**). The *RI* values for the hypoxic and high CO_2 treatment were similar as the differences in pO_2 and pCO_2 had a similar effect on *RI*. All treatments matched the target values and were held to an acceptable level and variability within each treatment (**Table 1**).

The animals held at $H_{O2}L_{CO2}$ conditions of high oxygen and normal pH did not experience mortality, indicating that mortality observed in the $L_{O2}L_{CO2}$, $H_{O2}H_{CO2}$, and $L_{O2}H_{CO2}$ treatments was due to the low pH and/or low DO concentration and not to other potential. Yet, survival rates were very high, with only 10 individuals dying out of a total of 320 specimens tested in the experiment after 3 or 6 days. As most of the individuals survived 3 days even in the $L_{O2}H_{CO2}$ treatment, they were kept in the aquaria up to 6 days. The species were mortality was observed were limpets *Fisurella* sp. (1x $H_{O2}H_{CO2}$ and 1x $L_{O2}H_{CO2}$ on day 4), the polyplacophora *Chiton granosus* (1x $L_{O2}H_{CO2}$ on day 3) and *Tonica* sp. (2x $L_{O2}L_{CO2}$ and 1x $L_{O2}H_{CO2}$ on day 3); and the anomura crustaceans *Petrolisthes violaceus* (1x $L_{O2}H_{CO2}$ on day 3), *Petrolisthes tuberculatus* (1x $L_{O2}L_{CO2}$ on day 3), and *Allopetrolisthes angulosus* (2x $H_{O2}H_{CO2}$ on day 3), respectively. However, survival rates were higher than 97% across treatments and species (**Table 2**), indicating that the experimental conditions represented sublethal stresses.

After the exposition to experimental conditions, the metabolic rate differed between species and taxa. Generally, echinoderms displayed lower respiration rates and the gastropod species *Tegula atra* and *Diloma nigerrima* the highest (Table S1). There were significant differences in metabolic rates between treatments ($p < 0.001$) and species ($p < 0.001$) but not with the duration of the experiment ($p = 0.69$; **Table 3**). The majority of species (65%) showed metabolic depression, which was reflected in reduced respiration rates, when exposed to hypoxia, high CO_2 or both stressors (**Figure 1**). Their negative responses increased over time, although not significant. The fraction of species showing a significant difference in respiration rate with high CO_2 increased from 41% after 3 days to 60% after 6 days and those showing significant responses to hypoxia increased from 65% after 3 days to 90% after 6 days, with 100% of the species showing significant responses to both stressors acting together already

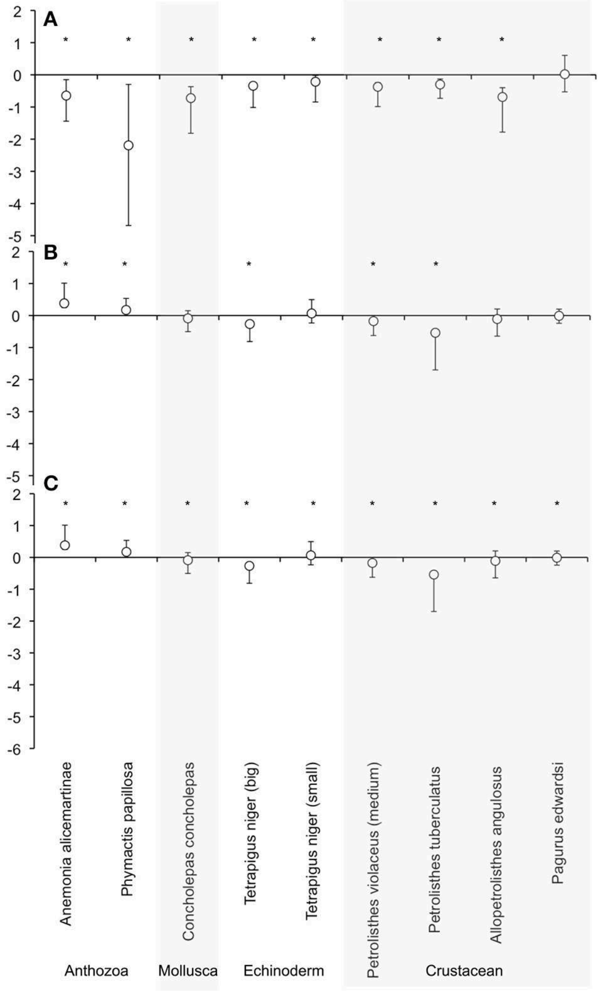

FIGURE 1 | Effect size off of the respiration rate of each species calculated with dry weight after 6 days. Where **(A)** is $L_{O2}L_{CO2}$, **(B)** $H_{O2}H_{CO2}$, and **(C)** $L_{O2}H_{CO2}$ treatment vs. $H_{O2}L_{CO2}$. LnRR = ln(treatment - $H_{O2}L_{CO2}$) ± Confidence interval (after Kroeker et al., 2010). *Marks the significant difference between $H_{O2}H_{CO2}$ and experimental treatments of the effect size.

TABLE 3 | Results of the Three-Way ANOVA describing the effects of species, treatment and day on the respiration rate.

	Df	Sum Sq	Mean Sq	*F*-value	Pr(>F)
Species	19	1670.8	87.94	84	<0.00001***
Treatment	1	11.3	11.35	458	0.00108**
Day	1	0.2	0.17	10.898	0.68748
Treatment:Species	19	41.6	2.19	0.162	0.00504**
Treatment:Day	1	0.0	0.00	2.103	0.98996
Species:Day	8	1.8	0.22	0.000	0.98801
Treatment:Species:Day	8	0.2	0.03	0.216	1.00000
Residuals	299	311.3	1.04	0.025	

*Signif. codes: 0 "***", 0.001 "**", 0.01 "*", 0.05.*

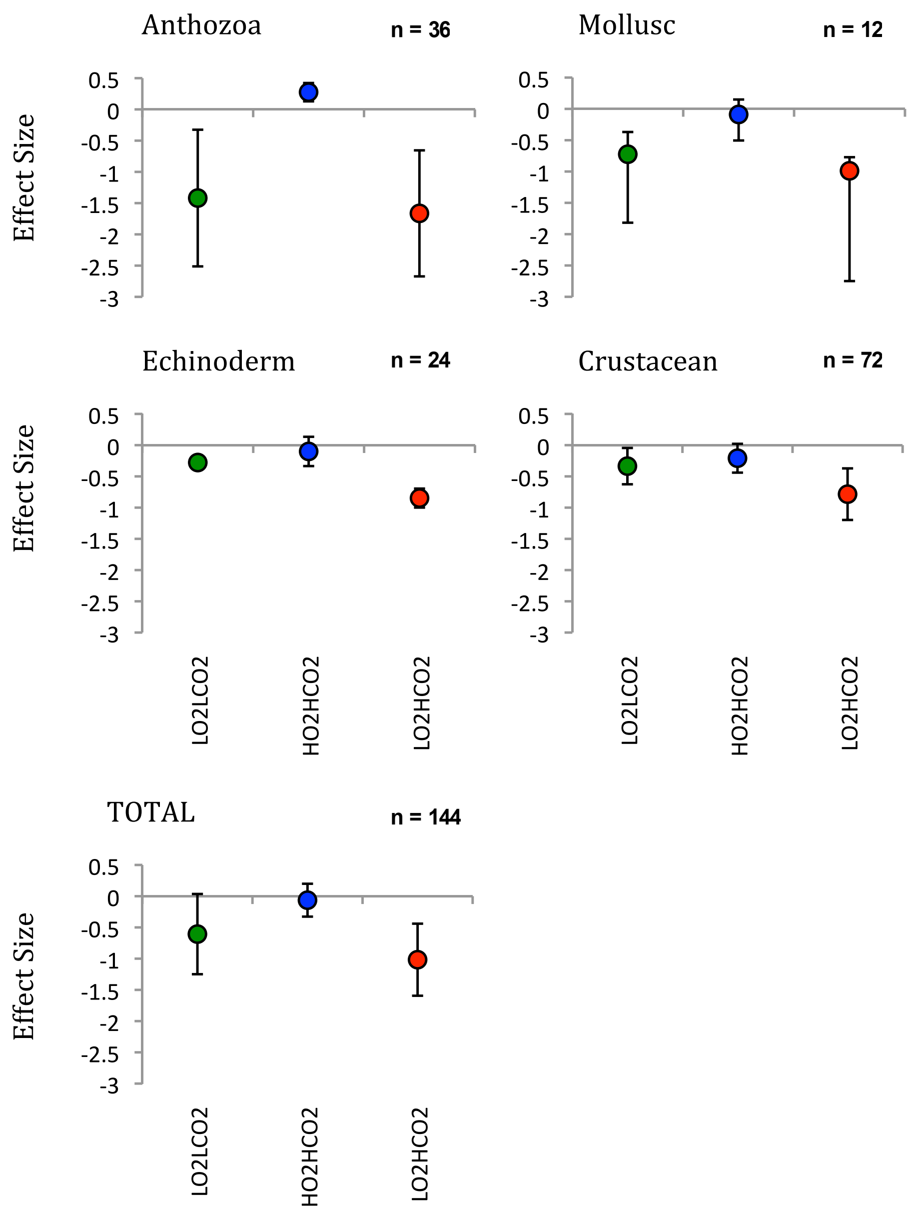

FIGURE 2 | Effect size off of the respiration rate of taxonomic groups calculated with dry weight after 6 days. LnRR = ln(treatment - $H_{O2}L_{CO2}$) ± Confidence interval (after Kroeker et al., 2010).

after 3 and 6 days (**Figure 1** and Figure S1). Anthozoans where the most sensitive taxa as there was a significant difference in all 3 treatments compared to the $H_{O2}L_{CO2}$ (**Figure 2**). For all other taxa, the result was significantly different for the $L_{O2}L_{CO2}$ and $L_{O2}H_{CO2}$ treatment but not always for the $H_{O2}H_{CO2}$, respectively (**Figure 2**). The combination of both stressors ($L_{O2}H_{CO2}$) led to a greater metabolic depression than either stressor alone (**Figure 3**).

Regression analysis of respiration rate in the presence of stressors vs. that in the $H_{O2}L_{CO2}$ treatment showed that the effects of hypoxia and high CO_2 were additive (**Figure 4**), as the deviations of the slope of the regression line for the $L_{O2}H_{CO2}$treatment from 1 (1 – slope $L_{O2}H_{CO2}$ = 0.48± 0.11) does not differ from that resulting from the sum of those of the individual treatments (1 – slope $L_{O2}L_{CO2}$ = 0.24± 0.17; 1 – slope $H_{O2}H_{CO2}$ = 0.15± 0.20; expected $L_{O2}H_{CO2}$ = 0.39± 0.18). This finding shows that, overall, the metabolic responses to the stressors tested was additive, and not synergistic or antagonistic, as also confirmed by the general linear model of the metabolic responses of the individual species to the stressors, where after 6 days only in 4 out of the 9 species tested (4 out of 17 species after 3 days, Table S2) showed a significant interaction term between the two stressors (**Table 2**). The most tolerant taxa after 6 days was the Crustacea, as 3 out of 4 species didn't show significant

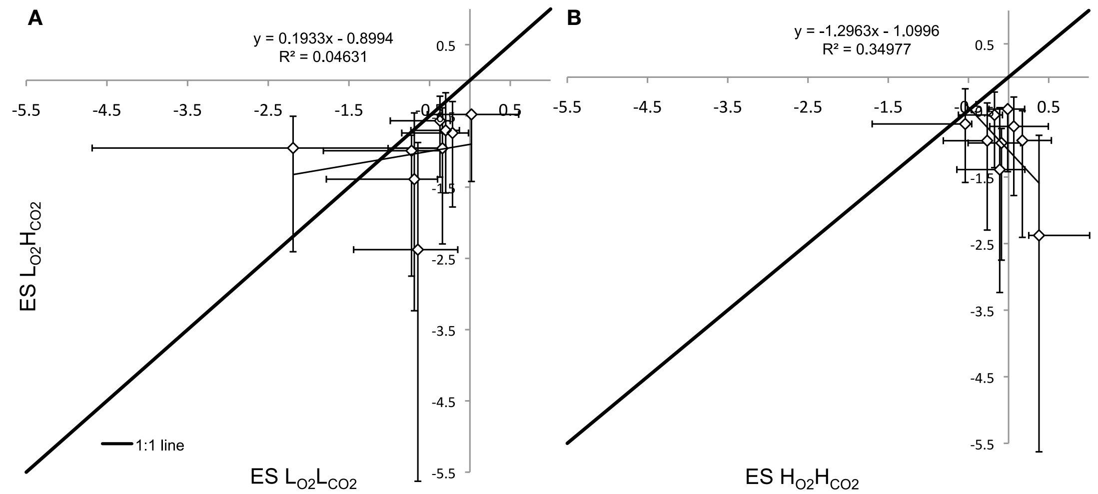

FIGURE 3 | Effect size off of the respiration rate of each species calculated with dry weight after 6 days. (A) $L_{O2}H_{CO2}$ vs. $L_{O2}L_{CO2}$ and **(B)** $L_{O2}H_{CO2}$ vs. $H_{O2}H_{CO2}$. LnRR = ln(treatment - $H_{O2}L_{CO2}$) ± Confidence interval (after Kroeker et al., 2010).

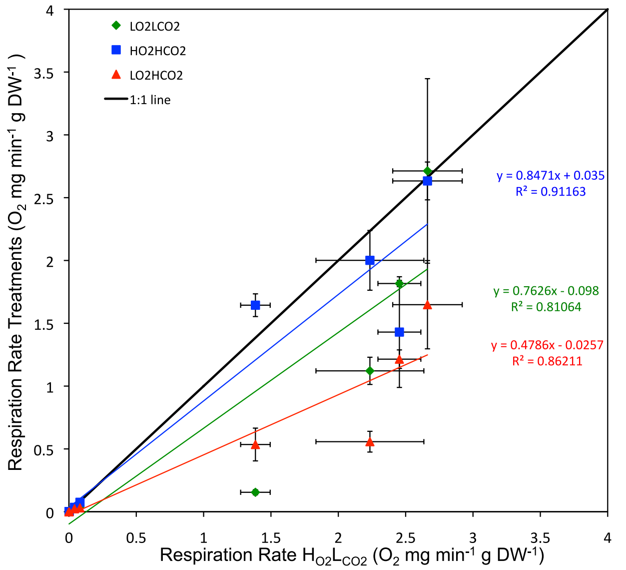

FIGURE 4 | Respiration rate (Average ± SE) after 6 days of all tested species: green – $L_{O2}L_{CO2}$, blue – $H_{O2}H_{CO2}$ and red – $L_{O2}H_{CO2}$.

differences and in *Petrolisthes violaceus* a significant antagonistic effect was observed.

The respiration rates decreased with decreasing RI in all species as expected (**Figure 5**), although the relationships between metabolic rates and RI was relatively weak within taxa, due to the different intensity of metabolic rate.

Discussion

The tested benthic invertebrates from the central Chilean coast were relatively resistant to hypoxia, high CO_2 and their combined effects, as the mortality rate was low across species and metabolic depression, while present, was relatively modest (**Table 2**). Anthozoans and Crustaceans were relatively vulnerable to hypoxia, while Molluscs and Echinoderms were tolerant. This is consistent with results from Vaquer-Sunyer and Duarte (2008), who showed Molluscs and Echinoderms to be particularly tolerant to hypoxic events compared to Crustaceans.

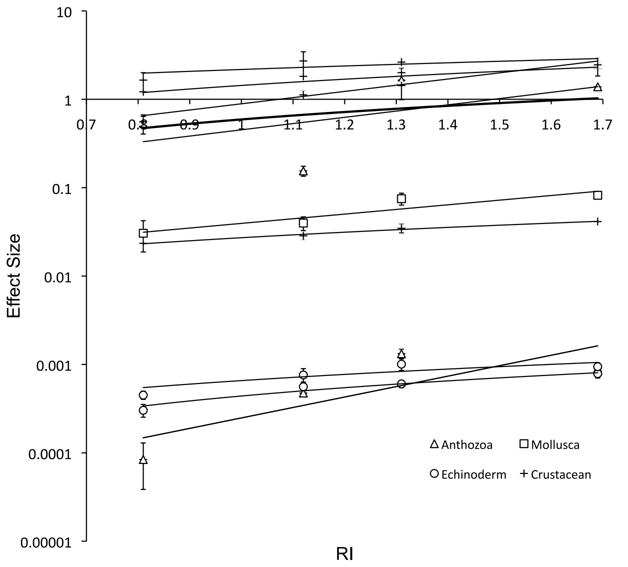

FIGURE 5 | Respiration rate vs. Respiration Index after 6 days (± SE; $y = 0.63x - 0.0385$, $R^2 = 0.04$). Solid lines show the fitted least squares regression lines for Anthozoa ($y = 0.637x - 0.32$; $R^2 = 0.1$), Mollusca ($y = 0.064x - 0.022$; $R^2 = 0.85$), Echinoderm ($y = 0.001x - 0.000$; $R^2 = 0.61$), Crustacean ($y = 1.083x + 0.079$; $R^2 = 0.12$), and Total (bold line; $y = 0.630x - 0.039$; $R^2 = 0.04$); and include the ± SE of the slope, and the *P*-value from the *F*-test for each regression.

The organisms were comparatively resistant to high CO_2 as they showed no significant mortality or metabolic depression when exposed to high CO_2. Indeed, exposure to high CO_2 showed increased respiration rate in Anthozoans and Echinoderms, as also reported in a recent meta-analysis (Kroeker et al., 2013), rather than a metabolic depression. Although it has been reported that food supply and not pCO_2 appears to be the primary factor driving biomass and biogenetic $CaCO_3$ production (Melzner et al., 2011; Thomsen et al., 2013), the effect on respiration rate is controversial (Lampert, 1984). Animals were fed previously, but not during the experiments, as feeding previously to the oxygen measurements was shown to increase respiration rate compared to starved animals. In the $H_{O2}H_{CO2}$ treatment the concentration of aragonite (Ω_{Ar}) was under-saturated ($\Omega_{Ar} < 1$) and in the $L_{O2}H_{CO2}$ treatment close to under-saturation ($\Omega_{Ar} = 1.14 \pm 0.15$), where calcifiers are expected to be under physiological stress (Doney et al., 2009). Molluscs, depositing mostly aragonite, are expected to be more vulnerable to high CO_2 (Porter, 2007) than Echinoderms and Crustaceans, which deposit calcite (Raup, 1959; Raabe et al., 2005).

Most importantly, our results showed that hypoxia and high CO_2 have additive effects and revealed no consistent synergetic or antagonistic effect for these stressors. Moreover, the observation of very low mortality rates and relatively modest metabolic depression (on average 52% reduction compared with the values in $H_{O2}L_{CO2}$ treatments) with both stressors reveals that the Chilean invertebrate species tested are relatively resistant to these stressors. The resistance of invertebrates in the central Chilean coast to hypoxia and high CO_2 is nonetheless not surprising as these organisms may experience these conditions in their natural habitat. Whereas pCO_2 of 1200 ppm as tested here are used in OA experiments to characterize values expected beyond year 2100 (Kroeker et al., 2013), these values are reached regularly in the Chilean coast (Torres et al., 2011; Mayol et al., 2012). Indeed, in the year preceding this experiments high pCO_2 values, of the order of those used in the high treatment here, were found twice, associated with upwelling conditions (N. Lagos, unpubl. data). Moreover, oxygen and pCO_2 are closely correlated in the water mass along the Chilean coast (Mayol et al., 2012), so that upwelling events leading to pCO_2 values around 1200 ppm are associated with oxygen values of $\sim 2\,\mathrm{mg\ L^{-1}}$ (Mayol et al., 2012). Hence, the hypoxia and high CO_2 treatments used here represent stresses already experienced by these organisms. Comparison of the CO_2 and O_2 conditions in the treatments with those experienced by the organisms in their habitat shows that the treatment best representing their environment is involving both high O_2 and low pH (**Figure 6**). Indeed, the pH environment in their environment is even lower than that imposed in the high CO_2 treatment in our experiment. Shall the organisms be vulnerable to high CO_2 they would have been already been sieved from the community and would not occur in this ecosystem. Indeed, the prevalence of high CO_2 in coastal waters (e.g., Borges, 2005) suggest that the use of CO_2 levels close to present atmospheric equilibrium as $H_{O2}L_{CO2}$ (cf. Hendriks et al., 2010) may not represent ambient conditions in many coastal ecosystems (Duarte et al., 2013), possibly confounding the interpretation of results. We suggest that the variability in responses to OA and hypoxia experiments (cf. Vaquer-Sunyer and Duarte, 2008; Kroeker et al., 2013, respectively) should be re-examined in terms of the conditions experienced *in situ* by the population from which the individuals were derived.

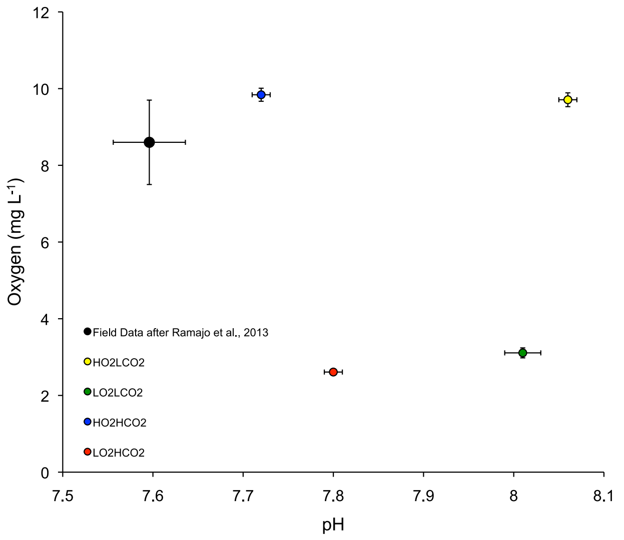

FIGURE 6 | The experimental range of variables from this experiment compared to the ecosystems ambient range of oxygen and pH from the study sites in central and southern Chile during November 2009 and January 2010 (Ramajo et al., 2013).

The fact that the ecosystem supports healthy populations of these invertebrate species despite regular upwelling events already suggests that they must be relatively resistant to at least short term exposure to these conditions. Indeed, exposure to such extreme conditions during upwelling events is typically in the order of 3–7 days (Narváez et al., 2004), the time scale to evaluate responses used here. That the previous history of exposure to the stressors affects the resistance of the organisms was shown experimentally by Brady and Targett (2013), who showed that previous diel-cycle hypoxia lowers the avoidance threshold from $<2.8\,\mathrm{mg\ O_2\ L^{-1}}$ (in saturation-acclimated fish) to $\sim 1.4\,\mathrm{mg\ O_2\ L^{-1}}$ (in diel-cycling hypoxia acclimated fish) in the juvenile weakfish *Cynoscion regalisthey*, showing that they become more resistant to hypoxia.

Whereas hypoxia and high CO_2 are expected to co-occur in nature (Brewer and Peltzer, 2009; Mayol et al., 2012), the responses of marine organisms to these stressors has been largely studied in isolation where either hypoxia (Vaquer-Sunyer et al., 2012) or high CO_2 (Doney et al., 2009; Hendriks et al., 2010; Kroeker et al., 2013) are tested. High CO_2 and hypoxia in the environment, affect the metabolic rates as they lead to a shift in the steady state acid-base equilibrium (Pörtner and Grieshaber, 1993; Pörtner and Heisler, 1998; Pörtner et al., 2005). The combination of hypoxia and increasing CO_2 reduces the rates of relevant trans-membrane ion exchange (Pörtner et al., 2000) and causes a synergistic metabolic depression via the effect of adenosine on central nervous functions if anoxia occurs (Reipschläger et al., 1997). Nevertheless, the examination of the responses to combined hypoxia and high CO_2 is based on a limited set of studies thus far. Kim et al. (2013) exposed juvenile abalone (*Haliotis rufescens*) to short term (3–6 h to 24 h) hypoxia and low pH and found that hypoxia had the greater influence on mortality (pH 7.5 vs. 8.0), but growth was lowest when both stressors where combined. Frieder et al. (2014) showed that low O_2 in combination with low pH did not affect the development and size of 2 mytilid mussels from the Scripps Institution of Oceanography pier (*Mytilus californianus*) and San Diego Bay (*M. galloprovincialis*), USA. Gobler et al. (2014) reported that the bay scallop, *Argopecten irradians*, showed additive responses on survivorship, growth and metamorphosis to low O_2 in combination with low pH, consistent with our findings. However, Gobler et al. (2014) reported that the later stages of the hard clam *Mercenaria mercenaria* were resistant to hypoxia or acidification separately but experienced significantly reduced growth rates when exposed to both conditions simultaneously. This indicates that responses to hypoxia, high CO_2 and their combined effects might be species specific.

The additive nature of the effects of hypoxia and high CO_2 lends weight to the use of the Respiration Index, *RI*, to reflect their combined stress on metabolic processes. Whereas the merit of the *RI* has been challenged recently (Seibel and Childress, 2013) no experimental test had been reported to date. Our results show that metabolic rates decline with decreasing *RI*, as expected (Brewer and Peltzer, 2009), confirming that the *RI* holds power as a predictor of effects, separate or combined, of hypoxia and high CO_2 on metabolic rates. However, our results also support the criticisms of Seibel and Childress (2013) to the predictive power of the thresholds proposed by Brewer and Peltzer (2009). The lowest *RI* we reached in our experiment was 0.81 ± 0.06, reached in the $L_{O2}H_{CO2}$ treatment. This is within the range of 0.7–1.0 where Brewer and Peltzer (2009) propose that aerobic respiration must be severely compromised. Yet, we observed little or no mortality, suggesting that the *RI* thresholds for marine invertebrates are well below those postulated by Brewer and Peltzer (2009). The test provided here is, to the best of our knowledge, the first experimental test, and more tests are required to confirm the merit of the *RI* index and to establish reliable thresholds for marine organisms. Moreover, in future studies measurement of calcification rates would be a good addition to assemble more data on the effects of future scenarios on marine invertebrates.

In summary, marine invertebrates inhabiting the upwelling ecosystems of the Chilean coast show additive but negative responses to hypoxia and high CO_2 and are relatively resistant to the combined effects of these stressors. We suggest that responses to the combined effects of hypoxia and high CO_2 are likely to be dependent on the conditions previously experienced by marine invertebrate populations and that organisms in upwelling-affected areas, such as those along the Chilean coast, are likely adapted, at least to brief exposures, to the occurrence of both stressors.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2015.00049

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REVIEW
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Coral Reef Ecosystems under Climate Change and Ocean Acidification

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Coral reefs are found in a wide range of environments, where they provide food and habitat to a large range of organisms as well as providing many other ecological goods and services. Warm-water coral reefs, for example, occupy shallow sunlit, warm, and alkaline waters in order to grow and calcify at the high rates necessary to build and maintain their calcium carbonate structures. At deeper locations (40–150 m), "mesophotic" (low light) coral reefs accumulate calcium carbonate at much lower rates (if at all in some cases) yet remain important as habitat for a wide range of organisms, including those important for fisheries. Finally, even deeper, down to 2,000 m or more, the so-called "cold-water" coral reefs are found in the dark depths. Despite their importance, coral reefs are facing significant challenges from human activities including pollution, over-harvesting, physical destruction, and climate change. In the latter case, even lower greenhouse gas emission scenarios (such as Representative Concentration Pathway RCP 4.5) are likely drive the elimination of most warm-water coral reefs by 2040–2050. Cold-water corals are also threatened by warming temperatures and ocean acidification although evidence of the direct effect of climate change is less clear. Evidence that coral reefs can adapt at rates which are sufficient for them to keep up with rapid ocean warming and acidification is minimal, especially given that corals are long-lived and hence have slow rates of evolution. Conclusions that coral reefs will migrate to higher latitudes as they warm are equally unfounded, with the observations of tropical species appearing at high latitudes "necessary but not sufficient" evidence that entire coral reef ecosystems are shifting. On the contrary, coral reefs are likely to degrade rapidly over the next 20 years, presenting fundamental challenges for the 500 million people who derive food, income, coastal protection, and a range of other services from coral reefs. Unless rapid advances to the goals of the Paris Climate Change Agreement occur over the next decade, hundreds of millions of people are likely to face increasing amounts of poverty and social disruption, and, in some cases, regional insecurity.

Keywords: corals, climate change, ecosystems goods and services, decline, warming ocean, ocean acidification

INTRODUCTION

Both warm- and cold-water corals secrete calcium carbonate skeletons that build up over time to create a three-dimensional reef matrix that provides habitat for thousands of fish and other species. The production of limestone-like calcium carbonate is high enough in many warm-water coral reefs to establish carbonate structures. High rates of calcification are sufficient to overcome significant rates of bioerosion and wave driven physical erosion. These structures underpin the framework of barrier reefs and islands, which are critically important to tropical coastlines. Although they occupy less than 0.1% of the ocean floor, tropical coral reef ecosystems provide habitat for at least 25% of known marine species, with many reef species still to be discovered (Fisher et al., 2015). The biological diversity of warm-water coral reefs has been estimated to include ∼1–9 million species that live in and around coral reefs (Reaka-Kudla, 1997, Census of Marine Life, http://www.coml.org/census-coral-reef-ecosystems-creefs). In deeper parts of these warm-water reef systems, the tendency toward carbonate dominated reef structures diminishes as light levels decrease (Bongaerts et al., 2010a). At low light levels, erosion and dissolution exceed calcium carbonate production, leading to coral communities that may be abundant yet with little or no three-dimensional calcium carbonate reef framework. Extending from 40 to 150 m, these "mesophotic" (low light) coral reefs also provide extensive habitat, with the rates of discovery of species remaining very high due to these reefs being difficult to visit (Bongaerts et al., 2010a, 2011). Mesophotic reef systems probably cover a comparable area to shallow warm-water coral reefs (Bongaerts et al., 2010a; Slattery et al., 2011).

Both shallow or deeper mesophotic coral reefs are dominated by scleractinian corals that form symbiosis with dinoflagellate protists from the genus, *Symbiodinium*. On the basis of this symbiosis, their intracellular symbionts (i.e., living within the gastrodermal or digestive tissues of their coral hosts) are able to photosynthesize and provide the host coral with a rich source of sugars, glycerol, lipids, and other organic compounds (Muscatine, 1990). This relationship enables corals to grow and calcify at high rates in the clear, warm, and shallow water conditions along tropical coastlines (Muscatine and Porter, 1977). The abundance of Scleractinian corals hosting *Symbiodinium* decreases with depth beyond 20–40 m, depending on the clarity of the water column. The deepest Scleractinian corals that are symbiotic with *Symbiodinium*, are found 100 m or more below the surface of tropical waters (Englebert et al., 2014). The productivity of this symbiosis is complemented by the ability of corals to capture and feed on waterborne particles and plankton (i.e., polytrophy). The combined ability to photosynthesise, as well as feed, underpins the success of the highly productive coral reef ecosystems that line many tropical coastlines. Evidence from isotope signatures within fossils reveal that Scleractinian corals have been symbiotic with *Symbiodinium* for over 230 million years (Stanley and Fautin, 2001; Muscatine et al., 2005), most probably driving productive and diverse ecosystems that were not too different from those of today.

Cold-water coral reefs extend to depths of 3,000 m although some cold-water corals can be found growing in waters as shallow as 50 m (e.g., Norwegian shelf). Below 200 m depth there is so little light that photosynthesis is no longer possible. As a result, cold-water corals do not form a symbiosis with *Symbiodinium* and depend instead on particle feeding. Discoveries of the locations and extent of cold-water reefs has primarily been driven by advances in underwater technologies for surveying and mapping (Turley et al., 2007; Ramirez-Llodra et al., 2010). For example, vast extents (∼2,000 km^2) of cold-water coral reefs, some shown to be thousands of years old (>8,000 years), have been found in Norwegian waters in past decades (Fosså et al., 2005). Cold-water coral reefs have now been discovered in every ocean, forming important assemblages within the deep ocean that provide critical habitat to thousands of other species, including many commercially important species.

Human communities derive many benefits from coral reefs including food, income, recreation, coastal protection, cultural settings, and many other ecological goods and services (Cinner et al., 2009; Costanza et al., 2014). Despite their biological diversity, productivity and importance to humans, both warm and cold-water coral reefs are being heavily impacted by human activities due to both local and global influences (Hall-Spencer et al., 2002; Burke et al., 2011). As a result, many coral reefs are rapidly declining across the world. While local factors can have significant impact on coral reefs (e.g., pollution, overfishing, and the physical destruction of reefs), changes in ocean temperature and chemistry due to anthropogenic activities are dramatically reducing the distribution, abundance, and survival of entire coral reef ecosystems (Gattuso et al., 2014b; Hoegh-Guldberg et al., 2014). Given these risks and the importance of coral reefs to humans and marine biodiversity, the present paper focuses on the challenges that warm and cold-water coral reef ecosystems and their human communities are facing, particularly those posed by rapidly warming and acidifying oceans.

DISTRIBUTION, ABUNDANCE, AND IMPORTANCE OF CORAL REEF ECOSYSTEMS

Warm-water coral reefs are prominent ecosystems within coastal areas of the Pacific, Indian, and Atlantic oceans (**Figures 1A,B**), where they are typically found in a broad band (30°S to 30°N) of warm, sunlit, alkaline, clear, and relatively nutrient deficient ocean waters (Kleypas et al., 1999b). Here, Scleractinian or reef-building corals proliferate, depositing copious amounts of calcium carbonate. As corals die, their dead skeletons build up over time and are "glued" together by the activities of other organisms such as encrusting red coralline algae (Glynn and Manzello, 2015). Other organisms such as calcifying green algae, invertebrates, and phytoplankton also contribute to the overall carbonate budget of warm water coral reefs (Hutchings and Hoegh-Guldberg, 2009), leading to three-dimensional calcium carbonate structures that build up over hundreds and thousands of years. In turn, the three-dimensional structures (**Figure 1C**) within warm-water reef systems creates habitat for hundreds of thousands of species, many of which support coastal human populations with food, income, and other ecological goods and services such as coastal protection. Coral reefs are also

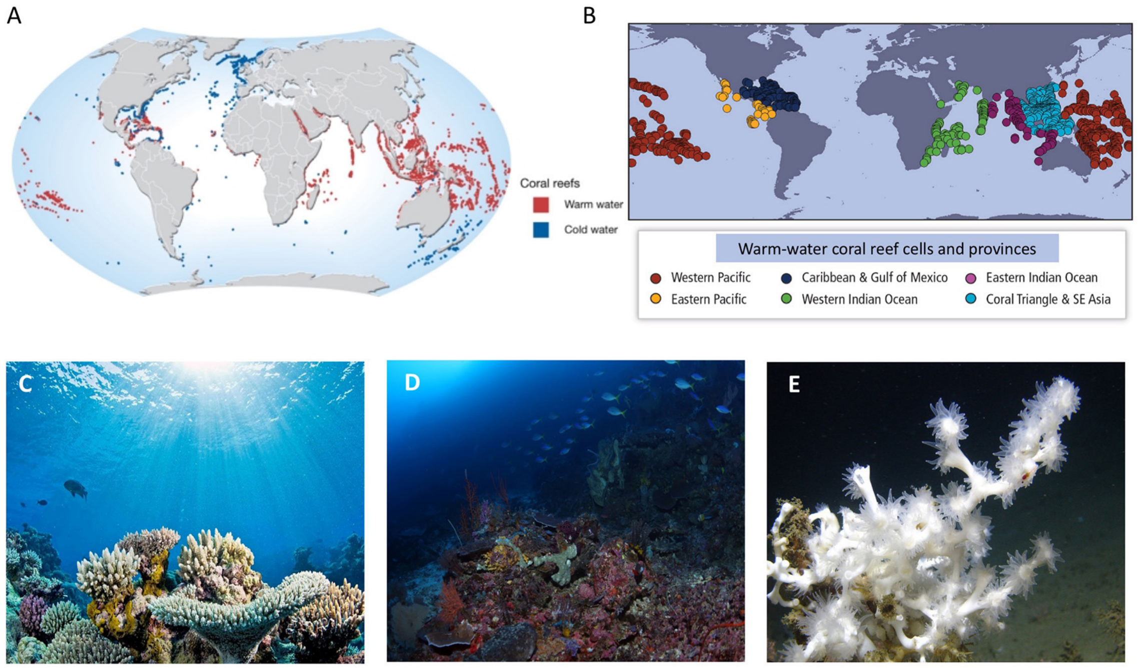

FIGURE 1 | (A) Distribution of warm-water and cold-water coral reefs (credit: Hugo Ahlenius, 2008, UNEP/GRID-Arendal, http://www.grida.no/resources/7197). **(B)** Location of warm-water coral reef cells and provinces, from Hoegh-Guldberg et al. (2014). **(C)** Warm-water carbonate coral reef from the Great Barrier Reef, Australia (credit: Ove Hoegh-Guldberg). **(D)** Mesophotic coral community of North Sulawesi, Indonesia. (Credit: Pim Bongaerts, University of Queensland). **(E)** Deep-water community of *Lophelia pertusa* from the Mississippi Canyon at ~450 m depth (Image from NOAA, licensed under the Creative Commons Attribution-Share Alike 2.0 Generic license).

important sources for bio-prospecting and the development of novel pharmaceuticals. The asset value of coral reefs has been estimated as close to \$1 trillion (Hoegh-Guldberg, 2015) with the economic value of goods and services from coral reefs exceeding \$375 billion annually, with benefits flowing to over 500 million people in at least 90 countries worldwide (Burke et al., 2011; Gattuso et al., 2014b).

As light levels decrease with depth, decalcification dominates and the overall carbonate balance of reef ecosystems shifts to negative (Barnes and Chalker, 1990; Bongaerts et al., 2010a). Under these conditions, Scleractinian corals and their symbionts persist with reefs being referred to as "mesophotic" (Bongaerts et al., 2010a, 2011; Robinson C. et al., 2010). In these habitats, colonies of Scleractinian corals are often platelike in shape, orientating themselves to maximize light harvesting under these dim light conditions (**Figure 1D**). Mesophotic reef systems are also primarily restricted to areas where water clarity, carbonate ion concentrations, and temperatures are relatively high. Like their counterparts in shallower regions, mesophotic reef systems play an important role in supporting fisheries and hence human livelihoods. Given the difficulty of working at depths of more than 30 m (beyond SCUBA-diving depth) many species remain to be discovered (Bongaerts et al., 2010a). Mesophotic reefs therefore have an unknown potential to be sources of novel pharmaceuticals and other potentially beneficial compounds (Leal et al., 2012). As a result, their true value has probably been underestimated.

Cold-water corals generally form reefs at much greater depths from 200 to 2,000 m however in some regions they are found at shallower depths (Fosså et al., 2002; Freiwald et al., 2004). Deep-water corals are not dependent on light levels as they are not symbiotic with *Symbiodinium*. Due to the colder and more CO_2 rich (and hence less alkaline) waters, deep-water corals grow slower than warm-water corals, forming aggregations that are variously termed patches, banks, thickets, bioherms, mounds, gardens, and massifs. In the absence of significant wave action, these fragile and slow growing reefs form aggregations that can cover vast tracks of the seabed (e.g., 2,000 km^2 in Norwegian waters http://www.lophelia.org/) (Hall-Spencer et al., 2002) and involve near mono-specific stands of Scleractinian corals such as *Lophelia pertusa* and *Oculina varicosa* (**Figure 1E**). In addition to Scleractinian corals, they often exhibit a wide variety of abundant coral-like organisms, including soft corals, gorgonians, and Alcyonaceans.

RECENT CHANGES IN THE EXTENT OF ANTHROPOGENIC STRESSES ON CORAL REEF ECOSYSTEMS

Coral reefs are facing growing challenges from the local to global effects of human activities. Over the past 200 years, human activities have fundamentally changed coastlines, overexploited resources such as fish stocks, and polluted coastal waters, to a point where many coral reef ecosystems are degrading rapidly (Jackson et al., 2001; Pandolfi et al., 2003; Hoegh-Guldberg, 2014b). Warm-water coral reefs, for example, have declined by at least 50% over the past 30–50 years in large parts of the world's tropical regions (Hughes, 1994; Gardner et al., 2003; Bruno and Selig, 2007; De'ath et al., 2012). Similar conclusions have been reached for cold-water reefs where human activities have put these systems under escalating pressure from the mid-1980s onwards. Key drivers of the destruction of cold-water reefs include commercial bottom trawling, hydrocarbon exploration and production, deep sea mining, cable and pipeline placement, pollution, waste disposal, coral exploitation, and trade, and destructive scientific sampling (Hall-Spencer et al., 2002; Turley et al., 2007; Roberts and Cairns, 2014). The increase in impacts from human activities is a result of rapid advances in technologies for visualizing and exploiting the biological and mineral resources of deep water habitats (Freiwald et al., 2004; Ramirez-Llodra et al., 2010). Many populations of deep-sea corals (Scleractinians, gorgonians) have very slow turn-over rates and may live for centuries, with some species such as black corals (Antipatharians) living for thousands of years. The longevity and slow growth rates of these taxa means that recovery from anthropogenic stressors will be very slow. The areas inhabited by the deep-sea reefs are also a "resource frontier" for hydrocarbon extraction and mining of high value and "high-tech" metals (Roberts and Cairns, 2014). Hence, it is likely that anthropogenic impacts on these reefs will expand. These impacts are also likely to interact with ocean warming and acidification (**Figure 2A**), which pose growing and serious risks to coral reef ecosystems on their own. The direct impact of these changes to coral reefs have been growing since the early 1980s (Hoegh-Guldberg et al., 2007, 2014; Eakin C. M. et al., 2010; Gattuso et al., 2014b). The latter are the direct result of the burning of fossil fuels and have been driving growing impacts on warm water coral reefs since the early 1980s. Understanding and solving both local and global threats to coral reefs will be critically important if they are to survive some of the greatest rates of environmental change in the recent history of the Earth (Hönisch et al., 2012; Pörtner et al., 2014).

Warm-water coral reefs are largely dependent on the physical and chemical changes occurring in the surface of the ocean, whereas cold-water reef systems are tied relatively more to the broad scale conditions of the bulk ocean (Freiwald et al., 2004; Eakin C. M. et al., 2010). In this respect, there are likely to be differences in terms of the rate and characteristics of the changes that are occurring. These differences also translate into different trajectories when it comes to near and long-term projections of planetary warming and ocean acidification.

Warm-water coral reef environments have experienced relatively small amounts of variability in terms of temperature and carbonate ion concentrations, even with the relatively substantial swings in average global temperature and atmospheric CO_2 concentration during the glacial cycle (**Figure 2B**). Warm-water coral reefs contracted toward the equator during glacial periods, and re-expanded along the tropical and subtropical coastlines of the world during the intervening warm periods (Hubbard, 2015). While these changes were rapid relative to geological time frames, they occurred over periods of 10,000 years or more and are slow when compared to climatic changes that have occurred since pre-industrial. While our understanding of how conditions have changed in terms of the habitat of deep-water coral reefs over geological time is limited, it is very likely that conditions varied even less over these long periods than those surrounding the warm-water coral reefs.

It is virtually certain that the upper ocean has warmed between 1971 and 2010 and likely that it has warmed between 1870s and 1971 (IPCC, 2013). These changes are consistent with those expected from the associated rise in greenhouse gas concentrations in the atmosphere (IPCC, 2013). The average sea surface temperatures (SST) of the Indian, Atlantic, and Pacific oceans have increased by 0.65, 0.41, and 0.31°C during 1950–2009 (Table 30-1 in Hoegh-Guldberg et al., 2014). The influence of long-term patterns of climate variability such as the Pacific Decadal Oscillation (PDO) contribute to variability at regional scales and confound efforts to detect and attribute regional changes to anthropogenic greenhouse gas emissions (Hoegh-Guldberg et al., 2014). Nonetheless, examination of the Hadley Centre HadISST1.1 data (Rayner et al., 2003) over 60 years (1950–2009) reveals significant warming trends in SST for many sub-regions of the ocean (Table 30-1 in Hoegh-Guldberg et al., 2014). Significant trends are clearly demonstrated within the six major warm-water coral reef regions, with the exception of the Gulf of Mexico/Caribbean Sea region (**Table 1**). Rates of increase in SST in the warm-water coral reef regions range from 0.07°C (west Pacific Ocean) to 0.13°C (Coral Triangle and southeast Asia) per decade, resulting in an overall increase in the regions of between 0.44 and 0.79°C during the period from 1950 to 2009.

In addition to the heat content and temperature of the upper layers of the ocean, the research community is virtually certain that ocean chemistry is also changing as a result of the increasing amounts of CO_2 entering the Ocean (IPCC, 2013). Observed increases in salinity at tropical latitudes are consistent with the amplification of the global hydrological cycle (Durack and Wijffels, 2010; Durack et al., 2012), including rainfall, which have significant implications for coastal ecosystems such as warm-water coral reefs. At regional levels, changes in storm and rainfall intensity also have the potential to influence coastal water quality, which is important to coral reefs, as a result of the interplay between droughts, coastal and catchment erosion, and sudden inundation (flood) events. The impact of climate change adds to those from other human activities that are already impacting water quality, coastal erosion and biological systems.

Average global sea levels are increasing by an average of 3.2 mm year^{-1} (over 1993–2010) as a result of warming of the ocean (thus increasing volume) and the melting of land ice (IPCC, 2013). Sea level rise varies between regions as a result of differences in local oceanography and geology and the influence of long-term variation in regional climate. Some areas that have significant warm-water coral reefs, such as Southeast Asia and northern Australia, have reported rates of sea level rise of around 10 mm year^{-1}. While the direct attribution of changes in regional wind strength, storm intensity and frequency to global warming is challenging due to long-term variability, there is considerable evidence that the frequency and intensity of the strongest tropical storms in some regions (e.g., North Atlantic ; IPCC, 2013) has increased since the 1970s. The combination of higher sea levels and more intense storm systems is likely to increase the amount

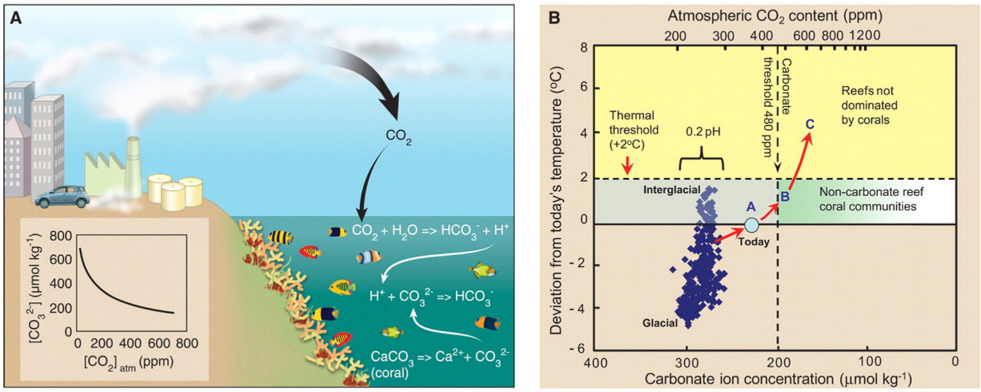

FIGURE 2 | (A) Linkages between the build-up of atmospheric CO$_2$ and the slowing of coral calcification due to ocean acidification. Approximately 30% of the atmospheric CO$_2$ emitted by humans has been taken up by the ocean (IPCC, 2013) where it combined with water to produce carbonic acid, which releases a proton that combines with a carbonate ion. This decreases the concentration of carbonate, making it unavailable to marine calcifiers such as corals. **(B)** Temperature, [CO$_2$]$_{atm}$, and carbonate-ion concentrations reconstructed for the past 420,000 years. Carbonate concentrations were calculated (Lewis et al., 1998) from [CO$_2$]$_{atm}$ and temperature deviations from conditions in the decade of the 2000s with the Vostok Ice Core data set (Petit et al., 1999), assuming constant salinity (34 parts per trillion), mean sea temperature (25°C), and total alkalinity (2,300 mmol kg^{-1}). Acidity of the ocean varies by ± 0.1 pH units over the past 420,000 years (individual values not shown). The thresholds for major changes to coral communities are indicated for thermal stress (+2°C) and carbonate-ion concentrations ([carbonate] = 200 µmol kg^{-1}, approximate aragonite saturation ~ $\Omega_{aragonite} = 3.3$; [CO$_2$]$_{atm}$ = 480 ppm). Coral Reef Scenarios CRS-A, CRS-B, and CRS-C are indicated as A, B, and C, respectively, with analogs from extant reefs. Red arrows pointing progressively toward the right-hand top square indicate the pathway that is being followed toward [CO$_2$]$_{atm}$ of more than 500 ppm. From Hoegh-Guldberg et al. (2007) with permission of Science Magazine.

TABLE 1 | Changes in sea surface temperature (SST) in six major warm-water coral reef provinces (Figure 1B) over the period 1950–2009 using 1 × 1 degree monthly SST data extracted from the Hadley Centre HadISST1.1 data set (Rayner et al., 2003).

Coral reef province	Regression slope: °C per decade			Total change over 60 years: °C			*p*-value, slope different from zero: °C per decade		
	Coolest month	All months	Warmest month	Coolest month	All months	Warmest month	Coolest month	All months	Warmest month
Caribbean Sea/Gulf of Mexico	0.026	0.024	0.023	0.156	0.144	0.138	0.107	0.382	0.203
Coral Triangle and Southeast Asia	0.137	0.131	0.098	0.822	0.786	0.588	0.000	0.000	0.000
Indian Ocean (east)	0.081	0.097	0.116	0.486	0.582	0.696	0.000	0.000	0.000
Indian Ocean (west)	0.091	0.100	0.102	0.546	0.600	0.612	0.000	0.000	0.000
Pacific Ocean (east)	0.079	0.094	0.101	0.474	0.564	0.606	0.106	0.000	0.023
Pacific Ocean (west)	0.072	0.073	0.073	0.432	0.438	0.438	0.000	0.000	0.000

The table includes the slope of the regression (°C per decade), the p-value for the slope being different from zero and the total change over 60 years (i.e., the slope of linear regression multiplied by six decades) for each category. The p-values that exceed 0.05 plus the associated slope and change values have a gray background, denoting the lower statistical confidence in the slope being different from zero (no slope). Note that changes with higher p-values may still describe informative trends even though the level of confidence that the slope is different from zero is lower. Full methods given in Table 30-1 in Hoegh-Guldberg et al. (2014), reprinted with permission of the United Nations Intergovernmental Panel on Climate Change, IPCC AR5).

of force exerted by wave action on coastal areas, which has implications for coastal infrastructure, as well as the state of ecosystems such as coral reefs, mangroves, and seagrass beds (Hamylton et al., 2013; Saunders et al., 2014).

Changes have also occurred in the pH of ocean surface waters over the past 100 years, a phenomenon which is referred to as ocean acidification (Kleypas et al., 1999a; Caldeira and Wickett, 2003; Gattuso et al., 2014a). As CO$_2$ enters the ocean, it reacts with water increasing hydrogen ion concentration (thus decreasing ocean pH) and decreasing the carbonate ion concentration. While the overall change in ocean pH appears small (0.1 pH units over the past 150 years), this is actually a 26% increase in the concentration of hydrogen ions. Experimental evidence shows a reduction in carbonate ions with ocean acidification is biologically significant, since it can affect the rate at which marine organisms, such as corals build their calcareous structures (Kroeker et al., 2013). However, understanding of the mechanisms driving the sensitivity of coral calcification to ocean chemistry, such as the response of the pH of the internal calcifying fluid in which the coral skeleton forms to the concentration of dissolved organic carbon, are only being untangled (Comeau et al., 2017). These changes in ocean

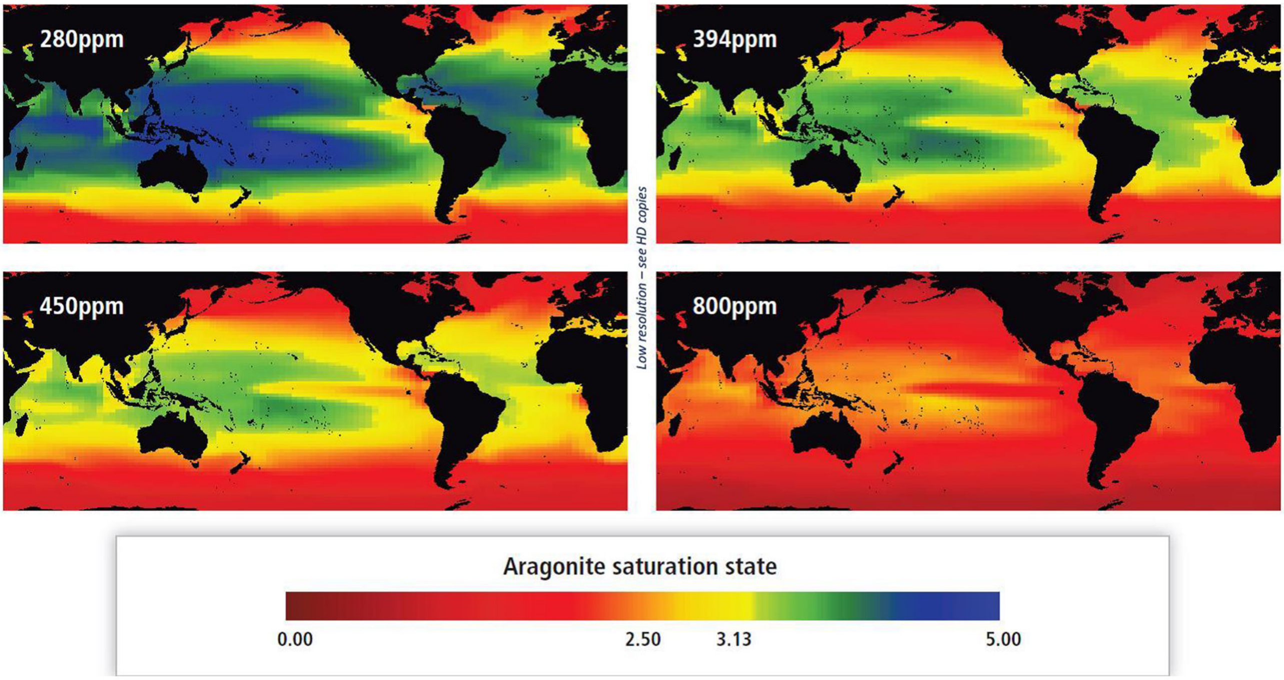

FIGURE 3 | Aragonite saturation state of the surface ocean simulated by the University of Victoria Earth System Model under different atmospheric concentrations of CO_2. 280 ppm represents pre-industrial and 394 ppm levels in 2012. Four hundred and fifty ppm is projected to be reached during 2030s under Representative Concentration Pathway (RCP) 4.5, 6.0, and 8.5, and to approach, but not reach 450 ppm, during 2040s under RCP 2.6 (IPCC 2013). Eight hundred ppm is projected to be reached during 2080s under RCP 8.5 only. Fields are calculated from the model output of dissolved inorganic carbon concentration, alkalinity concentration, temperature, and salinity, together with the chemistry routine from the OCMIP-3 project. Modified from Figure SM30-2 in Hoegh-Guldberg et al. (2014; reprinted with permission of IPCC AR5).

chemistry are temperature dependent, with the CO_2 absorption and consequently acidification being highest when waters are cooler. The aragonite (one form of calcium carbonate) saturation state (Ω_{arag}) is essentially the ratio between the concentrations of calcium and carbonate ions (Doney et al., 2009). The aragonite saturation state shows a similar distribution to sea surface temperature with Ω_{arag} being highest in the warmest ocean regions and lowest in polar regions (Jiang et al., 2015). Surface waters of the ocean are generally supersaturated with respect to aragonite ($\Omega_{arag} > 1$). However, in warmer waters where Ω_{arag} is not projected to fall to <1 (thus undersaturated with respect to aragonite, **Figure 3**), substantial impacts are likely to still occur on calcifying organisms. There is substantial evidence that carbonate accretion on warm-water coral reefs approaches zero or becomes negative when Ω_{arag} falls below 3.3 (Hoegh-Guldberg et al., 2007; Chan and Connolly, 2013), a level likely to be reached in tropical surface waters within the next few decades at current rates of greenhouse gas emission (Hoegh-Guldberg et al., 2007; Ricke et al., 2013).

The global distribution of cold-water corals is at least partly limited by the depth of the aragonite saturation horizon, $\Omega_{arag} = 1.0$ (Guinotte et al., 2006). Aragonite saturation state diminishes with depth, due partly to hydrostatic pressure and lower temperature, with a distinct aragonite "saturation horizon" below which waters become under-saturated for aragonite ($\Omega_{arag} < 1$) (Jiang et al., 2015). The saturation horizon is a complex outcome of ocean circulation, temperature, CO_2 concentrations, salinity, metabolic activity, and the concentrations of organic compounds and occurs at depths between 200 and 3,500 m, depending on the latitude and the ocean (Orr et al., 2005; Doney et al., 2009; Rhein et al., 2013; Jiang et al., 2015). Surface waters and waters at 50 m depth are mostly supersaturated throughout the global ocean (Jiang et al., 2015), however in western Arctic waters, the area of under-saturated waters in the upper 250 m north of 70°N has increased from 5 to 31% between 1990s and 2010 (Qi et al., 2017). At 500 m, large areas of undersaturated Ω_{arag} water are found in the northern and equatorial Pacific ocean. At 1,000 m, $\Omega_{arag} < 1.8$ over all ocean basins and at 2.000 m, $\Omega_{arag} < 1.0$ across all the Pacific and Indian Ocean and parts of the Atlantic Ocean. Ocean acidification is proceeding at higher rates at high latitudes than at lower latitudes (**Figure 3**) resulting in a shoaling of the aragonite saturation horizon. There is now evidence to show that the aragonite saturation horizon has shoaled since the Preindustrial Period (Turley et al., 2007). For example, in the north east Pacific (from 33.5 to 50.0°N) the aragonite saturation horizon has shoaled by 19.6 m in 11 years (2001–2012) and, at this rate, the entire water column in the northern section of this region is projected to become undersaturated within 50–90 years (Chu et al., 2016).

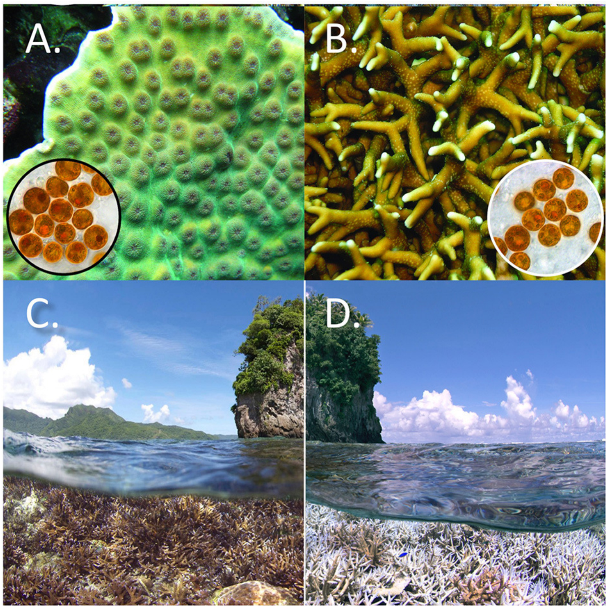

FIGURE 4 | (A) Scleractinian coral (*Turbinaria* sp) and **(B)** Hydrozoan coral (*Millepora* sp) showing respective *Symbiodinium* symbionts (each brown cell is about 10 μm in diameter) removed from coral tissues; Credit for **(A,B)**: Todd LaJeunesse, from Pennsylvania State University. (https://www.flickr.com/photos/tags/linkflickrset72157631573740050). **(C)** The photo at left, taken in December 2014, shows coral reef near runway in American Samoa, without obvious bleaching of corals. **(D)** The photo at right shows the same coral reef, now heavily bleached, in February 2014 (Credit for **C**,**D**: Richard Vevers, The Ocean Agency).

BIOLOGICAL RESPONSES TO A RAPIDLY WARMING AND ACIDIFYING OCEAN

Not surprisingly, the scale and pace of the physical and chemical changes occurring in the ocean are driving a large range of fundamental responses in marine organisms, ecosystems, and regions (Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). Equally significant, is the observation that relatively small amounts of change have resulted in quite substantial biological impacts, with clear evidence of non-linear trends, tipping points, and otherwise complex responses. Coral responses to changes in ocean conditions, in particular mass coral bleaching, provide particularly compelling examples of the consequences of a rapidly changing ocean for organisms, ecosystems, and dependent societies.

The symbiosis between warm-water corals and *Symbiodinium* (**Figures 4A,B**) is very sensitive to changes in the physical and chemical environment surrounding corals. Short periods of high or low temperature and/or light, or exposure to toxins like cyanide, can drive the breakdown of the symbiosis, resulting in the loss of the brown symbionts and a subsequent paling (hence "bleaching") of the coral host (Hoegh-Guldberg, 1999). Coral bleaching involves the breakdown of the symbiosis between Scleractinian corals and *Symbiodinium*, which may recover if conditions are not too anomalous for too long. While bleaching of coral tissues has been reported on the scale of colonies or groups of colonies for at least 100 years (Yonge and Nichols, 1931), reports of bleaching at large geographic scales (**Figures 4C,D**, example of affected coral reefs in American Samoa from late 2015) was unknown to the scientific literature until 1979. Since the early 1980s, however, mass coral bleaching has affected entire reefs and regions, often resulting in significant mortality of reef-building corals. The absence of pre 1979 scientific reports in addition to the close relationship between bleaching and elevated sea temperature, plus considerable laboratory, and mesocosm studies, strongly support the conclusion that mass coral bleaching and mortality are novel and are caused by warm water coral reefs being exposed to rising sea temperatures (Hoegh-Guldberg and Smith, 1989; Glynn, 1993, 2012; Hoegh-Guldberg, 1999; Glynn et al., 2001; Hoegh-Guldberg et al., 2007, 2014; Baker et al., 2008; Eakin C. M. et al., 2010; Strong et al., 2011; Gattuso et al., 2014b). The latest cycle of mass coral bleaching in 2016 (Hoegh-Guldberg and Ridgway, 2016) is reputedly the worst on record and accompanies the warmest years on record (King and Hawkins, 2016; https://www.nasa.gov/press-release/nasa-noaa-data-show-2016-warmest-year-on-record-globally).

Mass coral bleaching and mortality can be triggered by small (1–2°C) SST increases above the long-term summer maxima for a region (Strong et al., 2011). If temperatures are higher for longer, the amount of coral bleaching will increase, driving increased mortality (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Eakin C. M. et al., 2010). There is a strong link between the size and length of temperature extremes and mass coral bleaching and mortality (Hoegh-Guldberg, 1999; Strong et al., 2004, 2011; Eakin C. M. et al., 2010). These relationships are used with satellite data to derive anomalies in SST to monitor the frequency and intensity of mass coral bleaching and mortality (Strong et al., 2004, 2011). For this reason, there is a high level of confidence that the increases in mass coral bleaching and mortality since the early 1980s are due to anthropogenic climate change in particular ocean warming (Hoegh-Guldberg et al., 2014). The loss of symbionts from coral tissues can have immediate effects through the loss of photosynthetic energy, and lead to starvation, disease, reproductive failure, and a loss of competitive ability relative to other organisms on coral reefs (Hoegh-Guldberg and Smith, 1989; Glynn, 1993, 2012; Hoegh-Guldberg, 1999; Baker et al., 2008; Hoegh-Guldberg et al., 2014; Glynn and Manzello, 2015).

Understanding how the positions of ocean isotherms (lines of similar temperatures) are changing and how fast across the ocean surface ("velocity of climate change", Burrows et al., 2011, 2014) provides insight into whether or not coral populations will be able to move, adapt or acclimatize fast enough to changing sea temperatures (Hoegh-Guldberg, 2012; Pörtner et al., 2014). Some of the highest rates of climate velocity (up to 200 km per decade) were observed in ocean tropical regions (over 1960–2010), driven by shallow spatial gradients in temperature (Burrows et al., 2011, 2014). Observed rates of distribution shifts for individual warm-water coral species linked to increases in sea surface temperatures range from 0 to 150 km per decade, with an average shift rate of 30 km per decade (Yamano et al., 2011; Poloczanska et al., 2013), suggesting that corals and coral ecosystems may be unable to keep up with warming rates

(Hoegh-Guldberg, 2012; Burrows et al., 2014; García Molinos et al., 2015).

The possible reduced influence of extremes from climate change with depth has led to the speculation that deeper (>40 m) mesophotic coral reefs may offer a potential refuge against the otherwise rapid changes in temperature, storm intensity, and chemistry that are typical of shallow-water (0–30 m) coral reef environments (Bongaerts et al., 2010a). The "Deep Reef Refugia" hypothesis has been explored by a number of groups who are finding substantial differences in terms of the rate of warming and acidification with depth, as well as examples of species that may span the mesophotic zone to shallow reef areas. Recent work however, has revealed that mesophotic reefs may not be immune to the impacts of storms (Bongaerts et al., 2013). Also, populations of what appear to be the same coral species appear to have considerable genetic structure as a function of depth. This is important given that it implies a high degree of specialization, local adaptation, and even speciation, by corals living at different depths, with the implication that mesophotic corals may not be able to survive in shallow-water environments and *vice versa*, reducing the potential for mesophotic environments to provide refugia for shallow water Scleractinian corals. This reduces the significance of deeper water populations as a source of recruits for regenerating damaged areas on shallow water coral reefs (Bongaerts et al., 2010b, 2015). In addition to warming oceans, corals are also sensitive to changes to the pH and the carbonate chemistry of seawater as a result of ocean acidification (Kleypas et al., 1999a; Gattuso et al., 2014a). These changes affect organisms in a variety of ways, including reducing calcification rates in a wide array of corals and other organisms in laboratory, mesocosm, and field studies (Gattuso et al., 1998; Reynaud et al., 2003; Kleypas et al., 2006; Dove et al., 2013; Kroeker et al., 2013; Gattuso et al., 2014a).

Long-lived corals from the field have provided an opportunity for retrospective analysis of how growth has varied over long periods of time (De'ath et al., 2009; Lough, 2010, 2011). Calcification measurements from coral cores from 328 colonies of the massive coral *Porites* growing on the Great Barrier Reef in Australia, for example, have revealed that calcification by these corals has declined by 14.2% since 1990. This appears to unprecedented on the Great Barrier Reef for at least the last 400 years (De'ath et al., 2009) (but see D'Olivo et al., 2013; **Figure 5**). Given the complexity of the environmental changes occurring in places like the Great Barrier Reef, it is difficult to assign specific drivers of this decline. However, the combined effects of elevated warming and acidification from climate change, along with declining water quality, appear to be significant drivers of the changes observed (D'Olivo et al., 2013). Declining growth and calcification rates have also been detected for *Porites* colonies in the Red Sea (Cantin et al., 2010) and at several locations in Southeast Asia (Tanzil et al., 2009).

Studies of the influence of rapidly warming and acidifying conditions on mesophotic coral reefs are absent. Given that these reef systems cover roughly the equivalent area of shallow water coral reefs, understanding how environmental changes are likely to influence these important areas in terms of habitat the fisheries and biodiversity is important and should be a priority of future research (Bongaerts et al., 2010a). Linking the physiological and ecological response of mesophotic reefs to changes in pH and carbonate ion concentration will also be important in the context of understanding how mesophotic coral reef ecosystems will be affected by the shoaling of the saturation horizon in regions such as off Hawaii.

Our understanding of how deep ocean environments are likely to respond to changes in ocean temperature and chemistry are at an early stage. Like mesophotic coral reefs, little is known about the sensitivity of cold-water coral reefs to changes in temperature. As cold-water corals tend not to have a mutualistic symbiosis with *Symbiodinium*, their response is naturally different to that of symbiotic Scleractinian corals. As with mesophotic coral reefs, there is much more to be discovered with respect to how these critically important cold-water coral reefs are likely to respond to steadily warming and acidifying ocean. Coral reefs in the deep-sea have been identified as particularly vulnerable to the effects of ocean acidification; in part because of the numerical predominance of calcifying taxa, and in part because the pre-industrial carbonate levels at the depths and temperatures they inhabit were already low (Freiwald et al., 2004). Experimental studies reveal that short-term exposures of important deep-water corals such as *L. pertusa* to a reduction in pH of around 0.15–0.3 units resulted in a decrease in calcification rates of between 30 and 56% (Maier et al., 2009). However, subsequent work has shown that *L. pertusa* can acclimatize (i.e., maintain considerable calcification) to declining aragonite levels modifying skeletal structure and skeletal strength (Form and Riebesell, 2012; Hennige et al., 2015). Observations of deep-sea corals in under-saturated waters from the SW Pacific also suggest some species-specific tolerance, however growth rates are extremely low and in under-saturated conditions dead coral skeletons dissolve rapidly (Bostock et al., 2015; Thresher et al., 2015). Whether cold-water corals will be able to adjust to rapid warming and ocean acidification projected for the coming century is unknown. However, analyses of cold-water coral fossils suggest that a combination of declining aragonite and oxygen saturations will reduce the distribution of cold-water corals (Thiagarajan et al., 2013).

While coral species and their symbionts have received a major amount of focus in terms of the effect of ocean warming and acidification on warm-water coral reef ecosystems, there is a growing number of studies that have revealed impacts on a broader range of reef organisms. Among the most affected are calcifying algae, calcareous phytoplankton, molluscs, and echinoderms, with the larval stages of some organisms being more sensitive than the adult phase (Kroeker et al., 2013). Bioeroding organisms also respond to both warmer and more acidic conditions (Dove et al., 2013; Fang et al., 2013; Reyes-Nivia et al., 2013). The sponge, *Cliona orientalis,* increased biomass and bioerosion capability when exposed to warmer and more acidic conditions, implicating a role of this sponge in helping tip the carbonate balance of reefs toward net erosion (Dove et al., 2013; Fang et al., 2013). Similar observations have been made for bio-eroding endolithic algal communities, where small shifts in ocean temperature and acidity (i.e., CO_2 levels) enhanced skeletal dissolution and was associated with increased endolithic biomass and respiration under elevated temperatures and CO_2 levels (Reyes-Nivia et al., 2013).

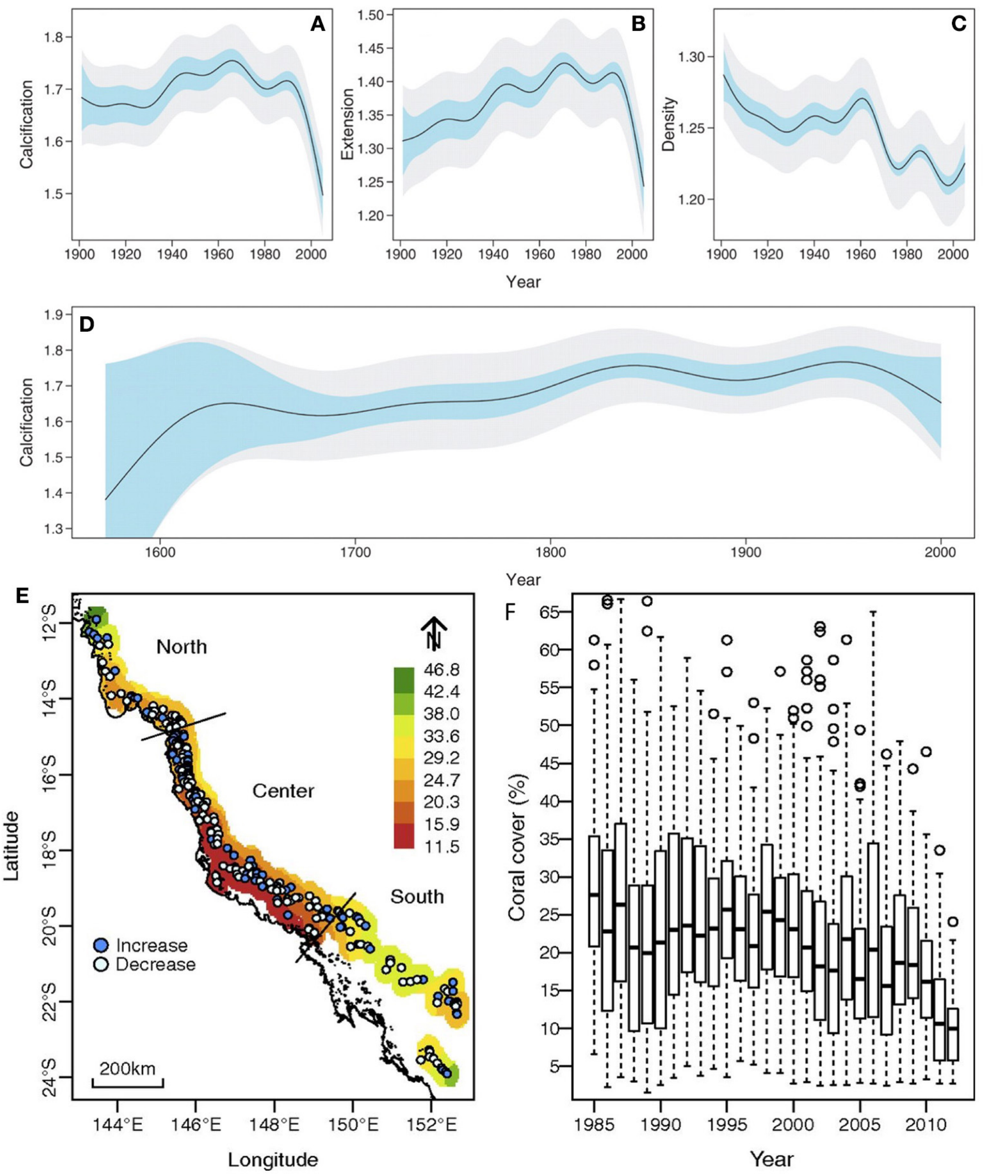

FIGURE 5 | (A–D) Partial-effects plots showing the variation of calcification (grams per square centimeter per year), linear extension (centimeters per year), and density (grams per cubic centimeter) in *Porites* from the Great Barrier Reef (GBR), Australia, over time. From De'ath et al. (2009). Plots **(A–C)** are based on 1900–2005 data from 328 *Porites* colonies, and plot **(D)** on data for ten long cores. Light blue bands indicate 95% confidence intervals for comparison between years, and gray bands indicate 95% confidence intervals for the predicted value for any given year. Calcification declines by 14.2% from 1990 to 2005 **(A)**, primarily due to declining extension **(B)**. Density declines from 1900 onward **(C)**. The 1572–2001 data show that calcification increased weakly from ∼1.62 before 1,700 to ∼1.76 in ∼1850, after which it remained relatively constant **(D)** before a weak decline since ∼1960. **(D–F)** Decline coral cover of the GBR over 1985–2012. **(E)** Map of GBR with color shading indicating mean coral cover averaged over 1985–2014. Points show the location of 214 survey reefs in the northern, central, and southern regions, and their color indicates the direction of change in cover over time. **(F)** Box plots indicate the percentiles (25, 50, and 70%) of the coral cover distributions within each year and suggest a substantial decline in coral cover over the 27 years. Adapted from De'ath et al. (2012) and with the permission according to PNAS policy.

In addition to impacts on growth, calcification, and reproduction, there is growing evidence of impacts on a range of physiological systems of coral reef organisms. Ocean acidification, for example, impairs the homing ability and olfactory discrimination of some coral reef fish, with potential consequences for the ability of fish to detect and avoid predators (Munday et al., 2009; Dixson et al., 2010). At present, there are few reports on the influence or not of ocean acidification on the metabolic performance of tropical fish species. In this regard, it will be important to explore whether or not tropical fish have the same challenges that temperate fish have when it comes to respiratory gas transport and acid–base balance (Esbaugh et al., 2012; Pörtner et al., 2014). Physiological impacts combined with ecological impacts and habitat degradation, are likely to generate "surprises" for complex ecosystems such as those associated with both cold and warm water coral reefs.

ECOLOGICAL RAMIFICATIONS OF RAPID CHANGE

The impact of climate change on coral reef organisms has ramifications for ecosystems, some of which may be transformative in terms of their effects on primary productivity, food web dynamics, habitat forming species, disease ecology, and many other aspects (Hoegh-Guldberg and Bruno, 2010). The recent decline in the abundance of warm-water coral reefs (Hughes, 1994; Gardner et al., 2003; Bruno and Selig, 2007; De'ath et al., 2012), however, illustrates the complex yet fundamental ways that marine ecosystems are changing in response to rapid rates of ocean warming and acidification. The ecological ramifications of rapid global change for mesophotic coral reefs are less well-known or understood than those of warm-water shallow reef systems. Similarly, threats to cold-water coral reefs less well-understood and undoubtedly involve a different mix of local and global drivers (Turley et al., 2007; Roberts and Cairns, 2014).

The major ecological responses of warm-water coral reefs to climate change have their origins in the response of reef-building corals to warming and acidification, and their role as framework builders within typical carbon reef systems (Gattuso et al., 1998; Kleypas et al., 1999a; Reynaud et al., 2003; Maier et al., 2009; Kroeker et al., 2013). As described above, corals are sensitive to small changes in temperature, light, and a number of other environmental variables, responding by disassociating from the dinoflagellate symbionts that populate their tissues (i.e., bleaching). Small changes in temperature are driving decreased growth and reproduction and increased mortality of corals in many parts of the world (Hoegh-Guldberg and Smith, 1989; Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2014). As corals lose their symbionts, they become vulnerable to death and disease, as well as being less able to compete with other benthic organisms. These changes have driven episodes of coral mortality associated with thermal stress, with the catastrophic loss of corals in particular regions over the past 30 years (Hoegh-Guldberg, 1999; Baker et al., 2008; Eakin C. M. et al., 2010; Glynn, 2012). While some coral reefs have recovered over subsequent decades many others have not. Regional differences in the ability to recover are linked to the presence and absence of other factors affecting the resilience of reef building corals and other reef related organisms such as levels of herbivory, macroalgal cover, and coral recruitment rates (Baker et al., 2008). The reduced resilience of reef building corals as a result of thermal stress is likely to be exacerbated by increasing ocean acidification, which has the potential to reduce the ability of corals to grow, calcify, and recover from disturbances. While teasing apart the effects of rising temperatures and increasing amounts of ocean acidification is difficult, both thermal stress, and acidification have the potential to reduce the ability of corals to recover from stresses (Hughes et al., 2007). This may help explain why stressors such as cyclones, which do not appear to have increased in frequency over the past 30 years (Callaghan and Power, 2011; IPCC, 2013), appear to be having longer-lasting impacts on coral communities on the Great Barrier Reef (De'ath et al., 2012).

Mass coral bleaching reduces the energy available to corals, leading to physiological compromise. Warm-water corals, for example, exude mucus which is rich with the excess carbohydrates which provides food for a large number of molluscs, crustaceans, worms, ciliates, fish, and many other organisms (Baker et al., 2008; Wild et al., 2011). It also appears to play an important role in preventing the settlement of fouling and disease organisms. Mucus secretion, however, is reduced in bleached corals, potentially leading to increased disease (Harvell et al., 2007). Bleaching can also directly influence growth and reproduction of corals, as well is their tendency to succumb to a range of diseases (Harvell et al., 1999, 2007; Bruno and Selig, 2007; Baker et al., 2008). A reduction in reef-building corals raises the threat that a considerable proportion of the mega-diversity associated with coral reefs will face extirpation or, for some species, global extinction (Glynn, 2012). A meta-analysis of 17 independent studies, undertaken by Wilson et al. (2006), revealed that fish species reliant on live coral cover for food and shelter (some 62% of reef fish species) decreased in abundance within 3 years of disturbance events such bleaching, storms, and outbreaks of crown-of-thorns starfish that reduced coral cover by 10% or more.

The loss of calcifiers such as corals and calcareous algae due to warming and other stressors contributes to a reduced rate of community calcification, which is exacerbated by increases in dissolution and bioerosion as the water column becomes more acidified. Coral bleaching events driven by elevated temperatures has also been shown to shift carbonate budgets of coral reefs from net accretion to net erosion (DeCarlo et al., 2017; Januchowski-Hartley et al., 2017). Sixteen years later, a third of reefs that were considered ecologically recovering (Graham et al., 2015) did not show positive carbon budgets (Januchowski-Hartley et al., 2017). Reefs remaining in negative carbonate budgets were those where massive coral loss was high and recovery of branched corals was low. The composition of reef benthic communities, which are sensitive to thermal stress, have an influence on the sensitivity of coral reef ecosystems to ocean acidification (DeCarlo et al., 2017). In long-term studies done in mesocosms, carbonate balance of reefs tips toward overall dissolution under concentrations of CO_2 of more than 450 ppm (Dove et al., 2013), which matches similar conclusions from previous experimental work (Anthony et al., 2008; Wild et al., 2011; Andersson and Gledhill, 2013) and from the geographical distribution of coral reefs in relation to the aragonite saturation state of seawater (Kleypas et al., 1999b; Hoegh-Guldberg et al., 2007).

EVIDENCE FOR EVOLUTIONARY RESPONSES AND THE RELOCATION OF ECOSYSTEMS

The strong relationship between short periods of elevated sea temperature in mass coral bleaching and mortality within warm-water coral reefs has been used to project how communities of reef building corals might change as ocean temperatures increase as a result of anthropogenic climate change (Hoegh-Guldberg, 1999; Done et al., 2003; Donner et al., 2005; Frieler et al., 2012). Inherent to the conclusions of these studies, however, is the requirement that the thermal threshold of corals remain relatively constant over time. Evidence from the past 25 years, over which time satellite measurement programmes have used a simple algorithm based on sea surface temperature anomalies (relative to the average summer-time maxima 1985–1993) to predict when and where mass coral bleaching and mortality is likely to occur. This strongly suggests that little change has occurred in the sensitivity of reef building corals to thermal stress (Eakin C. et al., 2010; Strong et al., 2011; Hoegh-Guldberg, 2012). Nonetheless, it is important to consider potential evolutionary responses of reef-building corals over the next 100 years as well as the potential for coral reef ecosystems to relocate, as conditions change. Due to the dearth of information available about mesophotic and cold-water corals, this discussion will be restricted to the evidence for warm-water coral reefs.

Other than dying, corals have the option of acclimatizing, evolving or relocating as conditions within a region become sub-optimal (Hoegh-Guldberg, 2014a). Reef -building corals, like all organisms, can adjust their phenotype or acclimate to match local conditions to some extent (Gates and Edmunds, 1999; Middlebrook et al., 2010, 2012). However, there is little or no evidence that acclimatization has resulted in an upward shift in the thermal tolerance of reef-building corals (Eakin C. et al., 2010; Hoegh-Guldberg, 2012; Hoegh-Guldberg et al., 2014). Corals appear able to shift the relative ratio of different genetic clades or varieties of *Symbiodinium* within the one coral colony, which is correlated with tolerance to extreme temperatures (Rowan et al., 1997; Berkelmans and van Oppen, 2006; Jones et al., 2008). Further investigation of these putatively more tolerant varieties reveals a physiological trade-off in terms of reduced growth and competitiveness (Jones and Berkelmans, 2011).

A few studies (Glynn et al., 2001; Maynard et al., 2008a,b) have proposed that the thermal tolerance of reef building corals has increased over time, with less corals bleaching for similar amounts of thermal stress. The problem with these studies is several-fold (Hoegh-Guldberg, 2009). For example, the assessment of stress levels was restricted to temperature alone despite the fact that variation in parameters such as the light intensity (Hoegh-Guldberg, 1999; Mumby et al., 2001) and water flow rates over a reef (Nakamura and Van Woesik, 2001) can significantly modify the overall stress levels arising from elevated temperature at small scales (Hoegh-Guldberg, 2014a). As well, studies like that of Maynard et al. (2008a) investigated community level responses, and hence are unable to distinguish the loss of fragile species as opposed to the specific acclimatization and/or adaptation of individual species. Evidence for acclimatization in other reef organisms has exposed some intriguing possibilities, such as transgenerational acclimatization, where organisms inherit improved tolerances from parents that have been previously exposed to high levels of stress. For example, some coral reef fishes being exposed to higher CO_2 levels prior to producing the next generation (Donelson et al., 2012; Miller et al., 2012). Whether or not this mechanism operates within corals is unknown, although the very observation that the same satellite temperature threshold still works after more than 25 years is evidence that thresholds are not changing very rapidly. As observed by Donner et al. (2005), the required rate of adaptation needs to match the rate of increase in sea temperatures or ∼0.1–0.2°C per decade.

Genetic adaptation has also been suggested as a mechanism by which coral populations might be able to keep up with rapid changes in ocean temperature. Like all organisms, corals and their symbionts have adapted to local temperature conditions, a fact embodied by the fact that thresholds used by satellites for predicting mass coral bleaching and mortality are tied closely to local temperature conditions (Strong et al., 2011). Adapting to local conditions, however, has probably taken hundreds if not thousands of years and is slowed by the fact that reef building corals have generation times from 5 to over 100 years (Babcock, 1991). As a result, reef building corals do not have the population characteristics that would favor rates of evolution that would enable them to keep up with an environment that is changing faster than any time in the past 65 million years if not 300 million years (Hönisch et al., 2012). Several researchers have suggested that corals might "evolve" by swapping their symbionts for more thermally adapted varieties (Buddemeier and Fautin, 1993). Evidence of this, however, has not eventuated. These propositions also suffer from the problem that both the coral and the symbiont need to adapt to temperature change (Hoegh-Guldberg et al., 2002; Stat et al., 2006, 2009; Hoegh-Guldberg, 2012, 2014a). There are several observations of the shuffling of strains of *Symbiodinium* within the one host in response to warming (Rowan et al., 1997). These changes, however, are examples of acclimatization as opposed to genetic adaptation (Hoegh-Guldberg et al., 2002). In this regard, the advent of completely new symbiotic association between coral and a novel strain of *Symbiodinium*, hence a "new symbiotic genotype" has never been observed.

A third and final response by organisms facing rapidly changing conditions might be to relocate to new areas, which has been documented for a large number of marine plants and animals (Poloczanska et al., 2013, 2014). New records of several coral reef species have been reported at high latitude locations (Precht and Aronson, 2004; Yamano et al., 2011) which is consistent with the proposition that corals might shift to higher latitudes. There is also ample evidence that small increases in ocean temperature in the past have resulted in the appearance of coral reefs at slightly higher latitudes than where they are found today (Precht and Aronson, 2004; Greenstein and Pandolfi, 2008). While these reports are interesting, they are not sufficient to support the notion that whole coral reef ecosystems will shift successfully to higher latitudes as anthropogenic warming of the ocean continues which raises some important considerations. Firstly, how will ecosystem structure and function of coral reefs be affected if only a portion of species in the ecosystem shift, and which of these are the critical components for ecosystem services. Secondly, reduced light levels along with decreasing aragonite saturation are also critical factors in determining whether or not carbonate coral reef ecosystems will form successfully at higher latitudes. As recognized by Greenstein and Pandolfi (2008), other factors (e.g., available shallow water shelf habitats) are crucially important for determining whether or not coral reef ecosystems will be able to move to higher latitudes. Thirdly, analogies to past shifts are limited given that current changes on coral reefs today include a multitude of other pressures in addition to temperature (e.g., pollution, ocean acidification). And finally, shifts in the past occurred over long periods of time during which conditions were relatively stable as compared to the extremely rapid changes typical of today. Current changes in ocean temperature and acidity will continue for centuries, if not millennia, under the current greenhouse gas emission pathway, thereby severely limiting the ability of populations and adaptive processes to keep up with a rapidly changing climate (Hoegh-Guldberg, 2012).

GLOBAL CHANGE: PROJECTED RESPONSES TO RAPID OCEAN WARMING AND ACIDIFICATION

The close relationship between mass coral bleaching and mortality, and short periods of elevated sea temperature, provides an opportunity to explore how warm-water coral reefs are likely to be affected under different climate change scenarios (Hoegh-Guldberg, 1999). Using projections of sea surface temperature (SST), future temperatures could be compared to established thermal thresholds for corals, and the frequency and intensity of future mass coral bleaching and estimated mortality. This led to the conclusion, which was somewhat controversial at the time, that coral reefs would experience mass coral bleaching and mortality on a yearly basis as early as 2030–2040. With field observations concluding that recovery from disturbances such as mass coral bleaching and mortality takes at least 10–20 years, the predictions of yearly mass coral bleaching and mortality events suggest strongly that coral dominated ecosystems would be unable to cope, and would start to disappear around this time. Subsequent studies revealed that these conclusions are not far-fetched and matched the expectations of a thermal threshold of corals was relatively fixed, as it appears to be (Hoegh-Guldberg, 1999; Done et al., 2003; Donner et al., 2005; Eakin C. et al., 2010; Eakin C. M. et al., 2010; Frieler et al., 2012).

Hoegh-Guldberg et al. (2014) repeated the analysis of Hoegh-Guldberg (1999) using Coupled Model Intercomparison Project Phase 5 (CMIP5) data from an ensemble of 10–16 independent models. Historical and unforced temperature trends were compared with those from Representative Concentration Pathway (RCP) 2.6 (global temperature "about as likely as not" to exceed 1.5°C by 2100 relative to 1986–2005) and RCP 8.5 (global temperature "very likely" to exceed 3.0°C by 2100 relative to 1986–2005) in terms of model projections of the future for coral reef provinces. Model outputs were constrained to geographic areas (coral regions) known to contain warm-water coral reefs. The range in each case represents differences between models and model assumptions. Three things become apparent. First, the amount of SST warming that we have seen so far is very significant in each coral region given that average global temperature has warmed by 0.85°C over the period 1880–2012 (**Table 1**, **Figure 6**). Second, differences between the two RCP scenarios do not become evident until mid to late century (**Table 2**, **Figure 6**). Third, only conditions associated with the RCP 2.6 scenario stabilize, which is important if evolutionary processes are to be able to operate and re-establish coral reef ecosystems in these regions. In the context of the preceding discussion, this is the only scenario in which coral reefs have any chance of replenishing tropical coastal regions.

Hoegh-Guldberg et al. (2014) also looked at the annual incidence of bleaching and mortality events. The proportion of a coral grid cells with a reef province (**Figures 1B**, **7A**) that would have a particular stress level in any 1 year was calculated and the maximum for each decade then plotted. Two levels of stress were examined. The first being the amount of warming required to trigger mass bleaching, which is around one Degree Heating Months (DHM) (Strong et al., 2011) and is shown in **Figure 7B**. The second was the amount of heat stress required to trigger mass mortality events like those that occurred in the Maldives, Okinawa, North-West Australia and Palau in 1998, and is calculated as five Degree Heating Months Hoegh-Guldberg, 1999; **Figure 7C**). The conclusions from this analysis are very clear. Firstly, the risk of mass coral bleaching (DHM ≥ 1) increases steadily over the next few decades, affecting all regions of the Caribbean, Gulf of Mexico and eastern Pacific. By contrast, the Western Pacific Ocean, Coral Triangle, and Indian Ocean are likely to experience less stress and will still have large areas unaffected by annual mass coral bleaching by the end of the century. Secondly, conditions that drive mass mortality events today (DHM > 5) will spread across most regions by the end of the century under RCP 8.5. This risk decreases from RCP 8.5 to zero under RCP 2.6 with no regions experiencing annual conditions that would cause mass mortality event. Given the time that it takes for coral reefs to recover from mass mortality events (10–20 years), there is significant risk associated with high greenhouse gas emission scenarios given that the damage from these events, even in managed reef systems. Even 10% of grid cells being at risk of experiencing a mass mortality event would eventually add up to a very low number of unaffected areas by the end of century.

Considering cold-water coral ecosystems, at pre-industrial atmospheric CO_2 level, 9% of known cold-water coral ecosystems were in under-saturated water (Cao et al., 2014). Under emission scenario IS92a (atmospheric CO_2 concentration 713 ppm and temperature increase of about 2.4°C by 2100), an estimated 70% of cold-water corals could be in under-saturated water by the end of the century with some ecosystems experiencing under-saturation by 2020s (Guinotte et al., 2006; Turley et al., 2007). Even if mitigation efforts (e.g., through geoengineering) could reduce atmospheric CO_2 levels to pre-industrial by the end of the century, the lag in the recovery of deep ocean chemistry would result in longer-lasting threats to cold-water coral ecosystems (Cao et al., 2014).

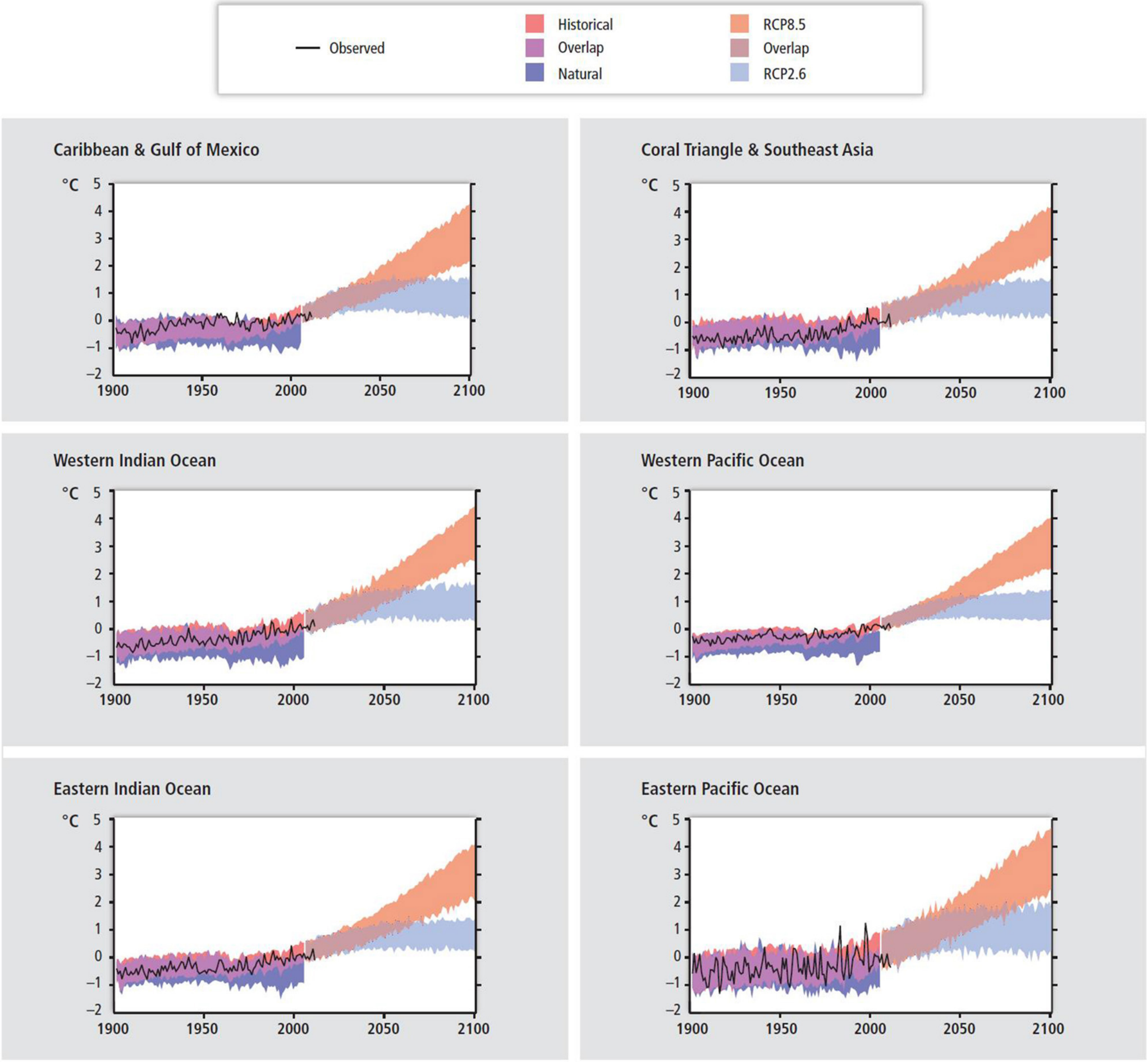

FIGURE 6 | Past and future sea surface temperatures (SST) in six major coral reef provinces and locations (Figure 1B) under historic, unforced (natural), and Representative Concentration Pathways (RCP)4.5 and 8.5 scenarios from Coupled Model Intercomparison Project Phase 5 (CMIP5) ensembles (see Table SM30-3 in Hoegh-Guldberg et al., 2014). Observed and simulated variation in past and projected annual SST over various sites where coral reefs are prominent ecosystems. The black line shows estimates from the Hadley Centre Interpolated sea surface temperature 1.1 (HADISST1.1) data set (Rayner et al., 2003) reconstructed historical SST dataset. Shading denotes the 5–95 percentile range of climate model simulations driven with "historical"changes in anthropogenic and natural drivers (62 simulations), historical changes in "natural" drivers only (25), the RCP4.5 emissions scenario (62), and the RCP8.5 (62). Data are anomalies from the 1986 to 2006 average of the HADISST1-1 data (for the HadISST1.q time series) or of the corresponding historical all-forcing simulations. Figure SM30-3 with the permission of IPCC AR5 (Hoegh-Guldberg et al., 2014).

LIVING WITH CHANGE: IMPLICATIONS FOR PEOPLE AND LIVELIHOODS

Overall, the evidence presented above confirms earlier work (Hoegh-Guldberg, 1999; Done et al., 2003; Donner et al., 2005; Frieler et al., 2012) and substantiates the serious concern regarding the vulnerability of carbonate coral reef systems to a rapidly changing world. Given the importance of coastal ecosystems such as warm-water coral reefs for hundreds of millions of humans (Burke et al., 2011; Hoegh-Guldberg, 2015), these changes are likely to have implications for people and livelihoods, as well as regional security in some instances. It is also clear that we must increase our understanding of the effects of warming and acidifying oceans on mesophotic and

TABLE 2 | Projected changes in sea surface temperature (SST °C) over the next 90 years for coral reef provinces (Figure 1B) from AOGCM model simulations from the Coupled Model Intercomparison Project Phase 5 (CMIP5, http://cmip-pcmdi.llnl.gov/cmip5/).

Coral reef province	Near-term (2010–2039)				Long-term (2010–2099)				RCP8.5 minus RCP4.5 (long-term)
	RCP2.6	RCP4.5	RCP6.0	RCP8.5	RCP2.6	RCP4.5	RCP6.0	RCP8.5	
Caribbean Sea/Gulf of Mexico	0.48	0.64	0.61	0.83	0.68	1.43	1.87	3.14	2.46
Coral Triangle and Southeast Asia	0.42	0.61	0.52	0.76	0.58	1.35	1.75	2.95	2.37
Indian Ocean (east)	0.32	0.56	0.46	0.67	0.37	1.18	1.59	2.76	2.40
Indian Ocean (west)	0.39	0.51	0.50	0.77	0.43	1.18	1.71	2.97	2.54
Pacific Ocean (east)	0.46	0.64	0.64	0.83	0.63	1.44	1.99	3.23	2.60
Pacific Ocean (west)	0.35	0.48	0.40	0.68	0.30	1.02	1.39	2.66	2.35

For each coral reef province, a linear regression was fitted to all 1 × 1 degree monthly SST data extracted from the models for each of three periods; 2010–2039, 2040–2069, and 2070–2099. Long-term change calculated by adding the average change of the three 30-year periods. This is a simplified method to account for slight non-linearity in SST change over the 90-year period. Full methods given in Table SM30-4 in Hoegh-Guldberg et al. (2014; reprinted with permission of the United Nations Intergovernmental Panel on Climate Change, IPCC AR5).

cold-water coral reefs. These coral reefs represent important stores of biodiversity as well as habitat for fish, many of which are commercially important. As the deep ocean warms, the aragonite saturation horizon shoals and dissolved oxygen declines, it will be important to understand how these ecosystems will be affected. It will also be important to get a better understanding of how environmental conditions differ in the case of mesophotic reefs and whether or not they have the potential to act as refugia for coral reef species from the greater environmental extremes of shallow regions (Bongaerts et al., 2010a, 2013, 2015).

With regard to cold-water corals, management interventions are likely to be limited to regulating or banning fishing and mineral extraction in the locality of reefs (Thresher et al., 2011). The highest priority for these sensitive ecosystems is to locate and protect sites that are likely to be refugia areas (Thresher et al., 2015).

The recent consensus of the Intergovernmental Panel on Climate Change (IPCC, 2014) identified a number of risks and vulnerabilities for coral reefs under rapid ocean warming and acidification, as well as exploring the ramifications and adaptation options (see Table 30.4 in Hoegh-Guldberg et al., 2014). Changes to the structure of ecosystems such as a loss of coral reefs, underpin a series of risks and vulnerabilities to fisheries production and consequently food and income security in tropical regions thus rates of unemployment and poverty. As coral reef ecosystems degrade or disappear, there is the risk that coastal fisheries production is reduced, decreasing food security and increasing unemployment. There is also a risk that the tourist appeal of tropical coastal assets may decrease as ecosystems take on less desirable states (i.e., from coral to seaweed domination), affecting the potential to attract tourist dollars. Reduced availability to food and income is likely to exacerbate coastal poverty in many equatorial countries. Strategies to reduce risks in both these cases involve strengthening integrated coastal zone management to reduce contributing stresses such as coastal pollution, overexploitation and physical damage to coastal resources.

As outlined by Poloczanska et al. (2013, 2014, 2016), marine species are already redistributing toward higher latitudes. This has the potential to reorganize ecosystems including commercial fish stocks, drive changes to the distribution, and abundance of predators and prey, as well as increasing the risks of invasive species taking hold in new locations and ecosystems. Changes to the distribution of fish species in coral reef regions are expected as oceans warm (Cheung et al., 2010; Pörtner et al., 2014; García Molinos et al., 2015). This has the potential to change national income in either direction, depending on location, as important fisheries stocks redistribute, increasing the likelihood of disputes over national ownership of fisheries resources (Robinson J. et al., 2010). In this regard, key management actions to reduce risks include increased international cooperation over key fisheries as well as developing a better understanding of the linkages between ocean productivity, recruitment and fisheries stock levels (Bell et al., 2011). International cooperation on measures which enable sustainable fishing of these valuable stocks that take into account the influence of climate change across international boundaries, are important adaptation measures that need to be implemented as soon as possible (Robinson J. et al., 2010). Changing ecosystem structures in a warming and acidifying ocean is also likely to increase the risk of disease such as ciguatera and harmful algal blooms, with ramifications for human health and well-being. Strategies in this case involve increased monitoring and education surrounding key risks, plus the development of alternative fisheries and income for periods in which disease incident increases (Bell et al., 2013).

CONCLUSION: THE KEY ROLE OF CLIMATE STABILIZATION AND NON-CLIMATE CHANGE FACTORS

A recurrent theme within this review is the fact that we are already seeing major and fundamental change occurring in the world's ocean in response to climate change and that the rate of change is largely outstripping the ability for coral reefs to adapt genetically or relocate. If greenhouse gas emissions are

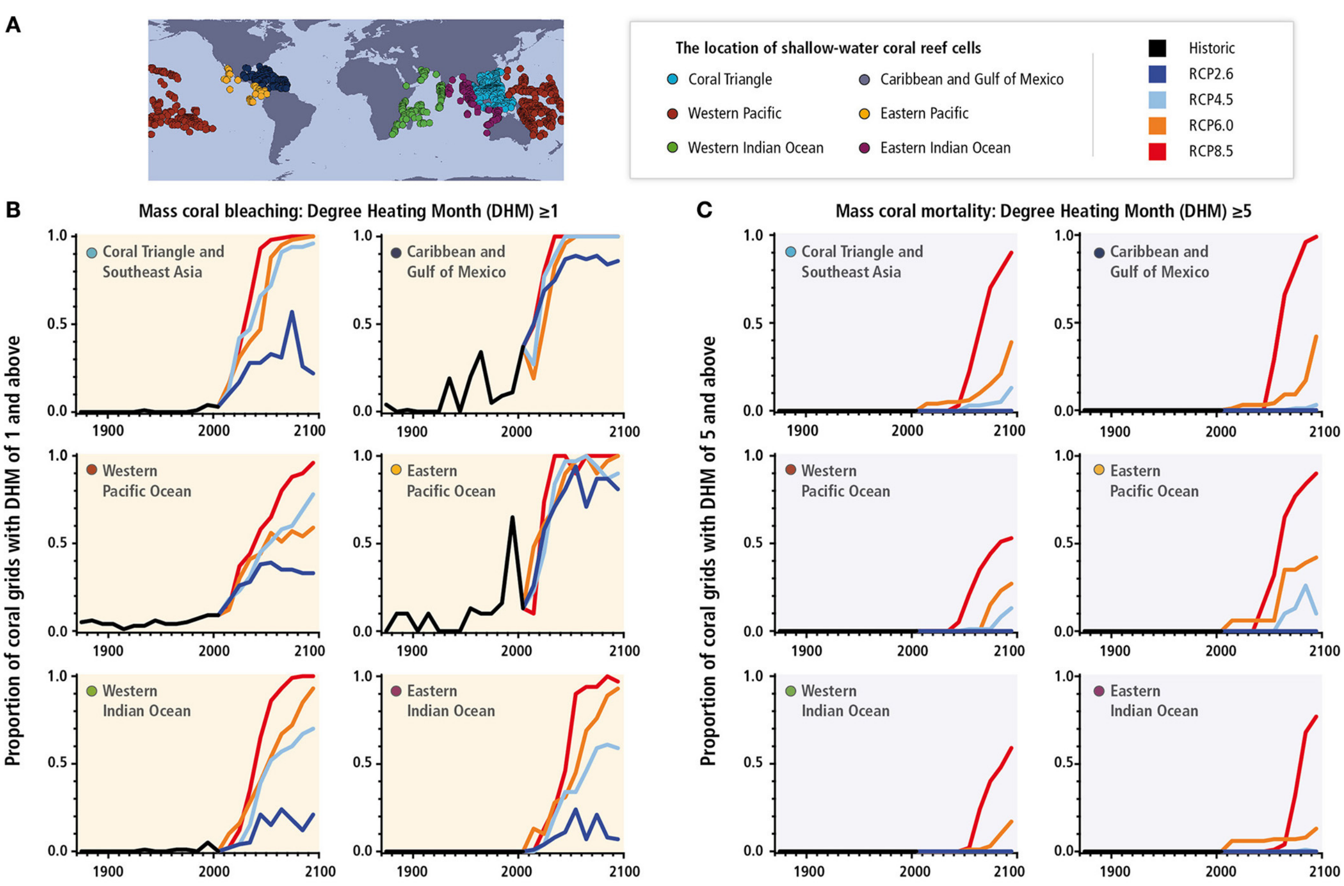

FIGURE 7 | Annual maximum proportions of reef pixels with Degree Heating Months (DHM, Donner et al., 2007) for each of the six coral regions (A). (B) DHM ≥1 (used for projecting the incidence of coral bleaching; Strong et al., 1997, 2011) and **(C)** DHM ≥5 (associated with bleaching followed by significant mortality; Eakin C. M. et al., 2010) for the period 1870–2009 using the Hadley Centre Interpolated sea surface temperature 1.1 (HadISST1.1) data set. The black line on each graph is the maximum annual area value for each decade over the period 1870–2009. This value is continued through 2010–2099 using Coupled Model Intercomparison Project Phase 5 (CMIP5) data and splits into the four Representative Concentration Pathways (RCP2.6, 4.5, 6.0, and 8.5). DHM were produced for each of the four RCPs using the ensembles of CMIP models. From these global maps of DHM, the annual percentage of grid cells with DHM ≥1 and DHM ≥5 were calculated for each coral region. These data were then grouped into decades from which the maximum annual proportions were derived. The plotted lines for 2010–2099 are the average of these maximum proportion values for each RCP. Monthly sea surface temperature anomalies were derived using a 1985–2000 maximum monthly mean climatology derived in the calculations for Figure 30-4 in Hoegh-Guldberg et al. (2014). This was done separately for HadISST1.1, the CMIP5 models, and each of the four RCPs, at each grid cell for every region. DHMs were then derived by adding up the monthly anomalies using a 4-month rolling sum. Figure SM30-3 presents past and future sea temperatures for the six major coral reef provinces under historic, un-forced (no anthropogenic forcing), RCP4.5 and RCP8.5 scenarios. Reprinted with permission of the PCC AR5, Figure 30-10 (Hoegh-Guldberg et al., 2014).

not mitigated, it is very clear that the ocean will be a vastly different place by the mid to late century (Gattuso et al., 2015). It is also clear that there are few or no adaptation strategies for humans to counter the risks of ocean warming and acidification at global scales. If they did exist, they would almost certainly be prohibitively expensive relative to the costs of developing solutions to the unprecedented rise of CO_2 in the earth's atmosphere.

This leaves us with two clear options with respect to preserving invaluable ecosystems such as coral reefs. The first is to stabilize planetary temperature and CO_2 concentrations as quickly as possible. Only then will biological responses such as acclimation and genetic adaptation have any chance of operating. The second is to dramatically reduce local stresses which are currently acting on coral reefs and which are reducing their resilience to climate change. By reducing these non-climate stresses, coral reefs will have the opportunity to develop greater robustness or resilience to the challenges of a changing planet. However, if this is not combined with stabilization of temperatures and acidification then it is likely to only temporarily put off the inevitable. If we do these two things, there is a chance that conditions will stabilize on planet earth by mid-to-late century, ensuring that some of the spectacular coral reef ecosystems will be able to flourish across the world's tropical regions.

AUTHOR CONTRIBUTIONS

OH led the project and wrote 50% of this manuscript. EP contributed to core concepts in the manuscript and contributed

30% of text. SD and WS contributed 15 and 5% respectively to the writing.

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Toward quantifying the response of the oceans' biological pump to climate change

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The biological pump makes a major global contribution to the sequestration of carbon-rich particles in the oceans' interior. This pump has many component parts from physics to ecology that together control its efficiency in exporting particles. Hence, the influence of climate change on the functioning and magnitude of the pump is likely to be complex and non-linear. Here, I employ a published 1-D coupled surface-subsurface Particulate Organic Carbon (POC) export flux model to systematically explore the potential influence of changing oceanic conditions on each of the pump's "moving parts," in both surface and subsurface waters. These simulations were run for typical high (High Nutrient Low Chlorophyll, HNLC) and low (Low Nutrient Low Chlorophyll, LNLC) latitude sites. Next, I couple pump components that have common drivers, such as temperature, to investigate more complex scenarios involving concurrent climate-change mediated alteration of multiple "moving parts" of the pump. Model simulations reveal that in the surface ocean, changes to algal community structure (i.e., a shift toward small cells) has the greatest individual influence (decreased flux) on downward POC flux in the coming decades. In subsurface waters, a shift in zooplankton community structure has the greatest single effect on POC flux (decreased) in a future ocean. More complex treatments, in which up to 10 individual factors (across both surface and subsurface processes) were concurrently altered, ∼ halved the POC flux at both high and low latitudes. In general climate-mediated changes to surface ocean processes had a greater effect on the magnitude of POC flux than alteration of subsurface processes, some of which negated one another. This relatively simple 1-D model provides initial insights into the most influential processes that may alter the future performance of this pump, and more importantly reveals many knowledge gaps that require urgent attention before we can accurately quantify future changes to the biological pump.

Keywords: POC export, biological pump, climate change, ocean microbes, zooplankton

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Introduction

Two ocean pumps play key roles in removing carbon from the surface ocean—the solubility pump is physico-chemically mediated whereas the biological pump is driven primarily by the interactions of marine biota from microbes to metazoa (Volk and Hoffert, 1985). In brief, in the euphotic zone (Ez) photosynthetic carbon fixation by autotrophs, and heterotrophic bacterial production, inputs POC (and dissolved organic carbon which is not considered in the present study) to the biological pump. This POC supply to the upper ocean is subsequently modified and attenuated by a wide range of grazing activities which transform most of the phytoplankton and bacterial carbon into heterogeneous particles which eventually settle out of the surface ocean after a residence time of days to weeks (Boyd and Stevens, 2002). Further transformations of these settling particles, by heterotrophic bacteria and grazers, further diminish this POC flux in subsurface waters (Steinberg et al., 2008). Despite, many processes attenuating this sinking particle flux, a small but significant (a few percent of the surface signature) proportion of this carbon supply will be sequestered into the deep ocean (Boyd and Trull, 2007).

Modeling studies have projected that an ocean without a biological pump would result in atmospheric CO_2 levels ~400 pmm higher than present day (Ito and Follows, 2005) and changes in the efficiency of the biological pump (driven by enhanced iron supply) are thought to explain up to a third of the ~80 ppm decreases in atmospheric CO_2 during the glacial terminations (Sigman and Boyle, 2000). More recent modeling studies investigating the implications of future changes to characteristics of the biological pump, such as particle remineralization length scales (Kwon et al., 2009) or Particulate Inorganic Carbon (PIC) (Roth et al., 2014), point to its potential influence as a significant feedback on a changing climate. For example—a 30 ppm change in atmospheric CO_2 is projected to result from climate-change mediated modification to particle remineralization length scales in the upper ocean (Kwon et al., 2009). Hence an increasing number of studies have focused on individual processes that will influence how the sign and magnitude of the pump is likely to change in a future ocean (Boyd and Trull, 2007; Riebesell et al., 2009; Passow and Carlson, 2012).

Investigations into the nature and performance of the future biological pump have ranged from modeling (Bopp et al., 2001, 2013; Taucher and Oschlies, 2011) to lab culture (Taucher et al., 2015) and field based mesocosm enclosures (Riebesell et al., 2007). Studies such as Bopp et al. (2013) have used global climate change biogeochemical models to capture the combined effects of climate-change mediated alteration of ocean circulation, properties such as temperature, pH and nutrient supply, and Net Primary Production (NPP) on the downward flux of POC. Other investigations, for example lab- and field-based experiments have targeted how aspects of climate-change (warming/ocean acidification, OA) will modify particular processes that influence the biological pump such as TEP (Transparent Exopolymer Particle) production (Taucher et al., 2015) or diurnal vertical migration (Berge et al., 2014). Pörtner et al. (2014) in the Working Group 2 Fifth Assessment Report of the Intergovernmental Panel on Climate Change attempted to synthesize the findings of the growing number of studies into the sensitivity of the component parts of the biological pump to climate change. They concluded that due to the many "moving parts" it was not possible state with confidence how the sign or magnitude of the pump would alter in the coming decades. Instead they put forward a first assessment of the integrated knowledge platform (see Table 6.1, Pörtner et al., 2014) required to project how the biological pump will function in a future ocean.

Passow and Carlson (2012) published a review of the status of our understanding of the biological pump—as a prerequisite to predicting how it will be altered under changing oceanic conditions. They used the study of Lomas et al. (2010) at BATS (Bermuda Atlantic Time Series) to illustrate the dangers of extrapolating results solely from investigations into the individual components of the pump. The Lomas et al. (2010) analysis demonstrates a zero sum outcome, over a decade at BATS, between alteration of upper ocean processes (NPP and downward POC export) vs. those in subsurface waters (mesopelagical attenuation of export flux). Thus, a holistic approach to assessing how the biological pump will be environmentally altered, in both the surface and the subsurface ocean, is essential if we are to begin to quantify how the functioning and magnitude of the pump will be transformed in the coming decades.

The present study has dual aims: to assess our current ability to quantify the response of the biological pump to complex and concurrent changes to oceanic conditions, and to refine the integrated knowledge platform needed to assess the performance of a future pump, presented by Pörtner et al. (2014). In this study, I employ a previously published 1-D coupled surface-subsurface biological model (Buesseler and Boyd, 2009) to explore the sensitivity of the downward POC flux to projected changes in a wide range of individual surface and subsurface processes. These range from physical (altered seawater viscosity) to ecological (differential vulnerability of organisms across trophic levels to changing oceanic conditions) processes. In addition to exploring the future role of the individual components of the biological pump, I also attempt to link the components that are controlled primarily by specific aspects of a changing climate, such as warming or OA, to explore the cumulative effects of these processes on downward POC export flux in a future ocean.

Methods

Rationale for the Employment of a 1-D Model

A wide range of models have been used to explore the functioning of the biological pump from conceptual (Michaels and Silver, 1988), to biological (i.e., Phytoplankton, Zooplankton, Detritus, Nutrient (PZDN), Taucher and Oschlies, 2011) to coupled ocean-atmosphere (Bopp et al., 2001; Kwon et al., 2009). Each different modeling approach has pros and cons (see later). Here, I selected a 1-D coupled surface-subsurface model that has previously been used to assess the relative roles of surface ocean processes [i.e., within the Euphotic zone (Ez)] vs. those in the subsurface mesopelagic (base of the Ez to ~300 m below this depth) across a wide range of oceanic provinces from tropical to polar (Buesseler and Boyd, 2009). Furthermore the model outputs from Buesseler and Boyd (2009), when compared with internally-consistent downward POC flux datasets (i.e., all based on the same techniques and measured by a sole laboratory) for each province, were successfully validated across the global ocean. My choice of this 1-D approach was based on its utility to explore the potential role of each of the many individual components of the biological pump.

The Coupled Surface-subsurface Model

There are benefits and drawbacks to using a 1-D approach. In this case the versatility of the model to represent, either directly or indirectly, each of more than 10 individual components of the biological pump (each shown to be sensitive to changing oceanic conditions) outweighs its inability to explore the “2D” space vs. time seasonality (*sensu* Lampitt and Antia, 1997), or the “3D animation” of the biological pump by ocean circulation (Kwon et al., 2009; Bopp et al., 2013).

The model structure is summarized in **Figure 1** which presents the flow pathways through the foodweb. The input to the model is a prescribed rate of Ez-integrated NPP (mg C m^{-2} d^{-1}), partitioned across different phytoplankton size categories, derived from published values for a particular region or season (e.g., Boyd et al., 2008). A further source of POC that is inputted into the model is Ez-integrated heterotrophic bacterial production (BP). The NPP and BP then flow through a pelagic foodweb typical of the surface ocean (**Figure 1**). The flows of POC follow size-based rules based on grazing constraints (such as maximum or minimum prey size), and are detailed in Buesseler and Boyd (2009). In addition to cell size, other phytoplankton traits (see Litchman and Klausmeier, 2008) that influence particle export include cell shape and coloniality. Both these traits are included implicitly in the direct sinking of a proportion of large phytoplankton (Jackson, 1990). **Table 1** summarizes the trophic transfer efficiencies that are applied to **Figure 2** to illustrate the attenuation of POC within the Ez and the subsequent POC flux to depth. As the NPP, within a phytoplankton size class, is consumed by grazers, the POC is attenuated based on published transfer efficiencies—for example 30% of the NPP grazed by ciliates is transferred to the next trophic level in the foodweb (**Figure 2**). All transfer efficiencies were derived from lab-based feeding experiments, the findings of which were synthesized by Straile (1997).

Published observations dictate that there are two major pathways for NPP to exit the surface mixed layer as sinking particles—as directly sinking aggregates of large phytoplankton (Jackson, 1990) and mesozooplankton fecal pellets (Lampitt et al., 1993). In the model, this simplification of the many pathways for particles to exit the surface ocean means that other vectors for particle export, such as marine snow as a carrier of small cells (Richardson and Jackson, 2007; Passow and Carlson, 2012), are not included. Moreover, only downward POC export, and not DOC vertical export (which is often seasonally-driven, Carlson et al., 2010) is considered in this model. Note, that as the model currency is POC, it cannot take climate-change mediated changes in downward PIC flux into consideration (Armstrong et al., 2001; Hofmann and Schellnhuber, 2009).

The POC exported out of the surface mixed layer is then inputted into the subsurface mesopelagic water column where it is further attenuated by three processes (**Figures 1**, **2**). These activities either act continuously (POC solubilization by microbes attached to sinking particles, Hoppe et al., 1993; Arístegui et al., 2005), or discretely (POC transformations by mesozooplankton grazing and residing within this stratum, Dagg, 1993) as reported by Steinberg et al. (2008). A further pathway for sinking POC in the subsurface ocean is via zooplankton diurnal vertical migration (DVM, Hays, 1996), which is represented in the model as a discrete vertical shunt of POC to depth without either microbial solubilization or zooplankton particle interception and transformation. Details of the attenuation of POC flux with depth by each of these subsurface activities are summarized in **Figure 2**, **Table 1B**.

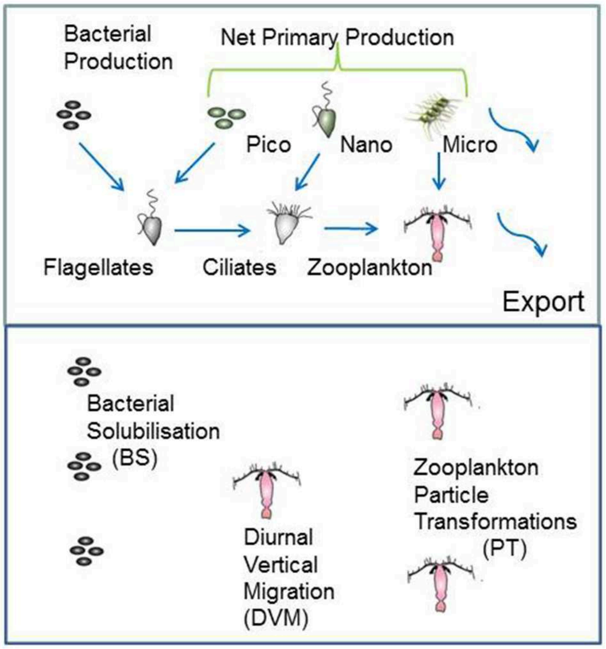

FIGURE 1 | Schematic of the coupled surface-subsurface model. The **upper panel** represents the euphotic zone (Ez) and the input of column-integrated net primary (NPP) and heterotrophic bacterial production (BP) to fuel downward POC export flux. NPP is partitioned between pico-, nano-, and micro-phytoplankton. Blue arrows show the grazing pathways the BP and NPP are routed through. Curved arrows denote the two pathways for POC to be exported from the Ez, direct sinking of a proportion of micro-phytoplankton NPP, and of mesozooplankton fecal pellets. For simplicity, pathways, such as bacterivory by ciliates (see Bernard and Rassoulzadegan, 1990) are not included. The **lower panel** denotes subsurface waters from the base of the Ez to 500 m depth, where attached microbes continuously solubilise POC, vertical migrators daily shunt POC to depth, and mesozooplankton transform particles via grazing.

High vs. Low Latitude Biological Pumps

Many other modeling studies compare and contrast how climate change will alter rates such as NPP or downward POC flux in high vs. low latitude oceanic regions (e.g., Bopp et al., 2001, 2013). In the present study I have also attempted such a comparison, and have used published datasets on NPP, depth of the Ez, and on the foodweb structures that characterize the low (LNLC) vs. high (HNLC) latitude oceans (**Table 2**) in the model standard runs. The high latitude standard run is presented in **Figure 2**. These runs are then compared with additional simulations that highlight the relative influence of each of the individual components of the biological pump in high vs. low latitude waters.

TABLE 1 | (A) Trophic transfer efficiencies through the pelagic foodweb in the surface ocean as represented by the upper panel in Figures 1, 2, and used in the control run. (B) Particle transformations in the subsurface ocean used in the control run and presented in Figure 2.

(A) Phytoplankton / microbial group	Grazer	Trophic transfer efficiency	References
Heterotrophic Bacteria	Heterotrophic flagellates	0.4	Michaels and Silver, 1988
Picophytoplankton	Heterotrophic flagellates	0.4	Michaels and Silver, 1988
Nanophytoplankton	Ciliates	0.3	Michaels and Silver, 1988; Straile, 1997
Microphytoplankton	Mesozooplankton	0.3	Michaels and Silver, 1988; Straile, 1997
Heterotrophic flagellates	Ciliates	0.3	Michaels and Silver, 1988; Straile, 1997
Ciliates	Mesozooplankton	0.3	Michaels and Silver, 1988; Straile, 1997
Microphytoplankton	Direct sinking	1.0	After Jackson, 1990
(B) Particle transformation	**Organisms**	**Alteration of POC flux**	**References**
Microbial solubilization	Particle-attached heterotrophic bacteria	0.2% m^{-1}	Buesseler and Boyd, 2009
Zooplankton shunt	Diurnal vertical migrators	One shunt of 20 mg C to 100 m below the Ez	Buesseler and Boyd, 2009
Mesozooplankton grazing	Specialist particle intercepting zooplankton (Dagg, 1993; Paffenhöfer, 2006)	one grazing event (0.4 transfer efficiency) every 100 m the particle settles below the Ez	Buesseler and Boyd, 2009

Projected Future Changes to the Oceans Biological Pump

A wide range of studies, from lab experiments (Taucher et al., 2015), mesocosm enclosures (Isla et al., 2008), synthesis of observations (Rose and Caron, 2007) to modeling experiments (Bopp et al., 2013) provide insights into how the multi-faceted components of the biological pump are projected to be altered in the coming decades. A synthesis of the individual components reported to both influence the performance of the biological pump, and which are sensitive to changing ocean conditions, is presented in **Table 3**. They include those cataloged by Pörtner et al. (2014) along with additional factors—such as seawater viscosity and its influence on particle sinking rates (Taucher et al., 2014) and the joint influence of warming/acidification on bacterial solubilization of particles (Piontek et al., 2015)—from recent research. **Table 3** lists the putative controlling environmental factor, such as warming, on each individual component that influences the biological pump, and the reported modification (where available) of each individual factor by changing ocean conditions for both surface and subsurface waters.

Representation of Climate Change Effects on the Biological Pump in the 1D model

The synthesis of climate change effects on component of the biological pump in **Table 3** is used to constrain the changes to individual components of the model to represent the biological pump in a future ocean (**Figure 3**). In some cases, such as future projections of NPP (Bopp et al., 2013) it was relatively straightforward to alter the 1-D model run (i.e., 10% more NPP at high latitudes, 10% less NPP at low latitudes) to reflect the future projected changes. For other pump components, such as changes to bacterial enzyme activity, I employed an intermediate value of a 10% increase (see **Table 3**). In other cases, such as climate-change mediated shifts in phytoplankton community structure, there are many different regional examples, driven by wide-ranging aspects of changing ocean conditions, such as warming, freshening, wind speed, nutrient supply, or OA (**Table 4**). Each of these floristic shifts can have different potential effects on the sign and magnitude of change to the biological pump, such that I have only considered illustrative examples in the model runs.

For other components of the pump, where the sign of the change is known, but not the magnitude—such as for the differential sensitivity of grazers vs. phytoplankton to warming, I applied arbitrary changes to the model in an attempt to represent these changes. For example, in the case of reports of the growth rate of microzooplankton responding more to warming than that of their prey (small phytoplankton) (Rose and Caron, 2007), the trophic transfer efficiency has been decreased to mimic a shift in the relationship between increased grazing pressure relative to phytoplankton growth rate (which is a complex coupling, see Apple et al., 2011) in this climate change scenario. In other studies, such as for mesozooplankton under warming scenarios (Isla et al., 2008), a wide range of responses—increased fecal pellet and egg production rates have to be reconciled against elevated mortality rates and reduced net growth efficiency (**Table 3A**). The cumulative outcome of such responses to a changing climate was problematic to represent simply in the model runs.

Table 5 summarizes how each of the individual components are represented in the model runs, which are each largely based on the trends from the literature collated in **Table 3**. In cases where the changes to the biological pump are not well constrained by published studies, or where I have employed an indirect representation of an individual process, I have used

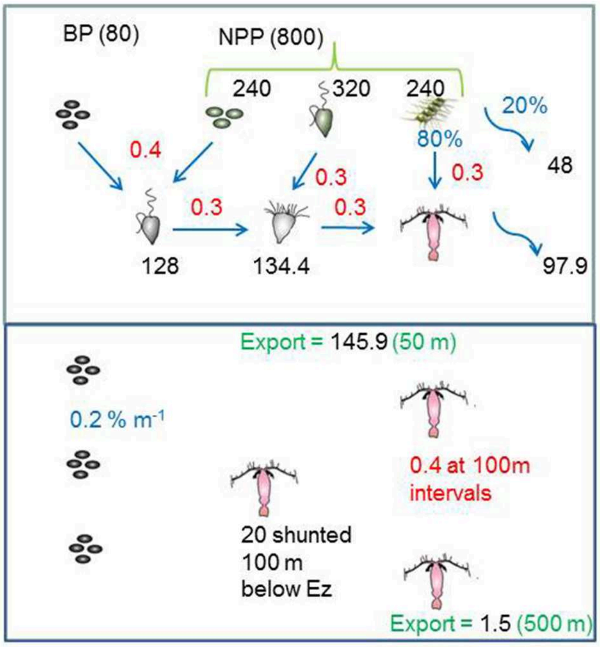

FIGURE 2 | The model standard run for the high latitude ocean case, that illustrates how the inputted POC in the Ez is transformed by trophic transfers (using published data from Table 1). In the subsurface ocean the export flux is further attenuated by continuous (microbes) and discrete (zooplankton) transformations, and supplemented by a shunt of POC to one discrete depth from vertical migrators. Black text denotes fluxes (mg C m^{-2} d^{-1}), red are trophic transfer efficiencies (proportion of 1), and blue represents (%) such as the partitioning of micro-phytoplankton NPP between grazing and direct sinking.

rudimentary sensitivity analysis to explore the effect of such uncertainties. Furthermore, in the concluding section of the Results, I have attempted to link the individual components that influence the performance of the biological pump to explore their cumulative effect on the pump in a future ocean. This linkage has focussed upon using comparable climate-change mediated forcing—such as warming or acidification—to move toward a joint outcome due to specific environmental forcing (see later). It has been problematic to cross-link the potential interactive effects of forcing by multiple environmental properties, the limits on which are presented in the Discussion.

Results

Influence of Alteration of Individual Factors Controlling Downward POC Flux

Simulations from the 1-D model are presented as vertical plots of downward POC flux vs. depth (presented for the base of the Ez, 150, 300, and 500 m), expressed as a systematic alteration of each of the climate-change mediated factors influencing POC export (**Tables 3, 5**), relative to the control, for the Ez (e.g., **Figure 4A**) and the subsurface Twilight Zone (e.g., **Figure 4B**). For the high latitude simulations, the export flux from the base of the 50 m deep Ez ranged from 109 mg C m^{-2} d^{-1} (shift to small phytoplankton cells) to ~160 mg C m^{-2} d^{-1} (higher NPP) relative to the control run (146 mg C m^{-2} d^{-1}, **Figure 4A**). As expected, the other runs (more photosynthate from NPP to BP; reduced energy transfer during grazing transformations) each resulted in 5–10% decreases in export flux at the base of the Ez. The amplitude of POC flux, across the range of model runs, was greatest at 50 m depth (base of the Ez in high latitude waters), and the span of these simulated POC fluxes declined with depth as the subsurface processes (each based on the standard run, **Figure 2**) further modified the sinking particles in the model (**Figure 4A**).

The model runs for each of the altered subsurface processes for the high latitude case also resulted in a wide range of POC fluxes [41 to ~59 (control, 55 mg C m^{-2} d^{-1})] at 150 m depth (**Figure 4B**). Increased exo-enzyme activity or a decrease in the transfer efficiency of energy after zooplankton-mediated particle transformations both reduced POC fluxes, whereas reduced viscosity (faster sinking particles), de-oxygenation (less microbial activity), or a larger DVM shunt led to higher POC fluxes at 150 m. These trends were also evident at 300 m depth, although with less spread across the range of model runs, but were almost undetectable by 500 m depth, due to the pivotal role in the model of zooplankton-mediated particle transformations removing 60% of the downward flux for every 100 m that the particles sink (Buesseler and Boyd, 2009).

At the low latitude site, the deeper Ez of 130 m (**Table 2**) led to a different vertical POC flux profile than in **Figure 4A**, with a flux of ~61 mg C m^{-2} d^{-1} for the control run as particle settled out of the zone of *de novo* particle production (**Figure 5A**). The trends for each of the model runs (for systematic alteration of upper ocean processes that each alters POC flux) were as for the high latitude case in **Figure 4A**. The range of POC fluxes at the base of the Ez (across the different model simulations) was 44 (altered size-partitioning of NPP) to 61 (control) mg C m^{-2} d^{-1}. As observed for the high latitude case, the spread of the POC fluxes across the various model runs decreased with depth as subsurface processes (all from the low latitude standard run, **Table 2**) further attenuated the POC flux to 500 m depth in the model simulations.

The trends in the downward POC flux from 150 to 300 m for the low latitude case differed slightly—due to the region-specific model parameterizations (**Table 2**)—than those for the high latitude simulation (**Figure 5B** c.f. **Figure 4B**). Specifically, the spread of POC export fluxes, across the range of simulations in which individual subsurface processes were modified, was greatest at 300 m (in contrast to the high latitude site where the amplitude of POC fluxes, across all simulations, was maximal at 150 m depth) due to several factors. First, the 150 m discrete depth selected for the model simulation—only 20 m deeper than the depth of the Ez at the low latitude site. Second, the DVM shunt and the first zooplankton-mediated particle transformation took place at a greater depth than in the high latitude simulation (**Table 2**).

In the low latitude simulations, the alteration of each subsurface process that influences POC export flux resulted in a different suite of trends, relative to the control, than was evident for the high latitude simulation (**Figure 5B** c.f. **Figure 4B**). Although the alteration of energy transfer during

TABLE 2 | Details of the standard runs for the representative cases for the high (HNLC subpolar waters, Boyd and Harrison, 1999; Boyd et al., 2008) vs. low (LNLC subtropical waters, Karl et al., 2008; Boyd et al., 2008) latitude ocean.

Property	High latitude case	References	Low latitude case	References
NPP (mg C m^{-2} d^{-1})	800	Boyd and Harrison, 1999	600	Karl et al., 2008
BP(mg C m^{-2} d^{-1})	80	Boyd et al., 2008	60	Boyd et al., 2008
Size partitioning (pico:nano:micro)	0.3:0.4:0.3	Boyd and Harrison, 1999	0.5:0.4:0.1	Boyd et al., 2008
Depth of Ez (m)	50	Buesseler and Boyd, 2009	130	Buesseler and Boyd, 2009
Foodweb structure (microzoo)	HNAN, CIL	Boyd et al., 2008	HNAN, CIL	Boyd et al., 2008
Mesozoo	Copepods	Boyd et al., 2008	Copepods	Boyd et al., 2008
Algal export	20% of microphytoplankton NPP	Buesseler and Boyd, 2009	20% of microphytoplankton NPP	Buesseler and Boyd, 2009
DVM shunt of POC	50 to 150 m	Buesseler and Boyd, 2009	130 m to 230 m	Buesseler and Boyd, 2009
PT length scale	100 m commencing from Ez	Buesseler and Boyd, 2009	100 m commencing from Ez	Buesseler and Boyd, 2009

The standard runs are each based on those presented in Table 4 of Buesseler and Boyd (2009) but do not directly correspond to them; in the present study the model simulations were not altered further to utilize site-specific observations, for example on particular feeding behavior of resident zooplankton (such as Ocean Station Papa, NE Pacific) that alters the particle transformation length scale.

TABLE 3 | Summary of projected climate-change mediated alteration of components of the biological pump for (A) surface and (B) subsurface waters.

Pump component	Oceanic driver	Projected change	References
(A)			
Phytoplankton growth	Temperature (warming)	~10% faster (nutrient-replete) no change (nutrient-deplete)	Boyd et al., 2013 E; Marañón et al., 2014 O$^{\&}$
Net Primary production	Climate change (temperature, nutrients, CO_2)	10–20% decrease (low latitudes); 10–20% increase (high latitudes)	Bopp et al., 2013 M
Partitioning of NPP (POC, TEP, DOC)	OA	~20% increase in TEP production	Engel, 2002; Engel et al., 2014 E; Riebesell et al., 2007 E; Seebah et al., 2014 E;
Floristic shifts	Climate change (warming/OA/Iron/Salinity	Shift to smaller cells (*less export*)	Morán et al., 2010 O; Li et al., 2009 O
Differential susceptibility	Temperature (warming)	Growth-rate of grazers more temperature dependent than prey (*less export*)	Rose and Caron, 2007 O;
Grazer physiological responses	Warming	Copepods had faster respiration and ingestion rates, but higher mortality (*inconclusive*)	Isla et al., 2008
Faunistic shifts	Temperate and subpolar zooplankton species shifts	Temperature (*inconclusive*)	Edwards et al., 2013
(B)			
Bacterial hydrolytic enzyme activity	Temperature	20% increase (resource-replete) to no change (resource-deplete)	Wohlers-Zöllner et al., 2011 E; Endres et al., 2014 E; Bendtsen et al., 2015 E; Piontek et al., 2015 E*
Particle sinking rates (viscosity)	Warming	5% faster sinking/degree C warming	Taucher et al., 2014 M
Mesozooplankton community composition	Temperature?	Shifts which increase/decrease Particle transformations (*less/more export, respectively*)	Jackson and Burd, 2002 M; Ikeda et al., 2001 O
Vertical migrators	Climate change (irradiance, temperature)	(*more export*)	Almén et al., 2014 O; Berge et al., 2014 O
Deoxygenation	Climate change	(*more export*)	Dunne, 2010 M; Cocco et al., 2014 O; Hofmann and Schellnhuber, 2009 M

*Environmental controls on individual factors that influence downward POC flux are based on published reports from experiments (denoted by E), modeling simulations (M), and observations (O). In some cases, due to the paucity, and regional specificity, of published reports I have indicated the sign of the projected change on export (in italics), as opposed to the magnitude. DOC is Dissolved Organic Carbon. Climate change denotes multiple controls such as nutrients, temperature and irradiance, as parameterised in coupled ocean atmosphere models. $^{\&}$Denotes observed for low latitudes only. ? Represents major uncertainty over environmental modulation of this component of the biological pump. *Denotes joint influence of temperature and acidification.*

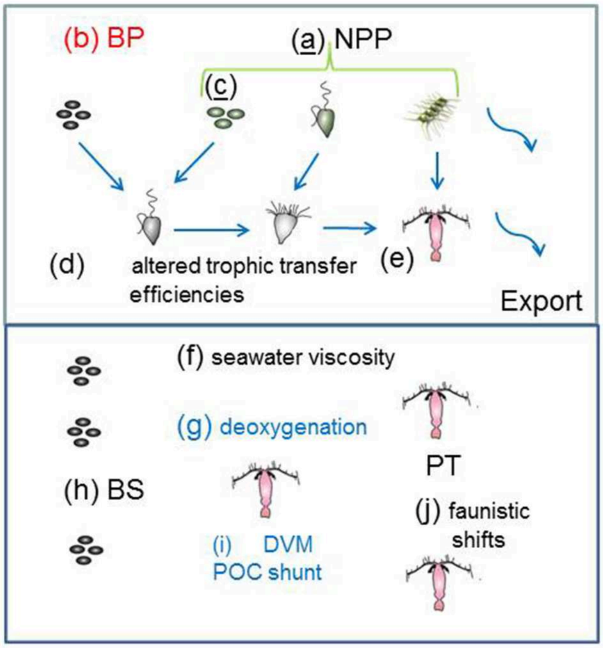

FIGURE 3 | Catalog of the climate-change model runs for the individual processes that influence the biological pump in both the surface and subsurface ocean. The schematic is as for **Figure 1** with the exception of the letters (a) to (j) which denote changes to: (a) NPP; (b) BP; (c) phytoplankton community structure; (d) and (e) efficiency of trophic transfer of POC In the subsurface ocean (f) to (j) represent alteration of: (f) seawater viscosity; (g) deoxygenation; (h) microbial solubilization; (i) vertical migration; and (j) mesozooplankton trophic transfer efficiency. Colored letters denote processes mediated by: temperature (black); OA (red); "climate change"(blue); and those underlined have more than one form of mediation—e.g., model run (c) is influenced by temperature, CO_2, salinity and/or iron supply (see **Table 4**).

zooplankton-mediated particle transformations led to the largest departure (faunistics, lowest POC flux) from the control run at 300 m depth at both the low and high latitude sites, the influence of other processes, such as DVM differed. The altered DVM run resulted in a flux that was higher than the control (at 300 m depth) at the low latitude site (**Figure 5B**) whereas the DVM simulation in **Figure 4B** was very similar to the control POC flux. As for the high latitude simulation, the spread of POC fluxes across these various subsurface simulations had declined by 500 m depth, again due to the dominant role of zooplankton-mediated particle transformations in attenuating the particle flux.

Cumulative Effects of Concurrent Alteration of Factors Controlling POC Flux

Many of the trends in **Figures 4**, **5**, such as the effect of increasing or decreasing NPP or decreasing the efficiency of energy transfer during zooplankton-mediated particle transformations in subsurface waters, were as anticipated. The outcome of next suite of model simulations was less readily predicted as they explored the cumulative effect on downward POC flux when multiple individual factors, representing both climate-change mediated surface and subsurface processes, are altered concurrently. The selection of which individual processes to combine in these model runs was based on published reports of the environmental forcing (see **Tables 3**, **6**) responsible for the observed changes in each individual process that alters the performance of the biological pump. This collation resulted in four categories—the individual effect of warming; the sole impact of Ocean Acidification (OA); the combined effect of multiple factors (including irradiance, nutrients, temperature evident from climate change models such as Bopp et al., 2013—termed here as "climate change"); and the cumulative effects of all the above factors (termed "All"). In addition, in several cases where the sign of the change in POC flux, due to alteration of an individual process such as alteration of energy transfer during grazing associated with faunistic shifts, is poorly constrained I also added runs where the sign of this process varied (see **Table 5**). These sensitivity analysis runs were termed A (i.e., less particle attenuation than the control or B and labeled on **Figures 6**, **7**).

The OA-mediated changes to export flux was the simplest of these simulations [with only altered photosynthate reported as a direct OA effect (**Table 6**, but see Piontek et al., 2015 in **Table 3B**), whereas for temperature seven individual factors (four associated with surface processes, and three with subsurface processes) were altered concurrently, **Table 6**]. The outcome of the cumulative effect of altering these processes, in different permutations, was an almost twofold range of POC fluxes exiting the base of the 50 m Ez at the high latitude site (**Figure 6A**). Most of these simulations resulted in lower POC fluxes, relative to the control, at 50 m depth, with the "climate change" run being the exception. In the simplest case—that of OA, there was little departure from the control, but increasing deviations (and lower POC fluxes) were evident for the temperature-mediated treatment and the largest reduction in the POC flux was for the "All A" treatment. Despite the inclusion of several subsurface processes in simulations such as "temperature," or "All," the trends in downward POC flux did not alter significantly with depth, but the amplitude of the POC fluxes, across the range of runs, did decline with depth—as was evident from **Figures 4**, **5**. However, at 150 m depth a substantial separation (1.5 fold) of the simulated POC fluxes, resulting from each of the treatments was evident, and the "climate change" and "all temps A" runs exhibited clear separation from the control at 300 m depth (**Figure 6B**).

Inter-comparison of the cumulative effects of different environmental controls on the downward POC flux in the low latitude case also revealed a wide range of export fluxes (> 2 fold) at the depth of the Ez (130 m) (**Figure 7A**). As for the high latitude case, the largest departures from the control run were driven by some of the more complex treatments ("all temps A" and "All A") in which six or more individual processes, straddling surface, and subsurface strata, were altered concurrently. The separation of the treatments, in terms of the magnitude of POC flux, at 150 m depth was similar to that at the base of the Ez (130 m), which was not surprising given that a 20 m vertical horizon separated these discrete depths in the simulations. However, between 150 and 300 m depth there was some "crossover" of the vertical profiles of POC flux—for "All A" and "all temps B" treatments, that was not evident at the high

TABLE 4 | Illustrative examples of the wide range of effects on the biological pump due to floristic shifts (see also Review by Boyd et al., 2010).

Shift	Region/province	Influence on the pump (driver)	References
More picocyanobacteria	Subtropical Atlantic Ocean	Shift to smaller phytoplankton cells (Temperature)	Morán et al., 2010
More picocyanobacteria	Arctic Ocean	Shift to smaller phytoplankton cells (Salinity)	Li et al., 2009
Poleward movement of coccolithophores	Subpolar waters	Altered carbonate PIC pump (Temperature and Salinity)	Winter et al., 2014
Diatoms and dinoflagellates	North Sea	More diatoms relative to dinoflagellates (temperature along with windier conditions)	Hinder et al., 2012
Diatoms	Subarctic Pacific	Blooms and changes in the partitioning of fixed C (Fe and CO_2 manipulation)	Yoshimura et al., 2014
Heterotrophic bacteria	Norwegian fjord	Higher growth rates (CO_2)	Endres et al., 2014

Note that such diverse responses have also been reported for other individual processes driving the biological pump but their inclusion is beyond the scope of this study.

TABLE 5 | Description of the model runs that each represent alteration, either directly or indirectly, of individual processes that influence the performance of the biological pump.

	Process	Direct alteration	Indirect alteration
Community NPP	Altered NPP toward export flux	+10% (High–Lat) or −10% (Low-Lat) relative to (C)	
Photosynthate to DOM	Less NPP toward export flux	10% of NPP directly to Het bacteria (0.4 transfer efficiency)	
Floristic shifts (high latitudes)	Altered size partitioning of NPP	0.3:0.4:0.3 (C) (pico:nano:micro) to 0.5:0.3:0.2	
Floristic shifts (low latitudes)	Altered size partitioning of NPP	0.5:0.4:0.1 (C) (pico:nano:micro) to 0.7:0.25:0.05	
Differential susceptibility to change	Lower transfer efficiency due to altered prey-predator relationship		0.4 (C)–0.3 (HNAN)
			0.3 (C)–0.25 (CIL)
Zooplankton Faunistic shifts	Altered transfer efficiency due to faunistic shifts		0.3 (C)–0.25 (MESOZOO)
Seawater Viscosity	Faster settling particles hence less solubilization by microbes	Altered particle transformation length scale	0.2% m^{-1} (C)–0.15% m^{-1} microbial POC flux attenuation
Bacterial enzymes	More particle solubilization by microbes	0.2–0.25% m^{-1} attenuation of POC flux	
Faunistic shifts in Zooplankton	Altered transfer efficiency due to faunistic shifts	Altered particle transformation length scale	(C) 0.4 (every 100 m) to 0.35 or 0.45 ("A" and "B" runs in **Figures 6**, **7**)
Vertical migrators	Alter DVM shunt	Altered POC shunt 20 (C) to 30 mg C m^{-2} d^{-1}	
Deoxygenation	Less respiration (Dunne, 2010) hence less microbial particle solubilization	Altered particle transformation length scale	0.2% m^{-1} (C)–0.15% m^{-1} POC flux attenuation

The magnitude of these alterations is either based on published findings/projections, or in some cases is arbitrary, but the sign of the change is based, where possible, on experimental, observational datasets or model projections reported in ***Table 3***. *HNAN denotes heterotrophic flagellates, CIL denotes ciliates, MESOZOO is mesozooplankton. (C) denotes value used in the control run.*

latitude case (**Figure 7B** c.f. **Figure 6B**). These "cross-overs" of the treatments were indicative of depth-dependent changes in the relative roles of the individual properties considered within each treatment (**Figure 7B**).

The relative roles of the processes setting export flux in the surface vs. the subsurface strata were explored by expressing the data from the control and the composite runs presented in **Figures 6**, **7** as the Ez ratio and T_{100} (from Buesseler and Boyd, 2009). The Ez ratio reveals the degree to which upper ocean particle transformations, which set the POC flux out of the Ez, decrease the input of new particles fuelled by NPP and BP. Deeper in the water column, T_{100} is a measure of the attenuation of the resulting export flux of particles as they traverse the 100 m horizon below the Ez (Buesseler and Boyd, 2009). In the high latitude case, the control run points to the surface ocean as having the greatest influence on the attenuation of the downward POC flux (Ez ratio of 0.18) whereas the T_{100} for the control was 0.37 (**Figure 8A**). The range of environmentally-mediated alteration of multiple properties resulted in Ez ratios ranging from 0.11 to 0.18, and corresponding T_{100} ratios of 0.37 to 0.48. The "All A" run (pink symbol) was a conspicuous end member with Ez and T_{100} ratios of 0.11 and 0.48, respectively.

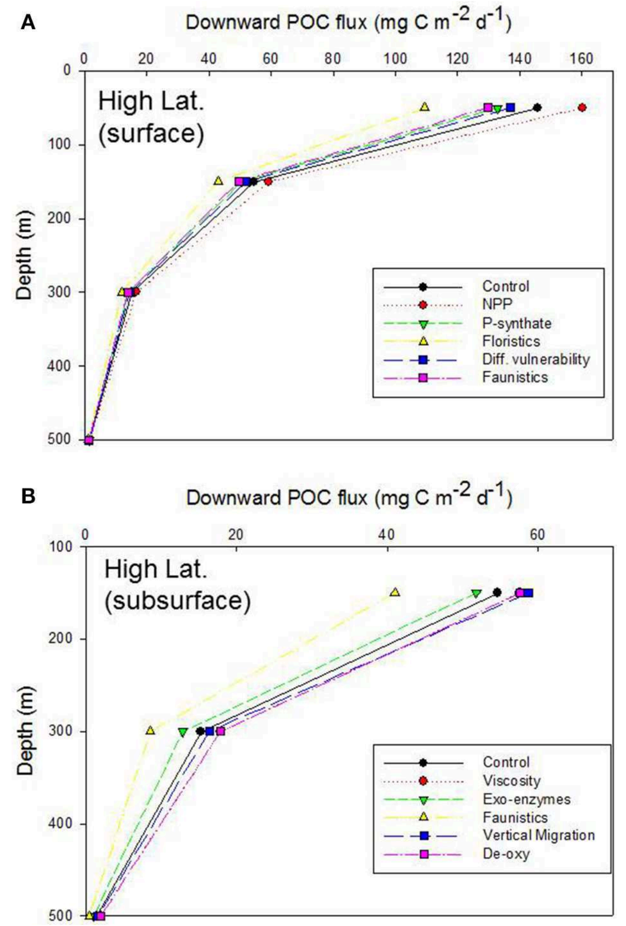

FIGURE 4 | Vertical profile of projected downward POC flux for the control run, high latitude case. Note that the profile for the Viscosity run is overlaid by that for De-oxygenation. **(A)** Additional simulations represent the systematic alteration of the individual components of the pump for the surface ocean: NPP, increased NPP; P-synthate, NPP directed to bacteria resulting in increased BP; Floristics, altered size-partitioning of NPP; Diff. vulnerability, altered microzooplankton trophic transfer efficiency; Faunistics, altered mesozooplankton trophic transfer efficiency. **(B)** As for **(A)**, but the simulations represent the systematic alteration of the pump components for subsurface waters: Viscosity, decreased seawater viscosity increasing particle sinking rates; Exo-enzymes, more microbial activity; Faunistics, altered mesozooplankton trophic transfer efficiency; Vertical migration, altered vertical POC shunt; De-oxy, decreased microbial remineralization due to de-oxygenation.

Examination of the trends in the Ez and T_{100} ratios from the "All A" and "all temps A" runs (**Figure 8A**), which exhibited the largest decreases in downward export flux (**Figures 6A**, **7A**), reveals that they have a larger effect on Ez than on T_{100}, with the latter ratios exceeding those for the control run. In contrast, the Ez ratios for these simulations were > 1.5 fold less than that for the controls at both the high and low latitude sites (**Figure 8**). Hence the effect of warming alone, and of all factors together being altered, has the largest effect on export out of the surface ocean, but less effect on downward POC flux in subsurface waters.

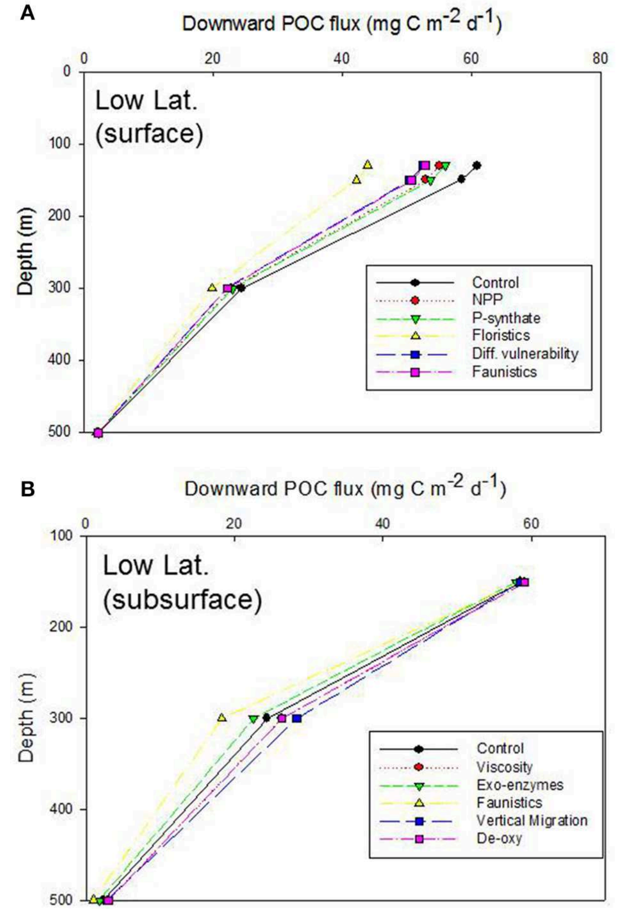

FIGURE 5 | Vertical profile of projected POC flux for the control run, low latitude case. The additional simulations for **(A,B)** are as described in **Figures 4A,B**. As for **Figure 4B**, the "Viscosity" profile is overlaid by "De-oxygenation." In the case of the NPP run, NPP is decreased for low latitudes (Bopp et al., 2013; Marañón et al., 2014). Note, the convergence of fluxes at 150 m depth is due to relatively little influence of altered subsurface processes over 20 m depth (i.e., 130 m deep Ez, **Table 2**).

The Ez and T_{100} ratios for the control in the low latitude simulation were both lower than in the high latitude run, reflecting differences in the surface and subsurface characteristics at each site (**Table 2**), as previously reported and discussed by Buesseler and Boyd (2009). The Ez ratio was 0.11 and T_{100} was 0.32 for the control (**Figure 8B**), and these ratio's ranged from 0.05 to ~0.1 for Ez and from 0.32 to 0.34 for T_{100}. As for high latitudes, the "All A" run (pink symbol) was an end member with Ez and T_{100} ratios of 0.05 and 0.34, respectively.

Discussion

The Cumulative Effects of Different Modes of Control on Export Fluxes

Stepwise investigation of the influence of altering each climate-change sensitive process reported to influence the biological pump (**Figures 4**, **5**) helps to interpret the cumulative effect

TABLE 6 | Summary of the coupling of individual processes used in model runs presented in Figures 6, 7.

	Strata	Export flux	Mode of control
Phytoplankton growth	Surface ocean	Altered flux (altered NPP)*	Temperature
Floristic shifts	Surface ocean	Less flux (higher proportion of small cells)	Temperature (but see **Table 4**)
Microzooplankton and their prey: Differential susceptibility	Surface ocean	Less flux (more efficient grazing)	Temperature
Mesozooplankton Faunistic shifts	Surface ocean	Less flux (more efficient grazing)	Temperature
Seawater Viscosity	Subsurface	More flux (faster sinking particles)	Temperature
Bacterial enzymes	Subsurface	Less flux (more solubilization of particles)	Temperature
Faunistics	Subsurface	Less or more flux (more / less efficient grazing parameterizations)	Temperature?
Photosynthate to DOM	Surface ocean	Less flux (NPP to bacteria and not to phytoplankton carbon)	Acidification
NPP	Surface ocean	More flux (More NPP)	Climate Change
Vertical migrators	Subsurface	More flux (greater DVM shunt)	Climate Change
Deoxygenation	Subsurface	More flux (less particle solubilization	Climate Change

*Processes were coupled by their mode(s) of control, for example processes that have been revealed to be primarily mediated by temperature. Other modes of control that have been reported include OA, and multiple factors. Note some effects of environmental forcing, such as of OA (see Discussion in Passow and Carlson, 2012) on the degree of calcification of coccolithophores (Langer et al., 2006) are species-specific and so are beyond the scope of this study. *Differences in the future alteration of NPP have been reported for high (more NPP) vs. low (less NPP) latitudes. ? Denotes uncertainties over environmental modes of control.*

of joint alteration of the pump in a future ocean by multiple factors (**Figures 6**, **7**). In surface waters for both the high and low latitude cases, climate-change mediated alteration of each individual factor mainly results in decreased POC downward flux out of the surface ocean (**Figures 4**, **5**). At both sites, shifts in phytoplankton community structure, and their ramifications for the altered flows of energy through the pelagic foodweb (**Figures 1**, **3**), result in the largest decrease in POC flux. These shifts in the model are based on widespread reports of environmentally-mediated shifts toward smaller cells that are driven regionally by temperature in low latitudes (Morán et al., 2010) or salinity in high latitudes (Li et al., 2009).

Changes to the flows of energy through the pelagic foodweb (**Figure 3**) due to altered predator-prey interactions, or more NPP going to the dissolved phase, also decrease export flux (**Figures 4**, **5**) but may be offset by increased phytoplankton growth due to warming (under nutrient-replete conditions, Boyd et al., 2013) and/or increased high latitude NPP driven by "climate-change" (Bopp et al., 2013). When these individual factors are considered together they result in a substantial decrease in downward POC flux from the base of the Ez (**Figure 6A**). In the model runs, where the cumulative effects of individual properties was investigated, no attempt was made to explore whether there are any interactive effects between these properties, and if any such interplay would result in synergistic amplification or antagonistic diminution of the POC export flux (Folt et al., 1999).

In the subsurface waters below the Ez, alteration of each of two individual processes decreased export flux, relative to the control, while modification of three other processes increased this flux, resulting in changes to downward POC flux that were more akin to a "zero sum" outcome. For example, the effects of decreased seawater viscosity and increased microbial solubilization of particles, as parameterized in the model, cancel one another out. The parameterization of altered mesozooplankton assemblages in subsurface waters had the largest effect on POC fluxes, but little is known, apart from exploratory modeling studies (Jackson and Burd, 2002) about how the subsurface community will be altered by climate change. However, temperature does influence zooplankton rates such as respiration (Ikeda et al., 2001) and hence likely grazing rates also. In the case of the DVM of mesozooplankton, such migration it is likely to be a complex effect driven by temperature, irradiance, and phytoplankton stocks (Berge et al., 2014). There is also the likelihood of feedbacks between the resulting changes to such biogeochemically-influential processes as DVM (alteration of dissolved oxygen inventories, Bianchi et al., 2013) and more intense microbially-mediated remineralization (more subsurface nutrient recycling, Bendtsen et al., 2015) that will have further consequences for export flux, but are beyond the parameterization limits of this 1-D model.

The combined effect of concurrent alteration of climate-change sensitive individual processes that influence the functioning of the biological pump is evident to depths of 300 m, but difficult to discern below 300 m (**Figures 6B**, **7B**). The marked decrease in simulated POC flux below 300 m depth in the control run (to rates less than reported from Thorium disequilibria or state-of-the-art neutrally buoyant sediment traps, Buesseler et al., 2007) is probably due to the constant length-scale (100 m) imposed in the model parameterization for biologically-mediated particle transformations such as zooplankton grazing on sinking particles. The concept of such a length-scale for particle transformations was introduced by Buesseler and Boyd (2009) to accommodate a wide range of regional particle transformation processes and to represent them simply within a 1-D model. However, due to the paucity of studies of mesozooplankton grazing on sinking particles and its depth dependency (Wilson et al., 2008) it is fatuous to further alter this parameterization in the model.

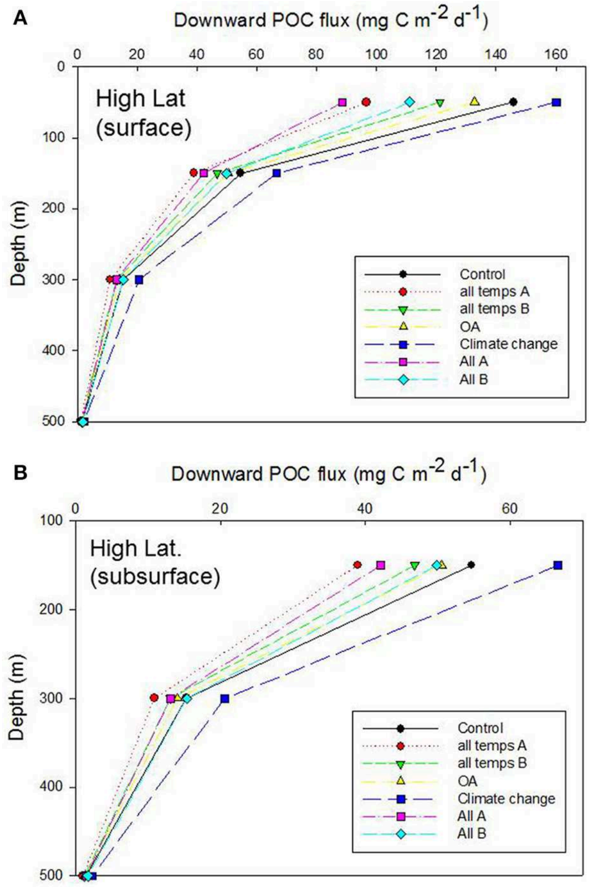

FIGURE 6 | Vertical profile of projected POC flux for the control run, high latitude case, for (A) surface and (B) subsurface processes. Additional simulations represent the cumulative effect of alteration of individual properties that influence the functioning of the biological pump: "all temps" denotes all the temperature-mediated individual processes described in **Table 6** ("A" and "B" are runs in which the mesozooplankton trophic transfer efficiency for surface waters is decreased and increased, respectively, relative to the control); OA denoted all OA-mediated individual processes; "Climate change" is the alteration of more complex processes (NPP, DVM, and deoxygenation) which are controlled by multiple factors; "All" is the cumulative effect of altering all of the temperature-, OA- and climate-change- mediated individual factors ("A" and "B" are as described earlier).

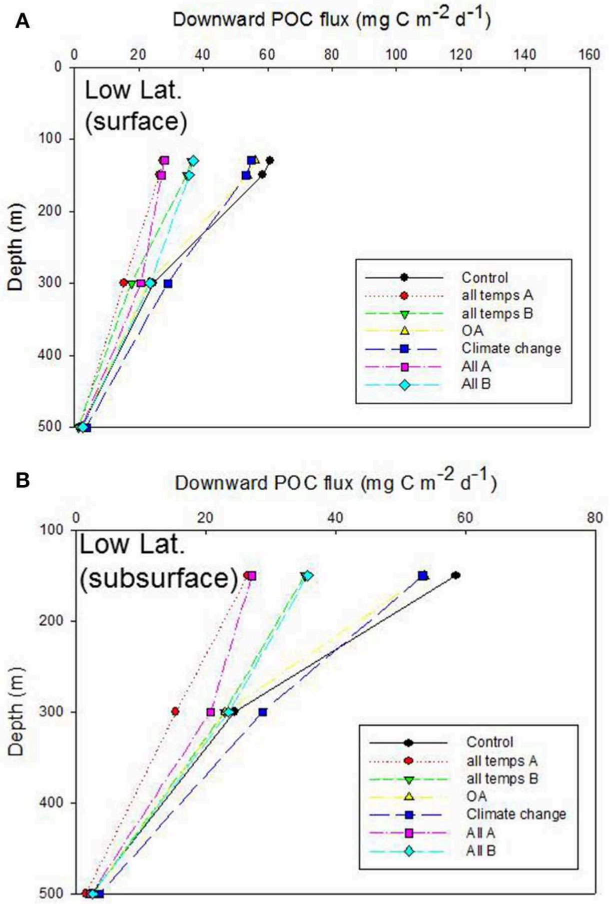

FIGURE 7 | Vertical profile of projected POC flux for the control run, low latitude case. The additional simulations in **(A,B)** are as described in **Figures 6A,B**.

A confounding factor in assessing the cumulative effects of climate change on the individual processes, that set the functioning of the biological pump, is that across the global ocean there will likely be regionally-specific effects, such as different environmental drivers causing similar trends. For example, the freshening of the Arctic Ocean is reported to be leading to a floristic shift toward small phytoplankton (Li et al., 2009), whereas warming has a similar effect on restructuring phytoplankton community structure in lower latitudes (Morán et al., 2010). **Table 4** reveals that other factors that cannot be considered in this 1-D model, such as nutrient supply or multiple environmental controls, may be equally important in driving such floristic shifts and that some changes, such as more iron to higher latitudes (Boyd et al., 2015a), could result in higher export flux out of the surface ocean. Hence, a range of different outcomes may arise from the regional climate-change mediated alteration of processes that shape the biological pump, and in some cases different environmental forcing may trigger similar responses in such influential processes.

The Role of Altered Surface vs. Subsurface Processes

The Ez ratio and T_{100} ratios permit robust inter-comparisons of sites with different Ez depths, and also reveal which processes—surface or subsurface—these regions are more sensitive to under both present day ambient and future perturbed conditions. The Ez and T_{100} ratios also provide insights into how sensitive the surface vs. subsurface processes are to environmental forcing—and hence where future research efforts to better quantify the effect of a changing climate on the biological pump should be directed.

A comparison of these metrics—in **Figure 8** indicates that the attenuation of the NPP signal in the surface mixed layer (for the control and climate-change model runs) is greater than the consequent decline in the POC export flux within the subsurface

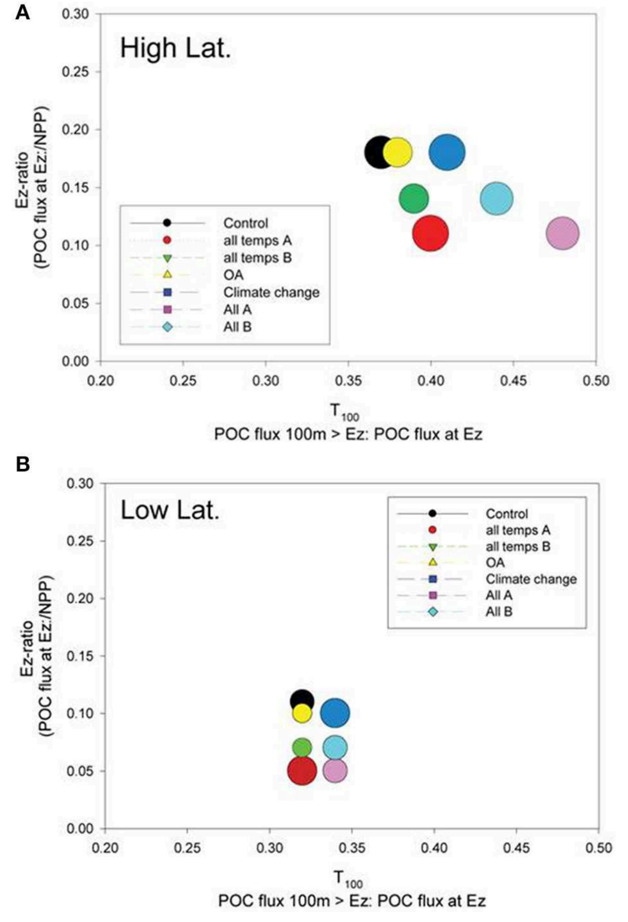

FIGURE 8 | A bubble plot of the Ez ratio vs. T_{100} (both defined in the plot labels) for the (A) high latitude and (B) low latitude cases. The model simulation represented by each bubble is color-coded as for **Figures 6**, **7**. The diameter of the bubble is scaled to column-integrated NPP used in the model simulations.

ocean at both the selected high latitude and low latitude sites. This trend, based on observations, has also been reported by Buesseler and Boyd (2009) for lower productivity regions (relative to high productivity water characterized by blooms). Buesseler and Boyd proposed that the lower attenuation in POC flux in subsurface waters was likely due to many particle transformations in the surface ocean resulting in sinking particles that were compact and less prone to further re-processing by the subsurface biota.

The climate-change model runs, which spanned simple (OA) to complex (concurrent alteration of nine processes) resulted in a ~two- and three-fold range of Ez ratios in the surface ocean for the high and low latitude cases, respectively. In contrast, the range of T_{100} ratios across the model simulations was ~30% (0.37–0.48) for the high latitude runs, and less (0.32–0.34) for the low latitude simulations. Hence, based on these model runs (but with the caveat of our present day undeveloped understanding of many of these processes, Riebesell et al., 2009; Passow and Carlson, 2012) climate change will have a greater influence on surface ocean controls on the biological pump. One reason why climate-change mediated alteration of subsurface ocean components may have less influence on the biological pump is because the effects of some individual factors may cancel each other out (**Figure 4B**)—for example decreased seawater viscosity results in faster sinking particles (enhancing flux) but also in faster rates of particle remineralization by microbes (decreasing flux). Moreover, the surface ocean is also characterized by a wider range of climate-change sensitive forcing (light, nutrients, CO_2, temperature) than the subsurface ocean, which may also partially explain its greater influence on downward POC flux relative to the subsurface ocean.

Extrapolation of Trends for High vs. Low Latitude Sites

The trends in Ez and T_{100} for the model simulations are similar to those reported for observations by Buesseler and Boyd (2009)—with T_{100} exceeding Ez at subtropical (ALOHA, off Hawaii) and subpolar (Ocean Station Papa, in the NE Pacific) sites. The HNLC characteristics of the high latitude site (**Table 2**) are also observed across about 30% of the global ocean (Moore et al., 2004), and the properties assigned to the low latitude site are comparable to the subtropical ocean which contains the largest biome—the Subtropical North Pacific Gyre globally (Karl et al., 2008). However, Figure 9 in Buesseler and Boyd (2009) displays Ez and T_{100} ratios of up to 0.4 and 1.0, respectively, from observations for the North Atlantic during the spring bloom, and also reveals changes in these ratios with season for different oceanic provinces, such as the Southern Ocean. Hence, the outcomes from the high and low latitude simulations (**Figures 4–8**) will be broadly representative of some but not all other oceanic provinces, and also the 1-D model cannot accommodate temporal shifts in either POC export flux (Lutz et al., 2002; Henson et al., 2012; Stock et al., 2014a) or in ratios such as Ez or T_{100}.

The different magnitudes of POC export flux across the high and low latitude sites (**Figure 4** c.f. **Figure 5**) and trends in Ez and T_{100} largely reflect the different environmental characteristics of these sites (**Table 2**) such as the deeper Ez depth, and hence the point of entry of new particles into the subsurface ocean (see Discussion in Buesseler and Boyd, 2009). The small range of T_{100} ratios (0.32–0.34) for the low latitude compared to the high latitude (0.37–0.48) runs, probably reflects differences in the model parameterization for the subsurface ocean that are driven by the deeper Ez for low latitudes. The 130 m deep Ez exit for sinking particles also increases the depth at which the simulated DVM shunt takes place, and the particle transformation length-scale does not take effect until deeper in the water column at the low latitude compared to the high latitude site. Hence the trends from the model runs reflect both site-specific differences in model parameterization, and different environmental forcing, such as warming and acidification, which influences a suite of both surface and subsurface processes at these sites with different characteristics of their regional biological pumps.

Climate-change Controls on the Biological Pump

One utility of this relatively simple 1-D modeling approach is that it provides insights into how different climate-change forcing influences a suite of both surface and subsurface processes, such as warming or acidification. By making this connection it is possible to cross-link the sensitivities in the model to altered climate-change parameterizations, such as warming, with the degree of confidence that exists for temperature-sensitive processes. For example, temperature-modulated changes to the viscosity of seawater can be readily estimated (Taucher et al., 2015), whereas the effect of warming on rates of bacterial solubilization of particles (Cunha et al., 2010; Bendtsen et al., 2015) is more problematic particularly in the subsurface ocean where the effects of *in situ* pressure on microbes is difficult to mimic in the lab or shipboard (Giering et al., 2014; Boyd et al., 2015b). The present 1-D modeling approach provides the means to rank our understanding of each process, relative to its perceived influence on the performance of the biological pump. The model runs revealed that changes to phytoplankton community structure had the most marked effect of all the individual mechanisms on POC flux out of the surface ocean. In contrast, a change in mesozooplankton community structure had the greatest effect on the export flux signal in subsurface waters. The datasets that illustrate the former are much more widespread and well-established, than for the latter which is more speculative and relies on several strands of indirect evidence that: fauna have different feeding strategies in the mesopelagic (Ikeda et al., 2001; Jackson and Burd, 2002; Paffenhöfer, 2006); climate-mediated shifts in mesozooplankton distributions have been observed in the surface ocean (Edwards et al., 2013) (and hence are also likely in the subsurface ocean as conditions change), and zooplankton species display a wide range of grazing rates (Mauchline, 1998).

Improving Estimates of the Performance of an Altered Biological Pump

This 1-D modeling study reveals that the cumulative effect of the individual processes, reported so far to be altered by a changing climate, on the biological pump in the future will be considerable, with marked reductions in POC flux projected at both high and low latitude sites. These reduced POC fluxes are in excess of those reported from 3-D coupled ocean atmosphere models (Bopp et al., 2001, 2013). The 1-D and 3-D approaches bring different levels of analysis to bear—with the cumulative effects of nine different processes being examined in a 1-D water column in the present study, vs. the influence of several inter-related factors (nutrients, irradiance, temperature, NPP) on export within a dynamic global model being jointly investigated in Bopp et al. (2013). In particular, the interplay and feedbacks (on the input of POC into the pump) between altered performance of the biological pump, mesopelagic nutrient regeneration, and ocean circulation can only be addressed in 3-D models. Clearly a nested suite of modeling approaches is currently needed to reduce the gaps in our knowledge, and to refine the integrated knowledge platform required to better explore the climate change ramifications for downward export flux in the coming decades.

Based on our current understanding of the influence of climate change on the biological pump, the 1-D approach in the present study indicates that the surface ocean will have a more pronounced influence on altering the magnitude of POC export flux in a future ocean. However, our knowledge on how a changing environment influences upper ocean processes that influence the pump is better than that for subsurface ocean processes. In particular, little is known about environmental forcing of mesozooplankton in the mesopelagic realm, and the study of zooplankton functional traits (Litchman et al., 2013; Vogt et al., 2013) in conjunction with advanced foodweb modeling (Stock et al., 2014b) offers the best prospect of advancing this field. It is also evident that although up to nine individual properties were considered in the 1-D model here, there are many gaps in our understanding on how complex climate change (i.e., multi-stressors, for example see Yoshimura et al., 2014) will influence the many "moving parts" of the biological pump in both surface and subsurface waters. Hence, a regional approach to this issue may be necessary to simplify this task as much as possible, before we can address global changes to a future biological pump with more certainty.

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REVIEW
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Responses of Marine Organisms to Climate Change across Oceans

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Climate change is driving changes in the physical and chemical properties of the ocean that have consequences for marine ecosystems. Here, we review evidence for the responses of marine life to recent climate change across ocean regions, from tropical seas to polar oceans. We consider observed changes in calcification rates, demography, abundance, distribution, and phenology of marine species. We draw on a database of observed climate change impacts on marine species, supplemented with evidence in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. We discuss factors that limit or facilitate species' responses, such as fishing pressure, the availability of prey, habitat, light and other resources, and dispersal by ocean currents. We find that general trends in species' responses are consistent with expectations from climate change, including shifts in distribution to higher latitudes and to deeper locations, advances in spring phenology, declines in calcification, and increases in the abundance of warm-water species. The volume and type of evidence associated with species responses to climate change is variable across ocean regions and taxonomic groups, with predominance of evidence derived from the heavily-studied north Atlantic Ocean. Most investigations of the impact of climate change being associated with the impacts of changing temperature, with few observations of effects of changing oxygen, wave climate, precipitation (coastal waters), or ocean acidification. Observations of species responses that have been linked to anthropogenic climate change are widespread, but are still lacking for some taxonomic groups (e.g., phytoplankton, benthic invertebrates, marine mammals).

Keywords: climate change, range shifts, phenology, ocean acidification, demography, abundance

INTRODUCTION

Anthropogenic greenhouse gas emissions have resulted in profound changes in the physical and chemical properties of the ocean that have serious implications for marine species, with concomitant risks to marine industries dependent on those species (Hartmann et al., 2013; Rhein et al., 2013; Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). The global ocean has absorbed 93% of the extra energy arising from anthropogenic greenhouse gas emissions, resulting in an increase in average global sea surface temperatures since the beginning of the twentieth century, that approaches 1°C (0.89°C over the period 1901–2012; IPCC, 2013). The ocean has also taken up ∼30% of anthropogenic carbon dioxide (CO_2) that has been released into the atmosphere, decreasing ocean pH, and fundamentally changing ocean carbonate chemistry in all ocean regions, particularly in the cooler, high latitude waters (IPCC, 2013). Other chemical and physical changes in the ocean attributed to anthropogenic forcing include declines in dissolved oxygen concentrations (Andrews et al., 2013) and alteration of ocean circulation (Cai et al., 2005; Wu et al., 2012). These anthropogenic changes represent risks to marine life and ecosystems (Poloczanska et al., 2013; Gattuso et al., 2015; Nagelkerken and Connell, 2015).

General expectations for biological and ecological responses to warming oceans include poleward distribution shifts, earlier spring events and delayed autumn events at mid to high latitudes, and reductions in body sizes of marine ectotherms (O'Connor et al., 2014; Pörtner et al., 2014). Ocean acidification is expected to reduce calcification in marine calcifiers such as corals and coccolithophores as well as influence a range of other processes such as growth and reproduction (Kroeker et al., 2013). Meta-analyses, applied across diverse species and ecosystems, have provided strong evidence of global fingerprints of recent climate change on natural systems including those in the ocean (Parmesan and Yohe, 2003; Rosenzweig et al., 2008; Poloczanska et al., 2013). Marine organisms have, on average, expanded the leading edges of their distributions by 72.0 ± 13.5 km per decade (generally polewards), while marine phenology in spring has advanced by 4.4 ± 1.1 days decade (Poloczanska et al., 2013). Yet responses are variable among taxonomic groups and among ocean regions, suggesting biological interactions, as well as marine ecosystem functions and the goods and services marine systems provide, may be substantially reorganized at regional scales.

Many factors can influence responses to changes in the environment, including species' generation time, dispersal ability, physiological tolerances, habitat and food preferences, and the composition of existing or receiving communities in the case of range shifts (O'Connor et al., 2009; Gerber et al., 2014; Alexander et al., 2015; Nagelkerken et al., 2015). Marine species often have complex life-cycles, as many have a dispersive planktonic stage, with distinct life stages potentially occupying different habitats, each with different exposures and sensitivities to changing climate (Rijnsdorp et al., 2009). The detection and attribution of biological responses to climate change is thus challenging given the idiosyncratic responses of species and populations at local and regional levels, the potential for changes in species interactions, and uncertainty in climatic trends at regional or local scales (Brown et al., 2011; Parmesan et al., 2011; Hansen et al., 2015). Organisms are subjected to the multiple interacting aspects of a changing climate, the effects of which may be synergistic or even antagonistic depending on species sensitivities and ecological processes (Fulton, 2011; Seabra et al., 2015). The picture is further complicated by the interaction of climate change with many other human pressures at regional and local scales that affect our oceans, such as fishing pressure, eutrophication, and habitat modification (Halpern et al., 2008). Furthermore, modes of climatic variability, e.g., Pacific Decadal Oscillation (PDO), Atlantic Multi-decadal Oscillation (AMO) and El Niño-Southern Oscillation (ENSO), which are major drivers of regional ecology, influence statistical uncertainty in climate change signals at regional scales (Bindoff et al., 2013). The interplay of these modes of variability can have strong influence on marine ecosystems. For example, the Gulf of Alaska and Bering Sea fluctuated from one of the warmest years in the past century (2005) to one of the coldest (2008) in the space of 3 years driven by the modes of ENSO and PDO and other factors, with associated changes in plankton, fish and seabird communities (McKinnell and Dagg, 2010; Batten and Walne, 2011). Considerable evidence exists for thresholds in individual species and ecosystem responses to regimes of climate and extremes of weather associated with altered ecosystem structure and function (Smith, 2011). For example, a marine "heatwave" event off Western Australia during the austral summer of 2011 which was due to a combination of a record-strength Leeuwin Current, a near-record La Niña event and anomalously high air-sea flux into the ocean, resulted in a reduction in habitat-forming macroalgae and a tropicalization of fish communities (Pearce and Feng, 2013; Wernberg et al., 2013).

Here, we consider the observed responses of marine ecosystems and species to climate change across oceans, from the boreal regions with their highly seasonal peaks in primary production to oligotrophic tropical seas. The ocean represents a vast region that stretches from the high tide mark to the deepest oceanic trench (11,030 m), and occupies 71% of the Earth's surface. In our discussion of ecological responses and knowledge gaps, we restrict our focus to pelagic and mesopelagic waters, and for continental shelf systems we also include the benthos and intertidal. Evidence of climate-change impacts is sparse in the deep sea due to logistical challenges of working in this environment which, when coupled with the size of the habitat, requires fuller consideration than we could have committed in this review.

We draw on a marine climate-change impacts database (hereafter "MCID"), comprising 1900 observations of marine ecological impacts of climate change from 235 peer-reviewed publications and including examples where responses were equivocal (not consistent with theoretical expectations under climate change) or zero (Poloczanska et al., 2013). We also refer to the information, synthesis and conclusions of the "ocean chapters" of Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC), namely Chapter 3 (Observations: Ocean) of Working Group I (Rhein et al., 2013) and Chapters 6 (Ocean Systems) and 30 (The Ocean) of Working Group II (Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). These are available from a single site (https://ipcc-wg2.gov/publications/ocean/). Below, we discuss observations of ecological responses in the ocean (changes in abundance, distribution, phenology, demography, and calcification). We discuss factors that limit or facilitate ecological responses, such as the availability of prey, habitat and other resources, or dispersal by ocean currents. We consider the consequences of large-scale change in ocean ecosystems and conclude by identifying key knowledge gaps.

MARINE CLIMATE CHANGE IMPACTS DATABASE (MCID)

We use the Marine Climate Change Impacts Database (MCID) analyzed in Poloczanska et al. (2013) which comprised of 1735 observations of marine ecological impacts of climate change from 208 peer-reviewed publications. To develop MCID, Poloczanska et al. synthesized all available studies (published during 1990–2010) of the consistency of marine ecological observations of change that were tested, or at a minimum discussed, in relation to expected impacts of recent climate change. We updated MCID with a further 27 publications published during 2011–2015, giving a total of 1900 observations from 235 publications (**Figure 1**; Supplementary Tables S1–S3). We extracted information on the taxonomic group, study period, location, class of response, and statistical significance of the observed change (Poloczanska et al., 2013). We included instances of marine taxa responding in a direction consistent with theoretical expectations under climate change, in a manner inconsistent (equivocal) with expectations, and taxa demonstrating no response as long as the observation was considered in relation to climate change. Data were available for every ocean, however most reports were from Northern Hemisphere temperate oceans.

To be included in our database, a study had to meet three criteria: (i) authors inferred or directly tested for trends in biological and climatic variables; (ii) data after 1990 were included thus recent climate change effects considered; and (iii) observations spanned at least 19 years in order to minimize the chance of bias resulting from short-term biological responses to natural climate variability. We included data from continuous data series [number of years with datapoints $n(yr) > 80\%$ of timespan of study in years], comparisons of two periods in time [$n(yr) < 20\%$ of timespan and clustered at the start and end of timespan] and intermittent data series [$20\% < n(yr) < 80\%$ of timespan], if they met our criteria. We did not restrict our search to only studies that applied a statistical test of a relationship between observed climate change and observed biological response. Most studies supplied multiple lines of evidence from theory, process-understanding, historical overview and experimental and field results, to contextualize findings of a response to climate change. From each paper, we classified responses into classes: calcification, demography, abundance, distribution, and phenology. If species were encountered more than once within each response class for each ocean region, we retained only the observation from the longest time series or most robust analysis (regionalization is shown in **Figure 1** and details given in Hoegh-Guldberg et al., 2014).

Rates of change for distribution and phenology, in kilometers per decade or days per decade, were obtained from individual studies in the database where possible, either directly as reported in the text, calculated from figures, or by contacting a study's authors. For distribution shifts, positive values (km per decade) indicate an expansion of distributions and negative, a contraction. For phenology, positive values indicate a delay (days per decade) and negative an advancement. Null responses (0 km or days per decade) were also recorded.

LONG-TERM OBSERVATIONS

Long-term observations of ecological responses to climate change are rare and biased toward high-latitude spring-bloom systems of the Northern Hemisphere (Edwards et al., 2010; Richardson et al., 2012; Poloczanska et al., 2013). Even here, long-term data sets are biased toward European and North American shelf waters (**Figure 1**). These shelf seas, which include the North Sea, Mediterranean Sea, and Labrador-Newfoundland Shelf, are among the longest- and most intensively-studied marine regions and are also among the fastest-warming of ocean regions (Belkin, 2009) (Table 30-1 in Hoegh-Guldberg et al., 2014). Responses to climate change are widely reported from these regions, particularly the north-east Atlantic high-latitude spring-bloom system (41% of MCID), where many long-term survey and monitoring programs are in operation. Several of these are multi-species programs, including fisheries catch records, fisheries-related surveys (e.g., van Hal et al., 2010), regional scientific surveys (e.g., Genner et al., 2004) and Continuous Plankton Recorder surveys (e.g., Beaugrand, 2009) The Continuous Plankton Recorder survey (CPR), in operation since 1931, monitors near-surface plankton communities and has provided valuable insight into climate responses of lower trophic levels across the open ocean (Edwards and Richardson, 2004; Richardson and Schoeman, 2004; Beaugrand et al., 2009; Edwards et al., 2010). Other programs in the north-east Atlantic that have sampled intensively over many years at local sites, such as the Helgoland Roads program (since 1962; Wiltshire et al., 2010), or research programs of the Marine Biological Association (earliest records from 1888; Southward et al., 2005), provide evidence of change across multiple taxonomic groups, higher trophic levels and adult life stages. Examples from other ocean regions, include the California Cooperative Oceanic Fisheries Investigations programme (CalCOFI) which samples plankton in the California Current upwelling system. Programmes such as Continuous Plankton Recorder and CalCOFI were initiated from a desire to understand the population dynamics of commercial fish stocks (Southward et al., 2005).

Equatorial and southern hemisphere regions are sparsely observed with respect to long-term biological variables. The few exceptions include a long history of marine records from coastal waters of south-eastern Australia in the south-west Pacific high-latitude spring-bloom system (Pitt et al., 2010; Johnson et al.,

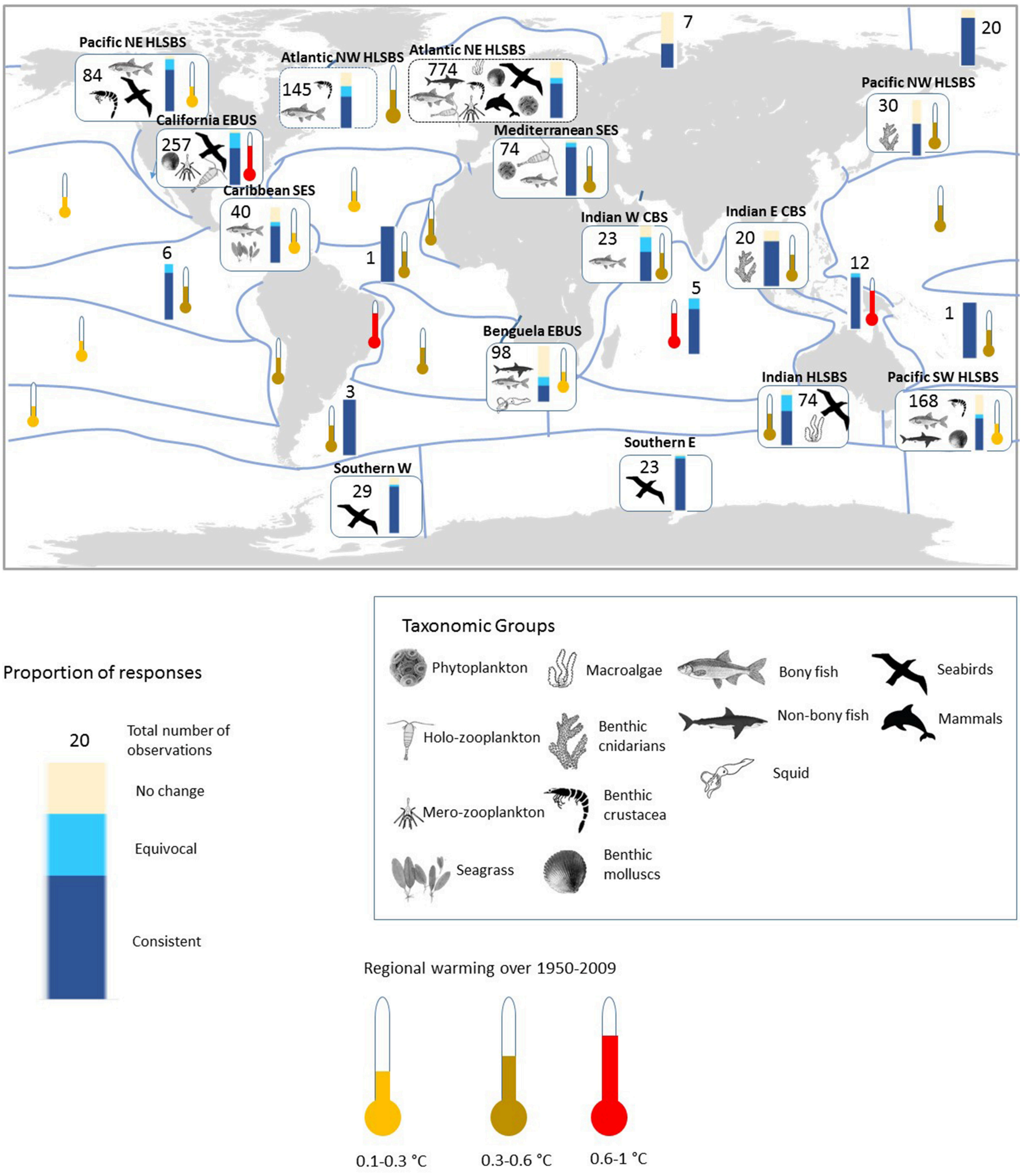

FIGURE 1 | Global distribution of marine ecological impacts across ocean regions. Distribution of climate change responses (including equivocal and no responses) in the abundance, distribution, phenology, demography, and calcification of marine species from the marine climate-change impacts meta-database of Poloczanska et al. (2013) updated with recent literature. The proportion of consistent (dark blue), equivocal (light blue), and no change (pale yellow) observations shown for each region. Numbers are total numbers of observed responses in each region—no number means no regional observations. Taxonomic groups with 10 or more observations in each region are indicated with symbols. Descriptions of taxonomic groups and criteria for selection of observations are given in Poloczanska et al. (2013). Regional temperature increase (all months) over 1950–2009 is shown in three categories: low (yellow 0.1–0.3°C), medium (orange 0.3–0.6°C), and high (red 0.6–1.0°C). The ocean separated into regions based on ecosystem structure and productivity, as well as key oceanographic features. HLSBS, high latitude spring bloom system; EBUS, eastern boundary upwelling system; SES, semi-enclosed sea; CBS, coastal boundary system. A full description of ocean regionalization and the calculation of regional warming increases are given in Hoegh-Guldberg et al. (2014) (Figure 30-1 and Table 30-1) and (Hoegh-Guldberg et al., 2014).

2011; Last et al., 2011) and from the Benguela eastern boundary upwelling system (Yemane et al., 2014). Many southern seabirds are well studied at their breeding colonies, such as penguin breeding colonies in Australia (south-west Pacific high-latitude spring-bloom system, e.g., Chambers et al., 2013) and Antarctica (Southern Ocean, e.g., Forcada and Trathan, 2009).

Although reef-building corals are conspicuous for their sensitivity to recent thermal stress, in terms of mass coral-bleaching, few observations for reef-building corals were included in MCID (3%). This likely reflects a scarcity of published long time series from these systems, despite a good mechanistic understanding of mass coral reef bleaching and mortality in response to thermal stress (Hoegh-Guldberg, 1999). However, retrospective studies, represented by analysis of cores taken from living corals (Lough, 2010), as well as baselines constructed from sediment cores for calcifying plankton (Moy et al., 2009), are supplying valuable information on both past local climates and biological responses of these organisms.

ECOLOGICAL RESPONSES ACROSS OCEAN REGIONS

Ecological responses to climate change are varied and many (Parmesan and Yohe, 2003; Parmesan, 2006; Pörtner et al., 2014). Observations related to abundance and distribution (including depth shifts) of marine species were widely reported in MCID (41 and 40%), while less evidence exists for changes in phenology (14%), demography (3%), and calcification (2%), largely due to the historical emphasis on certain measurements in marine research. Suites of these responses occur in concert, for example, coincident shifts in phenology and demography (Beaugrand, 2009). Observed responses of species to climate change across ocean regions show considerable variability both within and between taxonomic groups (**Figures 2**, **3**; Poloczanska et al., 2013). Species responses are complex and likely tempered by ecological characteristics, trophic interactions and resource availability, as well as other anthropogenic stressors, such as pollution and fishing. Fishing is a pervasive stressor in marine ecosystems (Worm et al., 2009; Branch et al., 2010) and its effects appear to increase sensitivities of ecological responses to climate change (Hsieh et al., 2008; Rijnsdorp et al., 2009; Hermant et al., 2010; Bates et al., 2014a).

Light is an abiotic factor that strongly influences the response of some marine species to climate change, particularly at higher latitudes. Seasonal fluctuations in the intensity, duration, and spectral composition of light change with latitude, and act as important phenological cues for a range of marine species, sometimes in combination with temperature. Light regime thresholds likely trigger events such as reproduction and migration (Davenport et al., 2005), in addition to temperature thresholds. Thus, temperature-driven shifts in distribution and phenology of species can be constrained by the influence of the seasonality of light on photoperiod, particularly at high latitudes (**Figure 4**; Saikkonen et al., 2012; Sundby et al., 2016). For example, in polar oceans, extreme light seasonality results in a short annual window of primary productivity and therefore food availability, thus restricting the potential for temperature-driven invasion of the high Arctic waters by species from lower latitudes (Kaartvedt, 2008).

Sensitivity of marine ectotherms (the majority of marine life) to temperature is well established. Thermal tolerance windows of marine fish and invertebrates roughly match the ambient temperature variability driven by climate regime and seasonality (Pörtner et al., 2014). The widest windows are found in species at temperate latitudes, where seasonality in temperature is strong. Polar species have the narrowest thermal windows and low energy-demand lifestyles, making them particularly sensitive to relatively small changes in temperature. Tropical species also have relatively narrow thermal windows and some species inhabit the warmest waters globally thus are near physiological temperature tolerance limits (Storch et al., 2014). The thermal range tolerated by a species can vary among life stages, with early stages (e.g., egg and larvae) generally being more sensitive (Pörtner and Peck, 2010). Similar sensitivities of early life stages are observed in response to changes in other environmental variables such as pH (Kroeker et al., 2013). Most observational studies consider just a single aspect and metric of climate change, generally annual mean sea surface temperature change (Brown et al., 2011; Poloczanska et al., 2013; Seabra et al., 2015), while the combined and indirect effects of environmental stressors on species and ecosystems are understudied and less well understood (Crain et al., 2008; Wernberg et al., 2012; Nagelkerken et al., 2015). Evidence suggests that sensitivities of fish and other ectotherms to temperature are generally increased when exposed to additional climate-change stressors such as reduced oxygen or ocean acidification and vice versa (Pörtner and Peck, 2010; Deutsch et al., 2015).

The ability of a species to colonize new areas as physical and chemical environments change will be regulated by rates of reproduction and dispersal, allied with the intrinsic capacity for a species to colonize and establish in new habitats and ecological communities. Factors such as high dispersal ability and large geographic ranges are hypothesized to influence the ability of a species to extend its range (O'Connor et al., 2012). Although some generalizations with regard to life-history and ecological traits are evident (Bates et al., 2014b), studies applying trait-based approaches to predict range expansions generally show low explanatory power (Angert et al., 2011; Pinsky et al., 2013). However, a study from south-east Australia identified species' traits common among range-shifting species, in particular swimming ability (thus dispersal potential), omnivory and initial range size (thus ecological generalization) (Sunday et al., 2015).

While the multiple factors that influence a species' ability to track climate change make simple prediction difficult, the use of multiple lines of evidence can inform understanding of species responses and increase confidence in the role of climate change (O'Connor et al., 2014; Hansen et al., 2015). Such lines of evidence include simple predictions holding true (e.g., abundance of warm-water species should increase and cold-water species should decrease), field and experimental studies showing species and populations are sensitive to past warm and cool periods (Southward et al., 1995; Hawkins et al., 2009) and theoretical tests of population models showing predicted

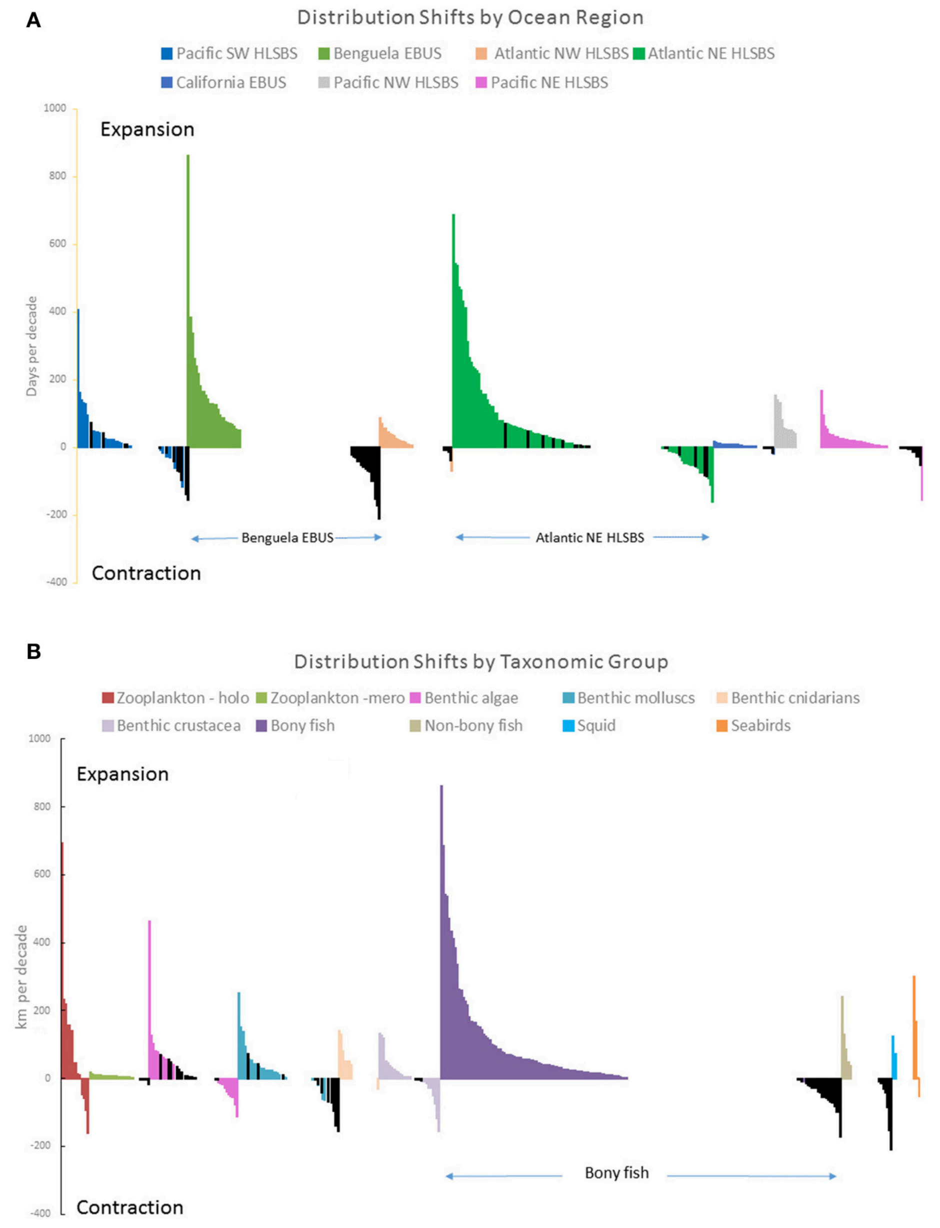

FIGURE 2 | Observed shifts in species distributions (km per decade) by (A) ocean regions and (B) taxonomic groups. Data from Poloczanska et al. (2013) updated with recent literature (2011–2015). Colored bars are consistent with expectations under climate change, black bars are equivocal, and zero values are no change. A description of ocean regions are given Fig 30-1 in Hoegh-Guldberg et al. (2014). Total number of observations = 659.

outcomes in nature (Poloczanska et al., 2008; Wethey and Woodin, 2008). In some cases, these lines of evidence provide understanding of the underlying mechanism(s) driving change, such as seasonal temperature thresholds for reproduction and recruitment success (Ling, 2008; Wethey et al., 2011). Below we discuss the evidence for changes in calcification, demography, abundance, distribution, and phenology.

Calcification

Ocean acidification will challenge marine calcifiers to grow and maintain their tests, shells and skeletons made from calcium carbonate. Experimental studies generally show negative responses of heterotrophs and calcified autotrophs to acidification, although results are highly variable and, of concern, show a trend overall toward enhanced sensitivity when thermal stress increases (Harvey et al., 2013; Kroeker et al., 2013; Nagelkerken and Connell, 2015). Observations of changing calcification are sparse in MCID (2%), with studies from tropical corals in the Indian (including Red Sea), Pacific and Atlantic (Caribbean) Oceans dominating (36 of 40 observations); the remaining 4 observations were of phytoplankton in the north-east Atlantic (Halloran et al., 2008; Iglesias-Rodriguez

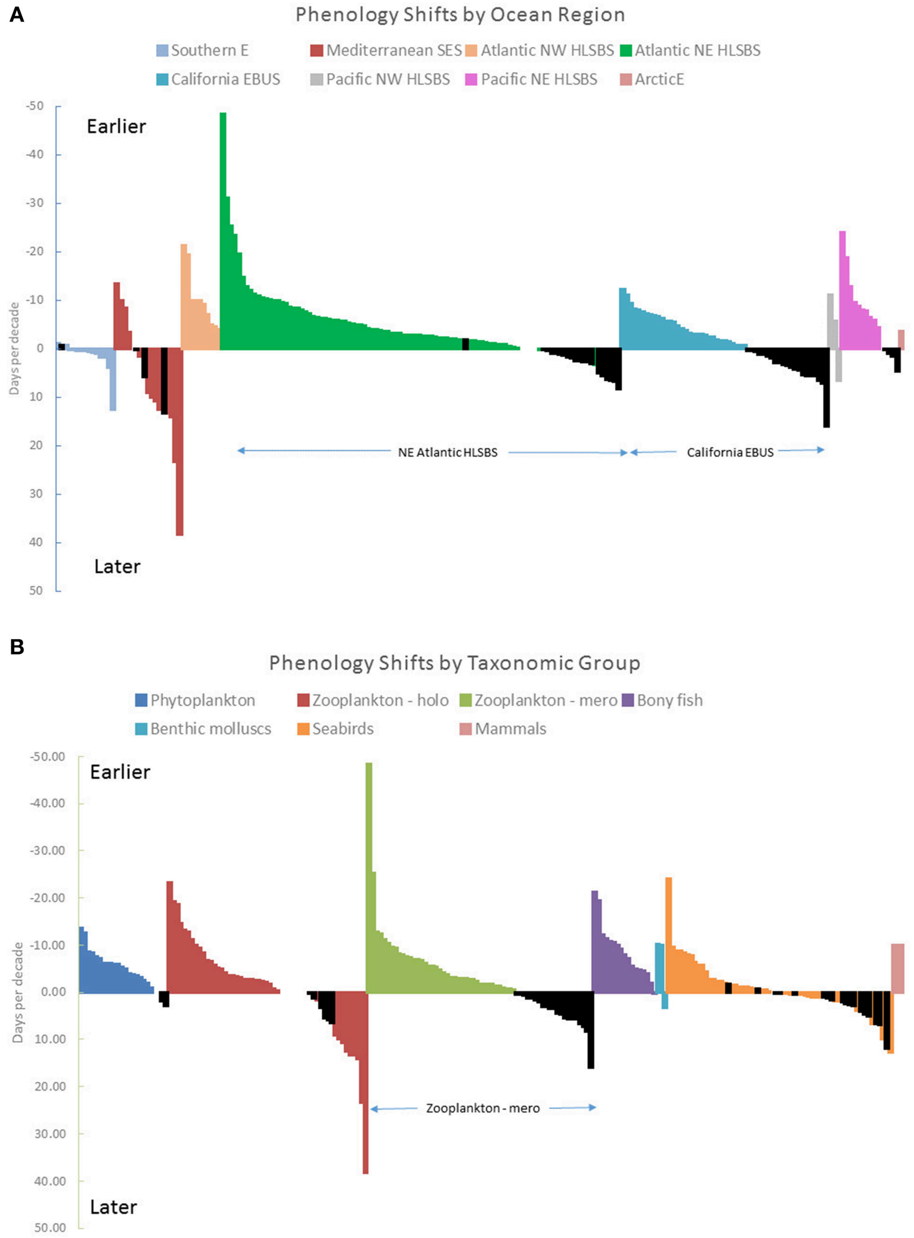

FIGURE 3 | Observed shifts phenology (days per decade) by (A) ocean regions and (B) taxonomic groups. Data from Poloczanska et al. (2013) and updated with recent literature (2011–2015). Colored bars are consistent with expectations under climate change, black bars are equivocal, and zero values are no change. A description of ocean regions are given Figure 30-1 in Hoegh-Guldberg et al. (2014). Total number of observations = 257.

et al., 2008) and zooplankton in the west Indian Ocean coastal boundary system (de Moel et al., 2009).

The skeletons of corals, contain valuable information on past environmental conditions and the calcification rates of species (Lough, 2010). Generally, cores from massive corals (e.g., Porites spp.) and sections from branching corals have revealed declines in calcification and/or growth rates (26 of 36 observations) consistent with expectations from warming and/or ocean acidification. The extension rates, calcification rates and skeletal density of corals are inter-related and need to be considered in combination to assess coral responses to changed environmental conditions (Lough and Cooper, 2011). Evidence of ocean acidification effects are currently scarce with temperature effects presently dominating. For example, in some cases, observed declines in coral calcification and/or growth rates have been ascribed solely to increasing temperature as thermal conditions exceed optimal conditions for growth, rather than the combined effects of warming and acidification. Examples come

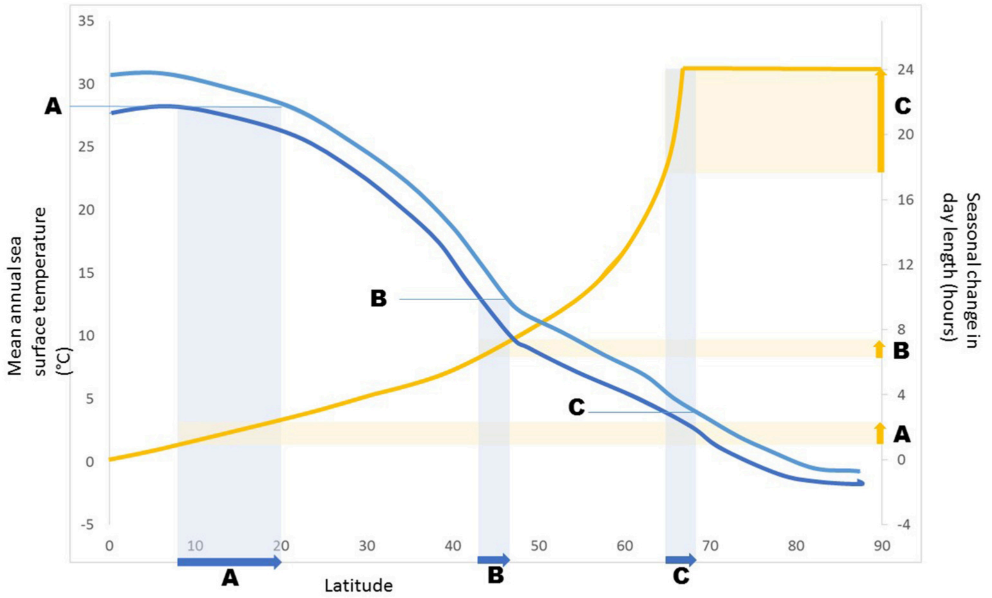

FIGURE 4 | Interaction among regional warming, latitudinal shifts, and seasonality in light for three hypothetical marine species. Dark blue line = current (1980–2005) zonal (5° latitude bands) mean annual sea surface temperature (SST) from Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST). Light blue line = future (2075–2100) zonal mean annual SST using ensemble data given in García Molinos et al. (2015). Temperature data for the Northern Hemisphere. Orange line = seasonal change in daylength, from the equator (no change) to polar seas (24 h daylight in summer to 0 h in winter) modified from Saikkonen et al. (2012). The shaded areas and arrows indicate shifts in latitude and daylength experienced as a species tracks its thermal niche. Species A lives in the tropics (29°C), to track its thermal niche requires a relatively large latitudinal shift (>10°) but experiences an intermediate change in light seasonality (~1 h). Species C is a sub-polar species (4°C), it requires an intermediate shift in latitude (~3°) to track its thermal niche but experiences a large change in light seasonality over this distance (>7 h). Species B lives in temperate regions (13°C) and experiences an intermediate change in light seasonality (<1 h) over an intermediate change in latitude (~3°) as it shifts distribution to track temperature.

from the Andaman Sea (in the Indian east coastal boundary system), the Red Sea and waters of Western Australia in the Indian Ocean (Cooper et al., 2008, 2012; Tanzil et al., 2009; Cantin et al., 2010). Similar mechanisms may explain the increase in growth and/or calcifications rates observed in a few Porites colonies off western and eastern Australia. These are consistent with expectations from warming as regional temperatures rise toward optimal temperatures for coral growth (Cooper et al., 2012; D'Olivo et al., 2013).

Cores taken from tropical corals from the Great Barrier Reef off eastern Australia show decreased growth rates since the early 1970s, initially ascribed to the combined effects of ocean acidification and thermal stress (De'ath et al., 2009). However, subsequent investigation suggests that temperature and land-based effects (nutrient and sediment loading of coastal waters) presently dominate over the signal from ocean acidification (D'Olivo et al., 2013). Mid- and outer-shelf reefs, removed from the major effects of river systems, exhibit a long-term (60 year) increase in calcification potentially related to the warming of minimum temperatures, which benefits calcification (D'Olivo et al., 2013). Of concern, these reefs appear to be undergoing a transition to declining rates of calcification, raising concerns that thermal stress is starting to emerge and/or the impacts of ocean acidification are starting to manifest.

Despite experimental evidence indicating sensitivity of many taxonomic groups to ocean acidification (Harvey et al., 2013; Kroeker et al., 2013; Nagelkerken and Connell, 2015), little observational evidence of observed responses to recent ocean acidification exists outside of reef-building corals. Changes in the plankton species are currently dominated by sensitivity to temperature change as well as the effects of nutrient availability and predation (Beaugrand et al., 2012; Beare et al., 2013). No relationship has been found between extensive data (60 years) of marine planktonic calcifiers in the north-east Atlantic and pH trends. However, longer-term perspectives are drawn from retrospective analysis of calcifying plankton and do indicate some impacts of recent ocean acidification. Studies of sediment cores reveal a decrease in shell mass of the planktonic foraminifera, *Globigerinoides ruber*, in the western Arabian Sea over ~250 years, as would be anticipated with recent ocean acidification (de Moel et al., 2009). A decline in shell mass, compared to specimens that are some 50,000 years old, was also found in *Globigerina bulloides* using sediment cores in the Southern Ocean (south of Australia) and ascribed to recent ocean acidification (Moy et al., 2009).

The lack of empirical evidence for changes in calcification is not surprising, given the very recent emergence of ocean acidification as a concern and the slow development of technologies for long-term monitoring of ocean acidification (Andersson et al., 2015). However, experimental and theoretical evidences indicates that ocean acidification is a major risk to marine ecosystems (Gattuso et al., 2015). Projections of changing temperature and ocean acidification, coupled with physiological thresholds, plus key information from large scale mesocosm studies (Dove et al., 2013) suggest that many reef-building corals globally will be severely impacted by ocean acidification within decades (Hoegh-Guldberg, 2004). Studies at volcanic CO_2 seeps and eruptions reveal a reduction in the abundance of calcifying invertebrates, including scleractinian corals and algae, along pH gradients (Hall-Spencer et al., 2008; Fabricius et al., 2014; Gil-Díaz et al., 2014). Further, herbarium records show a long-term (over three decades) decrease in calcification of the brown algae *Padina pavonica* from the Canary Islands coincident with a decrease in the pH of local ocean surface waters (Gil-Díaz et al., 2014). More broadly, a variety of lines of evidence from experimental and modeling studies indicate that ocean acidification will affect marine organisms over the twenty-first century, but the resulting long-term consequences for marine species' population dynamics and ecosystem functioning are yet to be identified and are areas of current research focus (Andersson et al., 2015; Riebesell and Gattuso, 2015).

Demography

Climate change will influence the demographics of marine species through differential effects on reproduction, growth and survival thus species abundance and population growth. Hypotheses regarding the response of populations to climate change include declines in recruitment/breeding success for populations near the equatorward edges of their ranges as temperatures warm, and corresponding increases near the poleward edges, although these will be tempered by a range of biotic and abiotic factors and differences in individual physiological responses (Poloczanska et al., 2013). Evidence of climate change impacts on demography of marine species, as recorded in MCID (3% of database), arises primarily from studies of recruitment variability in exploited fish and mollusc stocks and aspects of breeding for seabirds. Of the demography observations, 54% were measurements of reproductive success and productivity, 34% of observations were observations of growth and size parameters of organisms, and 12% were mortality measurements.

Recruitment may be a key process in driving population responses, in fish at least, to climate change (Rijnsdorp et al., 2009). Most fish spawn millions of eggs, and recruitment is influenced by growth and mortality integrated across the egg, larval, and post-larval phases, which can be highly sensitive to fluctuations in environmental conditions, particularly near range edges (Brunel and Boucher, 2006). For example, recent warming has allowed strong recruitment of subtropical wrasse, *Choerodon rubescens*, at the southern (polewards) edge of its range off Western Australia, where abundances of adult fish have historically been low or absent; in addition, its presence in angling catch records near its range edge has become more common in recent years (Cure et al., 2015). The increase in *C. rubescens* recruits coincides with warmer-than-average temperatures and an increase in intensity of the warm-water Leeuwin Current, the latter increasing seasonal advection of larvae and juveniles into newly-warming waters. Such patterns suggest that further warming could lead to a range expansion if suitable habitat is available. In Icelandic waters, a decade of warming has enhanced reproductive success of the monkfish, *Lophius piscatorius*, and expanded nursery and feeding habitats resulting in an increase in the monkfish stock near its poleward range edge, (Solmundsson et al., 2010). An enhanced delivery of eggs and larvae from distant stocks through changes in water inflow is also proposed as an additional mechanism.

In the north-east Atlantic, investigation of climate-driven recruitment variation (1970–1998) across 40 fish stocks belonging to nine species showed a general long-term decline in recruitment correlated with warming sea surface temperatures (Brunel and Boucher, 2007). While it is likely that fishing also played a role in observed trends in recruitment for some populations through depletion of spawning stock, for many such as cod, *Gadus morhua,* in the Irish Sea, the decline in recruitment commenced while stocks were still at high levels, implying a deterioration in favorable environmental conditions for early life stages. In contrast, recruitment for a few stocks, e.g., cod in the north-east Arctic, were positively correlated with strong year classes that preceded an increase in stock, suggesting that changes in the environment enhanced recruitment. The spawning intensity of Arcto-Norwegian cod, (using an egg production index from cod caught during the spawning season), is influenced by temperature with a recent (since 1976) decline in spawning in the southernmost areas and a northward displacement of spawning areas coincident with recent warming (Sundby and Nakken, 2008). Since 2003, cod spawning has been observed along the northernmost area, off the very top of Norway, which last occurred during the north Atlantic warm-period of the 1930–1950s.

An example of contrasting long-term responses of a fish species to ocean warming across a geographic range is that of the banded morwong, *Cheilodactylus spectabilis,* in south-east Australia and New Zealand (Neuheimer et al., 2011). Using growth rates over 90 years, estimated from otolith analysis, Neuheimer et al. (2011) showed that growth rates of fish living in the middle of the species' range increased with warming, while growth rates decreased in those living at the warm northern range edge. In the northern-most populations, warmer regional temperatures are no longer beneficial to growth due to greater metabolic cost and reduced energy for growth and reproduction.

Investigation of the long-term decline in recruitment of the bivalve *Macoma balthica* in the southern North Sea reveals the complexity of organismal response to changing climate. *M. balthica* has already disappeared from its equatorward range extremities along the southern French coast, with no or few individuals recorded at monitoring sites since the 1980s (Beukema et al., 2009). Evidence suggests that warmer temperatures decrease reproductive output (a direct physiological effect on adults) and advance spawning dates, resulting in a mismatch with both peak phytoplankton blooms and low predator abundance, the result being reduced food availability and increased predation pressure (Philippart et al., 2003). However, it is likely that the situation is more complex, with temperature also affecting mortality and growth rates of juvenile and adult life stages. For example, adult survival is reduced in warmer summers due to physiological stress, and winter weight loss by adults is higher when winters are milder. The latter results are driven by higher energetic demands, and thus reduced available energy for reproduction in the following spring (Beukema et al., 2009).

Numerous demographic responses to climate change have been observed for seabirds (Einoder, 2009; Chambers et al., 2014). For example, some of the longest seabird time series (spanning 50 years) are for Emperor penguin, *Aptenodytes forsteri*, colonies in Antarctica thus presenting data to investigate drivers of demographic responses (Barbraud and Weimerskirch, 2001; Barbraud et al., 2011). Loss of sea-ice reduces adult survival through multiple processes, including reduced food availability (abundance of krill, which form the base of Antarctic food webs, is lower in years with less winter-ice; Atkinson et al., 2004), but is also associated with increased hatching success, as the distance between colonies and foraging grounds (ice edge) is reduced. Overall however, long-term, climate-driven declines are expected for all Emperor penguin colonies this century as warming and sea ice loss continue (Jenouvrier et al., 2014).

Generally, climate change effects on seabird demography emerge through climate-mediated predator-prey interactions (Sydeman et al., 2015). Breeding success is negatively related to warming temperatures for fulmer, *Fulmarus glacialis*, (Lewis et al., 2009), manx shearwaters, *Puffinus puffinus*, (Riou et al., 2011), and black-legged kittiwakes, *Rissa tridactyla*, (Frederiksen et al., 2007) in the north-east Atlantic. These results are likely due to climate-driven changes in prey availability, although mechanisms differ among populations. For example, a reduction in fledging masses of manx shearwater chicks in the Celtic Sea was linked to higher sea surface temperatures in the preceding winter and a reduction in prey quality (Riou et al., 2011). A link between breeding productivity and winter sea surface temperatures in the preceding year was also shown for kittiwake breeding colonies in east Scotland and Orkney, but not for colonies in adjacent regions (west Scotland and east England) (Frederiksen et al., 2007). In addition, a positive relationship between breeding productivity and *Calanus* copepod abundance was found in East Scotland and a negative relationship in Orkney. *Calanus* is an important prey item of sandeels, *Ammodytes marinus,* the main food fed to kittiwake chicks, and relationships have been shown between sea surface temperature, sandeel abundance, and seabird breeding success (Arnott and Ruxton, 2002; Poloczanska et al., 2004). The unexpected finding in Orkney highlights that mechanisms are not fully understood, but variation in species' dependence on sandeel as prey among regions may help to explain the result.

Other examples of differing mechanisms by which climate change can influence foraging and diets of seabirds include flesh-footed shearwaters, *Puffinus carneipes*, in the eastern Indian Ocean and wandering albatross, *Diomedea exulans*, in the Southern Ocean (Weimerskirch et al., 2012; Bond and Lavers, 2014). Isotope analysis of the feathers of flesh-footed shearwaters from western and south Australia, where reproductive success has decreased and populations are in decline, shows that these seabirds have doubled their trophic niche and dropped a trophic level in 75 years (Bond and Lavers, 2014). By contrast, a recent increase in breeding success of wandering albatross in the Southern Ocean is linked to a strengthening and poleward shift of westerly wind fields. As a consequence, albatross travel rates (speed) have increased and foraging ranges shifted polewards, shortening the duration of foraging trips (Weimerskirch et al., 2012).

TABLE 1 | Observations of changing abundance in species classified as cold, warm, and cosmopolitan in their thermal preferences.

Response	Cold species	Warm species	Cosmopolitan species
Total observations	293	346	138
Increase	21%	52%	39%
Decrease	52%	19%	39%
No change	27%	29%	22%

Thermal affiliation is assigned in relation to the sampled region.

Abundance

Abundance changes were among the most commonly reported responses in MCID (41%). In a warming ocean, warm-water species are expected to increase and cold-water species decline. In MCID, species were classified as warm, cold or cosmopolitan relative to the region in which they were studied. Fifty-two percent of species classified as warm-water increased in abundance and 52% of cold-water species declined consistent with expectations under climate change; the remainder either showing no change or equivocal changes in abundance (**Table 1**). Of the cosmopolitan species, there was no bias in either direction with an equal number (39%) increasing and decreasing in abundance, with the remaining 22% showing no change.

Changes in abundance are observed as populations fluctuate across a range of time-scales from seasonal to decadal and beyond, reflecting the accumulation of demographic responses such as altered recruitment and survival. For example, fluctuations in abundances of intertidal invertebrates around the UK coastline have been observed during decadal warming and cooling periods (Hawkins et al., 2008, 2009). Poloczanska et al. (2008) investigated mechanisms underlying population fluctuations in two intertidal barnacle species and identified temperature impacts on recruitment as the dominant process influencing adult abundances. The presence of the cold-water barnacle, *Semibalanus balanoides*, which recruits to UK rocky shores in large numbers in early spring, can depress abundance of its later-recruiting, warm-water competitor, *Chthamalus* spp., through temperature-driven interference competition. *S. balanoides* recruits overgrow and undercut recruits of the subordinate *Chthamalus* spp. and effects are stronger during cool periods when *S. balanoides* recruitment success and juvenile survival are higher (Connell, 1961). Recent declines in abundance of *S. balanoides* in south-eastern UK and northern France are linked to warming as the frequency of recruitment failure increases, and with projected warming, *S. balanoides* could become locally extinct by 2050 (Poloczanska et al., 2008). Evidence of similar mechanisms are shown in other taxonomic groups. For example, variability in abundances of 20 flatfish species in the Bay of Biscay, north-east Atlantic (1987–2006), were linked to sea surface temperatures in the year of their birth, suggesting that larval survival and recruitment processes influenced adult abundances (Hermant et al., 2010).

Considerable evidence exists for changes in abundances of planktonic groups linked to recent warming. Declines in cold-water species and increases in warm-water species have been observed for mysids in Mediterranean caves (Chevaldonné and Lejeusne, 2003) and zooplankton communities in the north-east Atlantic (Beaugrand, 2003). Longer-term evidence of changes in foraminifera over ∼1400 years, reconstructed from sediment samples, revealed an increase in abundances of tropical/subtropical species over the last 100 years, and more recent declines in temperate/subpolar species (Field et al., 2006). In Antarctic waters the extent and duration of sea ice, as well as temperature, influences primary production. These effects cascade through Southern Ocean food webs. The density of krill has likely declined in the southwest Atlantic sector (1926–2003), while densities of salps, a warmer-water group, have likely increased (Atkinson et al., 2004) however, the magnitude of the decline is uneder debate (Constable et al., 2014). Krill density is influenced by seasonally important food sources; phytoplankton in the water column during summer and phytoplankton under winter sea ice (Atkinson et al., 2004). Both these food sources are declining with warming temperatures and decreasing sea ice extent.

Observations of changing abundance may be an early warning that large-scale shifts in distribution are about to occur, or that they are occurring (Bates et al., 2014b, 2015; Lenoir and Svenning, 2014), and indeed are often used to infer distribution shifts. For example, data spanning multiple decades from coastal localities off south-eastern South Africa (Lloyd et al., 2012), Rhode Island in north-west Pacific (Collie et al., 2008), the northern Gulf of Mexico (Fodrie et al., 2010), and south-east Australia (Last et al., 2011) all demonstrate increases in the abundance of warmer-water species and decreases in cooler-water species coincident with local warming temperatures leading authors to postulate that range shifts are occurring. In the South African example, regional warming was most pronounced during the Austral summer and was influenced by a southern extension of the warm-water Agulhas Current, as evidenced in a 178 km shift in the 27°C isotherm over the 19-year period (Lloyd et al., 2012). The abundance of temperate reef-fish species decreased over this period while that of tropical species increased. For south-east Australian waters Last et al. (2011), gathered data from a range of sources including spear-fishing competitions, scientific surveys and commercial catch, and showed evidence of southward distributional shifts and increased abundances of 45 fish species. The rapid warming of ocean temperatures in the region are driven, in part, by a southward extension of the warm East Australian Current by 350 km over 1944–2002. In both the South African and Australian examples, the observed shifts in the major current systems, driven by changes in westerly wind fields and an intensification of ocean gyre systems, have an anthropogenic signal (Cai et al., 2005; Rouault et al., 2009; Wu et al., 2012).

Distribution

Shifts in species distributions in relation to climate change are widely-reported (41% of MCID) with observational evidence from leading (polewards) and trailing (equatorwards) edges of species' distributions and from measurements at the centers of species distributions. Generally, where quantified data were available, leading edges are expanding (71 of 97 observations) and measurements taken within species ranges (centers) showed either polewards displacements (113 of 253 observations) or no change (104 of 253 observations), consistent with theoretical expectations under climate change (**Figure 2**). At trailing edges however, observations of expansions (26 of 83 observations), contractions (28), or no change (29) were similar (**Figure 2**). Differences in consistency of observations among range edges may be explained by differing processes (e.g., colonization vs. extinction) and detectability (Bates et al., 2014b, 2015).

The role of climate change in driving distribution shifts in marine biodiversity is currently garnering considerable attention (e.g., Bates et al., 2013; Poloczanska et al., 2013; Lenoir and Svenning, 2014) given the potential ramifications for fisheries, marine management, conservation, and policy (Cheung et al., 2010; Pinsky and Fogarty, 2012; García Molinos et al., 2015). The general expectation is that marine species will shift poleward, but some east-west distribution shifts and shifts toward the equator are expected in response to complex patterns of shifting isotherms, including areas of ocean surface cooling, and geographical barriers (Burrows et al., 2011, 2014; Pinsky et al., 2013). Depth shifts are expected where species can take refuge in cooler, deeper waters, or where local geographical features block latitudinal shifts. For example, in the northern Gulf of Mexico and Gulf of Maine, where the east-west coastlines prohibit poleward distributional shifts, demersal fish and invertebrate assemblages shifted deeper instead (Nye et al., 2009; Pinsky et al., 2013).

Ocean currents can rapidly advect phytoplankton and zooplankton, which include the early life stages of most marine ectotherms, as well as juveniles and adults vertebrates, thus facilitating marine distribution shifts (Berge et al., 2005; Banks et al., 2010; Sunday et al., 2015). Ocean currents have been implicated in observed species shifts in the north-east Atlantic (Beaugrand et al., 2009), north Pacific (Nye et al., 2009), and south-west Pacific (Johnson et al., 2011; Last et al., 2011). However, in many of these cases, changing temperature is the primary mechanism for the shift (Ling et al., 2008; Beaugrand, 2009), allowing larvae and juveniles to survive and thrive in new environments. For example, in south-Australia, the sea urchin *Centrostephanus rodgersii* spread from the mainland to Tasmania in the late 1970s and subsequently increased in both range and abundance coincident with regional warming (Johnson et al., 2011). The sequential poleward discovery of the sea urchin, a pattern of declining age, and a general poleward reduction in abundance along the eastern Tasmanian coastline is consistent with a model of range extension driven by recent change in patterns of larval dispersal (Ling et al., 2009b). Genetic studies indicate a high connectivity between pre- and post-extension zones, so the range shift appears to be an extension of the mainland population assisted by increased advection of larvae and warming of sea temperatures above the species' lower developmental threshold (Banks et al., 2010). The East Australian Current, which carries warm water and larvae and juveniles of marine organisms southward (Booth et al., 2007), has strengthened and penetrated further south since the 1940s (Ridgway, 2007), driven by a shift in westerly wind fields linked to greenhouse gas forcing (Cai et al., 2005; Wu et al., 2012). Consequently, coastal water temperatures in eastern Tasmania now fluctuate around the 12°C mark, which is the threshold for successful *C. rodgersii* larval development, during August when peak spawning occurs (Ling et al., 2008).

Range shifts of marine species, linked to warming temperatures, have been observed across all ocean regions (Poloczanska et al., 2013; **Figure 2**). Some of the highest rates of range expansion were observed for zooplankton in the north-east Atlantic, where the CPR survey has provided extensive data for climate change investigations. In response to anthropogenic ocean warming, warm-water calanoid copepod communities (108 species) extended poleward at rates of up to 231.6 km per decade, with corresponding declines in the abundances of cold-water species (Beaugrand et al., 2009). In particular, at higher latitudes such as south of Iceland and north of the North Sea, arctic/subarctic species have declined in abundance, while in the Bay of Biscay and southern Celtic Sea, subtropical species have increased in abundance. These rapid responses of zooplankton are attributed to their ecological characteristics, and particularly to the fact that they tend to be stenothermal, have short generation times (days to months) and be numerous and free-floating, so they can rapidly track shifts in environmental conditions (Mackas and Beaugrand, 2010). The redistribution of zooplankton has implications for marine food webs; warm-water species tend to be smaller and less energy-rich than polar/subpolar species. For example, changes in plankton communities driven by climate are a strong driver of cod, *G. morhua,* abundance in the North Sea (Beaugrand and Kirby, 2010).

The most concentrated evidence across taxonomic groups comes from the heavily studied North Sea in the north-east Atlantic, where waters have warmed just over 1°C in 40 years. This in turn has resulted in a shift in the 10°C isotherm of 217.5 km per decade (Beaugrand, 2009). Latitudinal distributional shifts were observed in a range of zooplankton (Beaugrand et al., 2009), exploited and non-exploited fish (Perry et al., 2005; Dulvy et al., 2008), and benthic invertebrates (Neumann et al., 2013; Hiddink et al., 2015), with ranges generally moving northwards (toward higher latitudes) as temperatures warm. Depth shifts, generally to deeper water, were also observed for benthic invertebrates (Beukema and Dekker, 2005; Hiddink et al., 2015) and demersal fish (Perry et al., 2005), with the whole demersal fish assemblage deepening by 3.6 m per decade (Dulvy et al., 2008). For demersal species, a latitudinal shift may necessarily incur a change in depth, depending on seabed topography. However, shifts in depth of individual species are often consistent with warming or cooling of deeper waters when taken into consideration with seabed bathymetry, local oceanography and species temperature preferences (Dulvy et al., 2008; Pinsky et al., 2013).

Fishing pressure can also strongly influence the distribution and abundance of fish populations, and acts in combination with temperature and thus challenge attribution of distribution shifts to climate change (ter Hofstede and Rijnsdorp, 2011). An example is the opposing shifts in flatfish species in the southern North Sea: over 90 years the distribution of plaice, *Pleuronectes platessa*, in the southern and central North Sea has shifted north-eastward by 142 km and deepened by 20 m, while sole, *Solea solea*, in the southern North Sea has shifted south-westward by 93 km and shoaled by <10 m (Engelhard et al., 2011). The distribution shifts in plaice are explained by warming, but the observed shift in sole distribution is explained by both warming and fishing. The southern North Sea is very shallow (<35 m) and shows the greatest range in seasonal sea surface temperatures, i.e., some of the coolest North Sea temperatures in winter and warmest in summer. Recent warming in the southern section has facilitated the southward expansion of flatfish species, previously excluded by cold winter temperatures, into southern coastal areas. Similarly, the distribution of North Sea cod, *G. morhua*, has shifted northeastward and deepened over 100 years (Engelhard et al., 2014). The northward shift is explained by warming and the eastward shift by fishing, through a serial depletion of cod from the western section of its historical distribution.

Other ocean regions where examples of climate-driven range shifts were observed include the Bering Sea in the north-east Pacific high latitude spring bloom system, the Benguela eastern boundary upwelling system, around Japan in the north-west Pacific high-latitude spring-bloom regions, and in south-west Australia in the Indian Ocean high-latitude spring-bloom system (**Figure 2A**). In the highly productive Bering Sea on the fringes of the Arctic Ocean, the extent of the "cold pool" (<2°C water) on the shelf separates polar and subpolar fauna. The cold pool is formed as a consequence of winter sea ice and is maintained over summer (Hunt et al., 2010). The region appears to be warming, and the loss of sea ice and resultant poleward retreat of the cold pool is driving a community-wide poleward distribution shift in demersal fauna, with range extensions of subarctic fauna into former cold-pool areas (Wang et al., 2006; Mueter and Litzow, 2008; Grebmeier, 2012). Range extensions of up to 98 km per decade were observed across a range of demersal fish and invertebrates. However, variable responses among individual species in the community (some leading, some lagging temperature change, and some not responding) are probably the result of interacting factors such as population size, dispersal ability, dependence on habitat or prey availability, resource competition, migratory strategy, latitudinal gradient in light regime, and fisheries impacts.

Variable changes in distribution and depth were also observed in the demersal fish community in the Benguela Current over 1985–2010 (Yemane et al., 2014). In the northern section of the system, off Angola, both mean sea surface temperatures and bottom temperatures have warmed. Many of the fish species sampled shifted polewards and deeper. In the southern section, off Namibia and South Africa, where regional ocean temperatures are influenced cold upwelling, different responses were observed. Bottom waters off Namibia have gradually cooled whereas off South Africa a recent warming is observed following a period of cooling. By contrast, sea surface temperatures have warmed off Namibia and cooled off South Africa. In this region of the Benguela system, no clear direction was observed in fish responses; around half the species that showed changes in distribution shifted polewards and the rest shifted equatorwards. However, all the depth shifts observed off South Africa were into shallower warmer waters as were most of those off Namibia.

In Japanese waters in the north-west Pacific high-latitude spring bloom system, four taxonomic groups of corals expanded poleward into temperate waters since 1930 at rates of up to 140 km per decade, coincident with significant warming of sea surface temperatures, while five other taxonomic groups remained stable (Yamano et al., 2011). Range shifts may have been facilitated by increased transport and southern expansion of the warm-water Kuroshio Current. Impacts were also observed in subtidal macroalgae: expansions were noted in tropical species such as *Sargassum* spp. and contractions in the ranges of temperate species such as the kelps *Ecklonia* spp. (Tanaka et al., 2012). In the Indian Ocean high-latitude spring bloom system, contractions in macroalgae at the equatorwards (warm) edges of their distributions were also observed along the southern section of the west Australian coastline consistent with regional warming (Wernberg et al., 2011).

Phenology

Seasons in the ocean are changing (Stine et al., 2009; Burrows et al., 2011), but observations of changes in marine phenology are relatively rare compared to those on land (Parmesan, 2007; Chambers et al., 2013), only 14% of MCID are phenology observations. The majority of marine phenological studies come from the north-east Atlantic, across a range of trophic levels from plankton to seabirds, and from Antarctic seabird colonies (**Figure 3**). Sparser evidence also arises from studies of highly migratory fish such as salmon and tuna (Juanes et al., 2004; Dufour et al., 2010).

The timing and production of plankton communities at the base of marine food webs are driven by temperature, nutrient and light availability. At higher latitudes, such as those in the north-east Atlantic, strong seasonal variability in primary and secondary production, formed by successive peaks in abundance of plankton groups, is pronounced because of seasonally varying photoperiod and water-column stability (Racault et al., 2012). Efficient transfer of marine primary and secondary production to higher trophic levels, including commercial fish species, is synchronized with successive plankton peaks (Hjort, 1914; Cushing, 1990). The plankton community (66 plankton taxa, including seasonal fish and invertebrate larvae) in the central North Sea is responding to climate change (1958–2002), but with substantial variation among species and functional groups (Edwards and Richardson, 2004). Spring- and summer-blooming species showed either an advance to some degree in peak abundance or stasis, as was the case for the majority of diatom species. The greatest advancements were observed in fish eggs and larvae (12.9 and 9.5 days per decade), echinoderm larvae (10.3 days per decade), *Ceratium* spp. (phytoplankton, ∼8.5 days per decade), and two diatom species (phytoplankton, ∼7.4 days per decade). In contrast, delays were observed in autumn- and winter-peaking species, with *Thalassiosira* spp (phytoplankton) delaying by 6.5 days per decade and larvae of *Limacina retroversa* (benthic mollusc) delaying by 8.4 days per decade. Some species, e.g., *Temora longicornis* (copepod), showed no statistically significant delay.

The potential decoupling of production peaks, and thus prey availability, has potential to cascade through trophic webs, particularly given the fast spring advancements in fish and invertebrate larvae. These latter cases suggest that reproductive phenologies have also shifted. An example is the advance in spawning in the bivalve *M. balthica* in the southern North Sea, which leads to a mismatch with timing of the phytoplankton bloom and also reduces avoidance of peak predation pressure for recruits (Philippart et al., 2003). An advance in spring phenology and delay in autumn phenology, coincident with warming, is also shown in reproduction of two conspecific intertidal limpets near their range limits in south-west England over 60 years (Moore et al., 2011). Spring reproduction in warm-water *Patella depressa* advanced by 10.2 days per decade, leading to a longer reproductive season (multiple spawning events), while autumn-spawning cold-water *P. vulgata* delayed breeding by 3.3 days per decade. The rapid decline in sea surface temperatures in autumn is thought to be the phenological cue for *P. vulgata* spawning, thus spawning is delayed toward cooler conditions more favorable for successful reproduction. However, the delay could potentially lead to a mismatch with larval food sources, which, coupled with declines in the proportion of the population reproducing and increasing thermal stress of adults during summer might eventually lead to local extirpation. In a rare study of fish spawning phenology, Fincham et al. (2013) show a shift toward earlier spawning in four stocks of sole, *S. solea*, in the north-east Atlantic. Warming of winter temperatures was linked to an advancement of ∼11 days per decade, through an effect on maturation rates, raising questions about potential mismatch with food sources and effects on juvenile survival.

Shifts in phenology for upper-trophic-level predators, such as seabirds, are variable, even among species breeding in the same region. Investigation of dates that the first eggs were laid (first egg date) of 10 species at two breeding colonies in the north-west North Sea showed advances of up to 8.4 days per decade for Arctic terns, *Sterna paradisaea*, European shags, *Phalacrocorax aristotelis*, and common guillemots, *Uria aalge* (Wanless et al., 2009). However, at the same colonies a number of delays in first egg date of up to 7 days per decade were noted amongst other species, including black-legged kittiwakes, *R. tridactyla*, northern fulmars, *F. glacialis*, and Atlantic puffins, *Fratercula arctica*, whilst no significant shift in phenology was recorded for remaining species. The species have different feeding methods, diets and dispersal patterns outside of the breeding season (e.g., local dispersal vs. long-distance migrant), and it is likely that an integration of environmental signals, including food availability across foraging grounds outside of breeding seasons, influences the timing of spring migrations and breeding phenologies.

The delays in seabird phenologies at Antarctic/sub-Antarctic breeding colonies appear, at first, to be inconsistent with the general expectation of earlier spring events (Barbraud and Weimerskirch, 2006; Hindell et al., 2012). Over 55 years, seabirds in the western Antarctic have, on average, delayed arrival by 1.6 days per decade, and first egg laying by 0.4 days per decade and no regional trend in temperature was found (Barbraud and Weimerskirch, 2006). However, some of the variation in arrival and egg laying was linked to a regional reduction in Antarctic sea ice and a lengthening of sea ice duration, which reduce access to and the quantity of marine food sources in early spring, thus presumably breeding condition of adult seabird.

Changes in phenology have been observed in other highly migratory species. Tuna are arriving earlier at productive feeding grounds in the north-east Atlantic by 5.6 days per decade (bluefin, *Thunnus thynnus*) and 2 days per decade (albacore, *T. alalunga*) (Dufour et al., 2010). These responses are linked to a regional climate shift toward warmer conditions. Earlier arrivals (up to 21 days per decade) into river systems have also been observed in Atlantic salmon, *Salmo salar*, breeding migrations to eastern North America. These shifts are positively correlated with warming temperatures (northern stocks) and river discharge rates (southern stocks), presumably reflecting the different migration patterns, and hence phenological triggers, of salmon populations (Juanes et al., 2004).

DISCUSSION

The volume and type of evidence of species responses to climate change is variable across ocean regions and taxonomic groups (**Figures 1–3**). Much evidence derives from the north-east Atlantic, a region that is heavily fished and studied, thus hosting many long-term observation programmes. A lack of observations from other regions does not imply that climate change is not having an impact, but rather represents our current state of knowledge (Hansen and Cramer, 2015). Most investigations of marine biological impacts of climate change have focused on the impacts of changing temperature, with few observations of effects of changing oxygen, wave climate, precipitation (coastal waters) or ocean acidification (Brown et al., 2011), despite an extensive theoretical, experimental and modeling base for understanding impacts on marine species. For example, models suggest declining oxygen will impact distribution and biomass of marine species through physiological responses and compression of habitat, and will result in a decline in body size of marine fish (Stramma et al., 2010, 2012; Cheung et al., 2011; Gilly et al., 2013). In addition, oxygen decline and ocean acidification in tandem will increase metabolic demands on marine species, particularly in northern hemisphere high-latitude oceans (Deutsch et al., 2015).

Evidence of impacts on phytoplankton at the base of marine food webs is limited with only a few studies in MCID. These studies suggest that phenology, abundance and calcification of phytoplankton species are changing in response to climate change. There is currently limited evidence and low agreement on the future direction and magnitude of change in primary production across ocean regions (Boyd et al., 2014). However, climate change is projected to strongly influence primary production in a multitude of ways through changes in a range of atmospheric and oceanic processes, including sea ice extent, stratification, cloud cover and upwelling (e.g., Sydeman et al., 2014).

There is substantial evidence for changes in the distribution, abundance and phenology of zooplankton in response to climate change. However, some differences in responses are evident between holo-zooplankton and mero-zooplankton (**Figures 2**, **3**). Holoplankton, or permanent members of plankton communities, show many and large shifts in distribution and phenology, which are generally consistent with expectations from climate change. These species may be particularly responsive to climate change given their short generation times, potential for rapid advection by ocean currents, and sensitivity to environmental conditions (Richardson, 2008; Beaugrand, 2009; Hays et al., 2015). In contrast, some of the largest shifts in phenology are seen in the meroplankton, the egg and larval stages of marine fish and invertebrates, but shifts in distribution are relatively small. We propose three factors that may influence results. First, most of the evidence for distribution shifts of meroplankton come from the California Current eastern boundary upwelling system (Hsieh et al., 2008, 2009), where thermal environments are complex given the upwelling of cold, nutrient-rich water that may reduce potential for distribution shifts. Second, many of the meroplankton species included are exploited as adults, and this may increase sensitivity to changing environmental conditions. In the California Current, larval fish species that are exploited as adults have greater distribution shifts that those that are unexploited (Hsieh et al., 2008). Third, the location and appearance of eggs and larvae in the plankton will ultimately be influenced by the location and timing of adult spawning. The capacity of adults to adjust or accommodate to changing environmental conditions may temper or exaggerate shifts in the timing of early life stages. Species may respond by first adjusting their phenological behavior, such as the timing of spawning, thus the timing of larval appearance in the plankton. Declines in abundance and distribution shifts may only occur once conditions change beyond physiological limits (Beaugrand, 2009).

How changes in the calcification, demography, abundance, distribution and phenology of the different life stages of marine species will manifest at an ecosystem level is a challenge for producing accurate predictions. Differential phenological responses across species will lead to temporal mismatches among trophic levels (Visser and Both, 2005; Thackeray et al., 2010). Climate change will alter the seasonal and temporal extent of areas favorable to reproduction, growth and survival for marine species (e.g., Shoji et al., 2011). Species may respond directly to changes in temperature and other climatic variables and also indirectly through changes in food and habitat resources (Stewart et al., 2014; Sydeman et al., 2015). Most marine species are ectothermic, so physiological functions are directly impacted by changes in ambient temperatures and other environmental variables (Pörtner and Knust, 2007; Pörtner and Peck, 2010). Direct impacts on metabolism and indirect impacts on food availability will alter growth rates and body sizes, and thus reproductive rates and ultimately population dynamics (Neuheimer et al., 2011; Rogers et al., 2011). Understanding the role of climatic variability and extremes, and their interaction with other stressors, in shaping species and ecosystem responses to long-term climatic change is important to predicting the ecological, social, and economic consequences of climate change at regional scales. Climate change will act with other anthropogenic stressors on marine ecosystems, such as fishing, pollution and intensification of shipping (risk of species introductions, Sorte et al., 2010) which also have potential to drive complex changes in ecosystems (Hoegh-Guldberg et al., 2014).

Observations of fish and other species moving to higher latitudes (Perry et al., 2005; Mueter and Litzow, 2008; Nye et al., 2009; Last et al., 2011; Magurran et al., 2015) are consistent with results of modeling exercises (Stenevik and Sundby, 2007; Cheung et al., 2009; García Molinos et al., 2015). The redistribution of species in response to temperature change, and in some cases also fishing pressure, has led to regional changes in species richness, particularly in northern hemisphere high-latitude spring-bloom systems (ter Hofstede et al., 2010; Simpson et al., 2011; Montero-Serra et al., 2015), and also to changes in community composition (Magurran et al., 2015). The high-latitude warming in the northern hemisphere over the past three decades has led to an increase in the size of fish stocks associated with some regional fisheries (Hoegh-Guldberg et al., 2014), and this may continue with further warming (Cheung et al., 2009; García Molinos et al., 2015) for some time into the future. In contrast, declines in species richness are projected in tropical areas, particularly in equatorial regions (García Molinos et al., 2015; Jones and Cheung, 2015). The redistribution of species with shifting climate zones will lead to the alteration of biotic interactions (Verges et al., 2014; García Molinos et al., 2015). For example, the climate-driven extension of the sea urchin, *C. rodgersii*, in south-east Australia has led to loss of macroalgae (kelp) beds through overgrazing, with loss of associated biodiversity (Ling, 2008). Intensive fishing of spiny lobsters *Jasus edwardsii,* the major predator of the urchin, may have reduced the resilience of kelp beds against the sea urchin threat (Ling et al., 2009a). In the north-east Atlantic, decline of the boreal intertidal barnacle, *S. balanoides*, with warming temperatures has resulted in an increase in abundance of a sub-dominant competing species (Poloczanska et al., 2008). In the Benguela Current, a temperature-driven shift in distribution of a coastal fish, *Argyrosomus coronus*, has resulted in an overlap with a related species, *A. inodorus*, during spawning events and thus a recent hybridization of these two species (Potts et al., 2014).

Climate change imposes strong selective pressures on species and populations, driving phenotypic and genetic responses (Chown et al., 2010). Plasticity in species traits and behavior are relatively well-studied and have been shown to allow species to compensate for changing climate (Crozier and Hutchings, 2014). For example, plasticity of foraging behavior has allowed the little Auk, *Alle alle*, to maintain fitness across a range of sea surface temperatures in the Greenland Sea (Gremillet et al., 2012). In the longer-term, as climate continues to change, evolutionary adaptation may be required. Trade-offs between phenotypic responses and genotypic responses will determine the capacity of individuals and populations to adjust to a rapidly changing climate (Chown et al., 2010; Chevin et al., 2013). Observations of evolutionary adaptation to modulate responses of marine species to climate change are notably lacking, despite increasing number of short-term experimental studies (Munday et al., 2013; Reusch, 2014).

Our review highlights the myriad and complex responses by species to recent changes in climate across ocean regions. We find that general trends in species responses that are consistent with expectations from climate change, including poleward and deeper distributional shifts, advances in spring phenology, declines in calcification and increases in the abundance of warm-water species. We also see the probable collapse of some ecosystems (e.g., coral reefs) if current changes in ocean conditions continue. Equally, we demonstrate that factors such as selection pressures for life history traits, resource availability, competition, predator-prey interactions and ocean currents also influence population and ecosystem dynamics, and whether a species can colonize and persist in new areas (Urban et al., 2007; Poloczanska et al., 2008; Burton et al., 2010; Comte et al., 2014). Observations of species responses that have been linked to anthropogenic climate change are widespread, but are still lacking for some taxonomic groups (e.g., phytoplankton, benthic invertebrates, marine mammals) and ocean regions (**Figure 1**; open ocean, tropics). Generally, responses to temperature are well studied, but notable gaps in observations and knowledge include responses to ocean acidification and changing oxygen concentration. Developing a greater capability for monitoring and understanding these changes will be critical for future management of ocean and coastal resources. The evidence of observed climate-change impacts is currently limited to the performance, phenology and distribution of marine organisms, with little understanding or evidence of evolutionary responses to recent climate change. The variability in responses across taxonomic groups are likely to lead to ecosystem reshuffling and shifts in ecosystem functions and benefits to people.

AUTHOR CONTRIBUTIONS

EP: conceived the manuscript, wrote the first draft, updated the database. CB: wrote the manuscript, updated the database. All others: wrote the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00062

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REVIEW
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Observed and Projected Impacts of Climate Change on Marine Fisheries, Aquaculture, Coastal Tourism, and Human Health: An Update

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The Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) states that climate change and ocean acidification are altering the oceans at a rate that is unprecedented compared with the recent past, leading to multifaceted impacts on marine ecosystems, associated goods and services, and human societies. AR5 underlined key uncertainties that remain regarding how synergistic changes in the ocean are likely to affect human systems, and how humans are likely to respond to these events. As climate change research has accelerated rapidly following AR5, an updated synthesis of available knowledge is necessary to identify emerging evidence, and to thereby better inform policy discussions. This paper reviews the literature to capture corroborating, conflicting, and novel findings published following the cut-off date for contribution to AR5. Specifically, we highlight key scientific developments on the impacts of climate-induced changes in the ocean on key socioeconomic sectors, including fisheries, aquaculture, and tourism. New evidence continues to support a climate-induced redistribution of benefits and losses at multiple scales and across coastal and marine socio-ecological systems, partly resulting from species and ecosystem range shifts and changes in primary productivity. New efforts have been made to characterize and value ecosystem services in the context of climate change, with specific relevance to ecosystem-based adaptation. Recent studies have also explored synergistic interactions between climatic drivers, and have found strong variability between impacts on species at different life stages. Although climate change may improve conditions for some types of freshwater aquaculture, potentially providing alternative opportunities to adapt to impacts on wild capture fisheries, ocean acidification poses a risk to shellfish fisheries and aquaculture. The risk of increased prevalence of disease under warmer temperatures is uncertain, and may detrimentally affect human health. Climate change may also induce changes in tourism flows, leading to substantial geospatial shifts in economic costs and benefits associated with tourism revenue and coastal infrastructure protection and repairs. While promising, ecosystem-based coastal adaptation approaches are still emerging, and

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require an improved understanding of key ecosystem services, and values for coastal communities in order to assess risk, aid coastal development planning, and build decision support systems.

Keywords: climate change impacts, fisheries, aquaculture, coastal tourism, human health, food security, ecosystem-based adaptation, ocean impacts

INTRODUCTION

The Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) states that climate change and ocean acidification are altering the global ocean at a rate that is unprecedented compared with the recent past, leading to multifaceted impacts on marine and coastal ecosystems, associated goods and services, and human societies (Church et al., 2013; Pörtner H. O. et al., 2014; Howes et al., 2015). Specifically, Working Group II (WGII) of the IPCC synthesized research regarding the observed and projected impacts of climate change on human and ecological systems. AR5 represents the first IPCC report to allocate two separate chapters to the ocean within WGII, thereby demonstrating the important contributions of the marine environment to discussions regarding climate change impacts and adaptation options.

As research regarding climate change, ocean acidification, and the ocean has accelerated rapidly, it is important to update the synthesis of available knowledge on these topics regularly to inform policy discussions. As a result of the need to ensure timely publication and peer review, the IPCC could only consider literature that had been published prior to August 2013 and now more than 2 years since WGII's deadline for inclusion of published literature have passed. Research findings published within this subsequent period may strengthen or alter the assessments and conclusions drawn in AR5.

To summarize progress toward addressing the uncertainties identified in AR5, this paper highlights key developments with respect to scientific understanding of the impacts of climate-induced changes in marine and coastal environments on socioeconomic sectors and human health, with a brief discussion on recent research regarding adaptation strategies that build from the AR5. Specifically, this review focuses on topics related to fisheries, aquaculture, and coastal tourism, as well as human health and food security, with the aim to capture corroborating, conflicting, and novel findings from literature published after the literature "cut-off date" of the IPCC report. To achieve this, the authors identified key findings from WGII of the IPCC's AR5 on CO_2-related impacts on living marine resources of importance to key marine and coastal sectors. Then, we undertook a systematic review of literature on these topics. Finally, we concluded by identifying areas of agreement and points of departure from the IPCC's AR5.

KEY FINDINGS IN IPCC AR5

Key findings from AR5 focused primarily on the ecological implications of climate change (Pörtner H. O. et al., 2014; Howes et al., 2015). In particular, global redistribution of marine species was highlighted, with observations and projections supporting further poleward range shifts under increased ocean temperatures (Poloczanska et al., 2014; Pörtner H. O. et al., 2014). Community size structures were projected to decrease under climate change, with reductions in maximum body sizes expected to occur in response to increased temperatures and reduced oxygen supply (Cheung et al., 2013b). Studies have indicated that impacts of acidification are likely to be both positive and negative, with severe impacts on calcifying organisms such as reef-building corals and bivalves, but with potential benefits for some vegetative habitats, such as seagrasses (Gattuso et al., 2014a). Net primary productivity (NPP) was projected to decrease moderately in the open ocean by 2100 under both low- and high-emission scenarios, comprising a mean increase in NPP at high latitudes and a decrease in the tropics (Boyd et al., 2014).

AR5 also highlighted socioeconomic impacts of climate change on coastal communities. Projections indicated that species' poleward range shifts would likely negatively impact tropical and subtropical communities that depend on these species for food and economic security (Pörtner H. O. et al., 2014). Adaptation options included maintaining important ecosystems, ensuring occupational flexibility, and developing early warning systems for extreme events (Portner J. R. et al., 2014). Other coastal impacts discussed included the prominent threat of sea level rise (SLR), the vulnerability of low-lying coastal areas, islands, and polar regions (Larsen et al., 2014; Nurse et al., 2014) and, to a lesser extent, impacts on coastal tourism through poleward redistribution of tourism flows associated with increased temperatures, loss of beaches through coastal erosion and SLR, and a reduction in water supplies (Wong et al., 2014). At the time, global estimates of observed or projected economic costs associated with ocean acidification were limited (Gattuso et al., 2014a), while evidence of impacts on human health focused primarily on increased frequency of disease transmission and range expansion, deaths associated with storm surges and flooding, increased prevalence of harmful algal blooms (HABs), and reduced food and water security (Nurse et al., 2014; Pörtner H. O. et al., 2014; Wong et al., 2014). The report called for additional research exploring climate-related impacts on other coastal sectors, such as tourism (Wong et al., 2014) and aquaculture (Portner J. R. et al., 2014).

AR5 underlined key uncertainties regarding how synergistic climate-induced changes in ecological systems are likely to affect human systems (Larsen et al., 2014; Pörtner H. O. et al., 2014), and how humans are likely to respond to climate-driven events (Portner J. R. et al., 2014). For instance, the capacity for different taxa to track or acclimate to (i.e., alter functional or morphological traits in response to) changes in climate and multiple stressors remained uncertain, with few studies addressing adaptation to multiple stressors over longer time series (Poloczanska et al., 2014; Pörtner

H. O. et al., 2014). Limited evidence existed regarding the directionality and magnitude of changes in NPP across different regions and ecosystems (Boyd et al., 2014) and, while acknowledged as a critical process influencing ecosystem productivity, the likelihood of climate-induced changes to major upwelling systems through increased or decreased upwelling remained uncertain (Lluch-Cota et al., 2014). Similarly, while the processes behind ocean acidification were well-understood, few comprehensive studies of biological, ecological, and biogeochemical impacts were available (Gattuso et al., 2014a). While climate change was projected to alter the yield, distribution, quality, and composition of fisheries' landings globally, details regarding these projected changes, such as quantification of risk and uncertainties, were still limited (Cheung et al., 2013c). Although socioeconomic vulnerability was projected to be highest in tropical countries (Pörtner H. O. et al., 2014), examples of successful adaptation for small island nations—beyond relocation—were limited and assessments of the social and economic costs of adaptation options were seldom available (Nurse et al., 2014), with relative costs of adaptation varying strongly between and within regions (Wong et al., 2014). Ecosystem-based adaptation also featured strongly in the report as a potential option for responding to climate change, yet examples were too few and too recent to facilitate a comprehensive assessment of benefits and risks (Shaw et al., 2014). Critically, authors of AR5 noted that the practice of adaptation often exceeds the rate at which peer-reviewed research describing and examining these practices can be produced and disseminated (Noble et al., 2014). Thus our knowledge of the effectiveness of these adaptation practices often lags behind their implementation.

SYSTEMATIC REVIEW OF LITERATURE

A search of the peer-reviewed literature was conducted to identify recent scientific developments globally with respect to our understanding of the impacts of greenhouse gas emissions on marine and coastal ecosystems and the sectors and communities that depend on them. Relevant studies, including regional examples where available, were obtained by browsing issues published in peer-reviewed journals between 1 January, 2013 and 31 October, 2014. The literature review was guided by the questions outlined in **Table 1**.

While the study does not intend to provide a comprehensive overview of climate-induced impacts on marine systems (see Howes et al., 2015), an understanding of the effects of ocean warming and acidification on living marine resources was required to examine corresponding impacts on coastal sectors and communities. Thus, the study examines relationships between ecological and socioeconomic impacts arising from climate change, focusing on impacts likely to occur within the twenty-first century.

Fisheries and Auxiliary Sectors

Healthy marine systems play a critical role in supporting fisheries, which contribute significantly to jobs, food security, and the wealth of nations. Recent studies have sought to characterize how climate-related drivers alter species' distributions and community size structures, with increased attention allocated toward synergistic effects (Hollowed et al., 2013; Brown and Thatje, 2014), early developmental stages and community size structures (Suikkanen et al., 2013; Woodworth-Jefcoats et al., 2013; Baudron et al., 2014; Calbet et al., 2014; Lefort et al., 2014), and genetic and phenotypic adaptation (Munday et al., 2013; Merilä and Hendry, 2014; Sunday et al., 2014). Each of these aspects is likely to affect the availability and abundance of fish stocks globally (Sumaila et al., 2011), with regional variation accompanying climatic trends. From an operational perspective, studies have also noted that changes in the frequency of extreme weather events may cause disruptions to fishing activities and land-based fisheries-related infrastructure (Noone et al., 2013).

TABLE 1 | Questions used to guide the literature review.

Topic	Question
Fisheries	How are climate change drivers expected to impact fish stocks (distribution, composition, quantity of individuals, etc.) that are currently exploited?
	How are these changes expected to vary by ecosystem and geographical region?
	How are these impacts expected to affect fisheries' catch potential?
	What economic impacts are expected for fishing and auxiliary industries?
	How are these impacts expected to alter food security?
	What ramifications may arise with respect to multilateral business agreements and international agreements? What geopolitical impacts are likely to occur?
	What new evidence supports the theory of an emerging “winners and losers” gap?
Aquaculture	How is climate change expected to impact future shellfish and fish aquaculture?
	What are the projected consequences of changes in aquaculture production on global food and economic security?
Coastal tourism	What are the consequences of ocean warming and acidification impacts on tourism flows?
	What are the consequences of ocean warming and acidification impacts on tourism operators' strategies?
	What are the economic consequences to be expected from ocean warming and acidification?
Human health	What are the possible impacts of climate-related drivers (e.g., diminished food and water security; extreme weather events; increased prevalence and transmission of disease) on human health?
Coastal adaptation	What evidence exists of the capacity for coastal communities and sectors to mitigate and adapt to climate change?

Projected Impacts on the Distribution of Fisheries Stocks

Empirical and theoretical evidence of range shifts in response to temperature gradients has continued to emerge for various taxa across many geographical locations (Poloczanska et al., 2013; Bates et al., 2014), with observations supporting the hypothesis that range shifts correspond with the rate and directionality of climate shifts—or "climate velocity"—across landscapes (Pinsky et al., 2013). In fact, variation in climate velocity was discovered to be a stronger predictor of the directionality and magnitude of taxon shifts than variations in life histories (Pinsky et al., 2013).

Studies have increasingly evaluated the degree to which taxa can track these climate velocities, with an aim to understand the factors that constrain range extension or contraction processes (Burrows et al., 2014). Supporting previous findings, Arctic and tropical fishes have been found occupying new habitats as temperatures change, further demonstrating the likelihood of continued poleward range shifts under ocean warming (Wenger et al., 2013). For instance, tropical fish species with larger body sizes, greater swimming capacities, larger sizes at settlement, and pelagic spawning behavior have exhibited greater success when colonizing temperate habitats, while habitat and food limitation during juvenile stages were likely to constrain movement (Feary et al., 2013). Latitudinal trends also suggest that fisheries stock sizes can increase polewards through higher growth rates accompanying increased temperatures, with a corresponding redistribution of fishing effort polewards (Hamon et al., 2013). However, recruitment is expected to exhibit an eventual decline under climate change, and thereby partially or fully counteract projected benefits (Hamon et al., 2013). Observed range shifts associated with ocean warming may also result in hybridization between native and invasive species through overlapping ranges, leading to reduced fitness and thus potentially increasing the risks of genetic extinction and reducing adaptability to environmental changes (Muhlfeld et al., 2014).

New examples have emerged regarding barriers to migration, with studies demonstrating that some taxa may be incapable of keeping pace with climate velocities, as observed with benthic invertebrates in the North Sea (Hiddink et al., 2014), and that there may be geographical barriers to migration associated with "climate sinks," where local climatic conditions differ from the temperature gradients tracked by migrating species (Burrows et al., 2014). Moreover, genetic bottlenecks can emerge where species exhibit limited dispersal capacity because of a lack of suitable habitat, thereby preventing population connectivity (e.g., lack of gene flow between populations of corkwing wrasse, *Symphodus melops*, in the North Sea and Portugal) (Knutsen et al., 2013). Significant correlation has been found between hypoxia thresholds and hyperbaric thresholds of taxonomic groups, suggesting that the synergistic effects of temperature, pressure, and oxygen concentration may constrain the capacity of marine invertebrates and fishes to respond to changes in environmental conditions through range shifts (Brown and Thatje, 2014). These results corroborate previous projections that polar species—and thus the fisheries that target them—are likely to be more vulnerable to climate change due to constrained ecological niches (e.g., Cheung et al., 2009), and further suggest that tropical and temperate fauna may experience substantial range expansion under the combined influence of ocean warming and deoxygenation (Brown and Thatje, 2014). Indeed, in some locations, it is thought that hypoxia may function as a greater driver of poleward shifts than warming (e.g., poleward shifts of southern groundfish communities in the Pacific Northwest basin Okey et al., 2014).

Climate-induced local (i.e., landward) and global (i.e., poleward) range shifts are also likely to occur for shallow tropical water systems and coastal mangroves, which support fisheries by providing nursery grounds and sheltered habitats that are critical for many species. Mangrove habitats are expected to respond to higher temperatures and CO_2 concentrations through poleward range shifts and faster growth rates, with species richness increasing at higher latitudes (Ross and Adam, 2013). Southern and eastern range expansions have already been reported in Australia (Ross and Adam, 2013). While research suggests that mangroves may be able to migrate landwards in response to low scenarios of SLR (e.g., Gazi Bay in Mombasa, Africa), adaptation probabilities have been shown to decrease under higher rates of SLR due to saline intrusion (Di Nitto et al., 2014), accompanied by decreased growth rates (Mitra, 2013). Species-specific adaptation is also influenced by interspecific competition and recruitment strength, which may alter community composition within mangrove forests (Di Nitto et al., 2014). Thus, evidence of the capacity of coastal habitats such as saltmarshes and mangroves to spatially respond to SLR is still considered inconclusive and site-specific (Spalding et al., 2014).

Strengthening AR5's findings, additional empirical evidence has been published demonstrating the effects of species' range shifts and habitat phase shifts—or the transformation of a habitat into an alternative state as a result of environmental pressures—on the structure, functionality, and health of marine ecosystems and the socioeconomic sectors that depend on them. For instance, the tropicalization of temperate marine ecosystems through poleward range shifts of tropical fish grazers has been shown to increase the grazing rate on temperate macroalgae, such as those in Japan and the Mediterranean, with similar trophic impacts expected to affect ecosystem structure in temperate reefs (Vergés et al., 2014a). Similarly, a heat wave event in western Australia altered biodiversity patterns of temperate seaweeds (90% dieback), invertebrates, and demersal fish, leading to a tropicalization of community structure (Thomson et al., 2014). The sensitivity of species' responses to ocean warming through range shifts can be affected by ecosystem status: for example, increased reef community resilience to tropicalization has been observed through protection from fishing (Bates et al., 2013). Thus, not only do phase shifts alter the availability of targeted species to fisheries, but fisheries can also play a synergistic role in reducing the resilience of ecosystems to climate change. As projected by Wong et al. (2014), temperature-mediated herbivory has since been shown to prevent kelp ecosystems from recovering from climatic drivers (e.g., effect of overgrazing of kelp beds in southern Japan (Vergés et al., 2014a); tropical herbivores preventing re-growth of kelp in Western Australia (Bennett et al., 2015); herbivorous tropical rabbitfish converting macroalgal forests into barrens in the Mediterranean (Vergés et al., 2014b). Phase shifts have also been documented in polar regions: for example, macroalgal colonization of newly ice-free regions has recently occurred in Antarctica (Quartino et al., 2013), and bluefin tuna have been found in the waters east of Greenland, having shifted northwards in response to warmer temperatures and to follow the northward shift of important prey species (MacKenzie et al., 2014).

Projected Impacts on Fisheries' Yield, Catch Quality, and Composition

New evidence suggests that range shifts can significantly alter the availability and composition of commercial fisheries catches, thereby having socioeconomic implications for fisheries, markets, and consumers. In Mexico, 10 of the top 12 highest fished species—including the South American pilchard (*Sardinops sagax*) and Penaeus shrimp—were projected to decline in catch by 2050 under the severe climate change scenario (Sumaila et al., 2014). The observed subtropicalization of European pelagic fish communities in the North and Baltic Seas has altered the availability of economically-important species, with a shift from Atlantic herring and European sprat (1960s to 1980s) to Atlantic mackerel, Atlantic horse mackerel, European pilchard, and European anchovy (1990s onwards) in response to warming (Montero-Serra et al., 2014). In tropical regions, evidence of community phase shifts from coral-to algal- or sponge-dominated reefs has been linked to reductions in reef functionality and fisheries yield (Bell J. J. et al., 2013). Altered interspecific interactions between sympatric coastal fishes have also been observed in the Mediterranean under warmer conditions, with a cooler-water fish (e.g., rainbow wrasse, *Coris julis*) being displaced by a more dominant warmer-water fish (e.g., ornate wrasse, *Thalassoma pavo*) (Milazzo et al., 2012). These examples support the theory that there will be "winners" and "losers" under climate change, with warm-adapted species outcompeting cold-adapted species in temperate marine ecosystems, accompanied by changes in the composition of fisheries' landings. However, increased temperature has also been shown to affect the physiology and interspecific competition exhibited by Arctic fish fauna, such as the Arctic staghorn sculpin, *Gymnocanthus tricuspis* (Seth et al., 2013), thereby potentially altering the quality, availability, and composition of traditional foods of polar communities.

Recent research continues to improve our understanding of potential future changes in primary productivity and zooplankton composition, which are important causal links to projecting future fisheries production. Models indicate an overall reduction in global primary production of 2–13% (Bopp et al., 2013), but a lack of understanding of the drivers of interannual and multidecadal climate variation and the influence of species-specific responses to climate change effects increases uncertainty regarding future primary production trends (Chavez et al., 2011). Development of high-resolution, shelf-seas, lower-trophic-level ecosystem models has improved projections of NPP in areas that are most important to fisheries (Barange et al., 2014). Moreover, an increasing number of Earth System Models with ocean biogeochemical components explicitly include zooplankton in their model structures, thereby providing projections of future changes in zooplankton production (e.g., Stock et al., 2014), which influences fisheries yield. Importantly synergistic effects have been found to alter projected outcomes: for example, despite individual stressors leading to declines in production, a combination of increased temperature and nutrient loads was shown to increase zooplankton production and food web efficiency in a microcosm experiment conducted in Baltic Sea conditions (Lefébure et al., 2013). However, despite these recent developments, the projected outcomes of synergistic effects on productivity are still supported by experimental evidence.

Studies continue to advance our understanding of how species' body sizes are likely to change under climate change, as supported by simulations of phase shifts between ecosystems (Ainsworth and Mumby, 2014) and by projections of climate-related impacts on ecophysiology through reduced oxygen availability (Cheung et al., 2013b). In a global model of pelagic communities, maximum body size and biomass were found to increase at high latitudes and to strongly decrease at low- to mid-latitudes in response to changes in the availability of food necessary to support metabolic requirements (Lefort et al., 2014), which agrees with previous projections. Such changes are likely to affect commercial fisheries through a reduction in the mean size of landed fish. For instance, empirical evidence of reductions in body sizes has been found for six of eight commercial fish species over a 40-year period in the North Sea, which coincided with a 1–2°C increase in water temperature and resulted in a 23% reduction of the mean yield-per-recruit (Baudron et al., 2014). A reduced supply of nutrients resulting from greater stratification may also yield a reduction in the average size of phytoplankton and increase the number of trophic links within food webs, which in turn would reduce energy transfer efficiency (Bell J. D. et al., 2013).

Recent studies have strengthened evidence that ocean acidification has a significant negative effect on the survival, calcification, growth, development and abundance of marine taxa (Kroeker et al., 2013), and interacts synergistically with increased temperatures to reduce species tolerance (Wittmann and Pörtner, 2013). However, recent research has shown that species' resilience to ocean acidification varies considerably across species (Range et al., 2013) and functional groups (Branch et al., 2013), with variable responses to synergistic factors. For instance, resilience to the synergistic impacts of ocean warming and acidification has been observed among juvenile sea urchins, yet conditions leading to shorter and weaker spines suggest increased vulnerability to predation (Wolfe et al., 2013). Research on species targeted by commercial fisheries—specifically, spider crabs (*Hyas araneus*), northern shrimp (*Pandalus borealis*), Antarctic krill (*Euphausia superba*), and European lobsters (*Homarus gammarus*)—suggests that crustaceans may be less severely impacted than molluscs by exposure to higher concentrations of CO_2 (Branch et al., 2013). Complex relationships arising from modeled food web responses to ocean acidification suggest that trophic cascades and contradictory effects are likely to arise from changes in predator-prey dynamics: for example, projected declines in copepod abundance in Puget Sound yield increases in microzooplankton (prey) and decreases in herring (predator) abundance, yet reduced macrozooplankton and euphausiid biomass release some pressure on copepods and, in turn, benefit herring (Busch et al., 2013). Acidification-induced changes in the flow of energy through, and dynamics of, food webs thereby illustrate the importance of key groups (e.g., copepods) to ecosystem structure and function (Busch et al., 2013), and to ensuring the availability of key commercial fisheries stocks (e.g., herring).

New studies continue to indicate that oxygen-depleted hypoxic conditions are a major global environmental issue influenced by anthropogenic and climatic drivers, with particular relevance to tropical and temperate coastal ecosystems and sectors (Bauer et al., 2013). Time-series observations in the Atlantic, Pacific, and Indian Oceans have shown declining oxygen levels since the 1950s (Keeling et al., 2010; Gilly et al., 2013). Studies indicate that the expansion of extreme oxygen minimum zones (eOMZs) in some regions may lead to habitat compression and reduced abundance of species of pelagic and mesopelagic fish and zooplankton with low hypoxic tolerances. Recent research has diverged from existing projections of expanding OMZs, arguing that a weakening of equatorial Pacific winds may lead to a contraction of anoxic conditions in the North Pacific despite the potential for a global, stratification-driven decline in O_2 supply (Deutsch et al., 2014). This global reduction in oxygen supply is expected to exacerbate reductions in the mean body sizes of fishes under warmer temperatures (Cheung et al., 2013a), thereby detrimentally affecting the quality and mean biomass of fisheries' yield. However, new opportunities for fisheries may arise from an increased abundance of hypoxia-tolerant organisms, which have also been shown to alter predator-prey dynamics and provide food for commercially-important species (e.g., Salvanes et al., 2015).

As reported in AR5, future changes in upwelling systems and the ramifications for fisheries' yields remain uncertain (Pörtner H. O. et al., 2014), but studies have contributed increasingly to strengthening our understanding of regional differences (de Lavergne et al., 2014; Sydeman et al., 2014). Stratification is projected to increase across most of the tropical Pacific, with synergistic interactions between temperature and salinity reinforcing stratification in the areas around the Pacific Warm Pool, South Pacific Convergence Zone (SPCZ), and intertropical converge zone (ITCZ) (Ganachaud et al., 2012). Ensemble projections obtained from 36 of the models from the fifth Coupled Model Intercomparison Project (CMIP5) support these projections, suggesting a weakening of deep Southern Ocean convection associated with surface freshening and stratification under climate change, which in turn may reduce the production rate of Antarctic Bottom Waters and alter ocean heat and carbon storage processes (de Lavergne et al., 2014). In contrast, a recent meta-analysis of 22 studies of eastern-boundary regions shows that upwelling-favorable winds have intensified in the California, Benguela, and Humboldt systems but weakened in the Iberian system in the past decades (up to 60 years), with the intensity of change consistent with warming pattern (Sydeman et al., 2014). This provides evidence to support the hypothesis of upwelling intensification in eastern boundary upwelling systems under climate change, which could lead to an enhanced nutrient supply in subtropical euphotic zones and a potential increase in fisheries production or, alternatively, to an increase in acidic and hypoxic conditions in shelf habitats (Sydeman et al., 2014), which could detrimentally impact species sensitive to these parameters.

In addition to changes in yield, the quality of fish stocks may be detrimentally affected by increased occurrence of disease transfer and cumulative mortality under warmer temperatures. For instance, diseases such as *ichthyophous* (ichthyophoniasis) reduce the market value of finfishes, thereby having wide-ranging and significant economic and ecological impacts (Burge et al., 2014). Likewise, the loss of keystone predators through disease, such as the dramatic die-off of sea stars along the Pacific coast of North America from a newly-identified densovirus (Hewson et al., 2014), can dramatically change ecosystems (Feehan and Scheibling, 2014) and, in turn, the composition and quantity of fisheries yield.

Regional Impacts on Fisheries

Studies continue to emphasize the vulnerability of tropical (Barange et al., 2014) and polar marine ecosystems (Clark et al., 2013) to climate change, with projected risks borne by the developing nations and communities that depend upon marine and coastal resources for food and economic security (Barange et al., 2014)**.** Recent projections suggest that ecosystems at higher latitudes will generally experience increases in primary production, while those at lower latitudes are likely to experience decreases (Barange et al., 2014). However, evidence of community phase shifts arising from climate-related drivers has been found for most regions, including tropical (Inoue et al., 2013; Ainsworth and Mumby, 2014), temperate ecosystems (Wernberg et al., 2012; Thomson et al., 2014; Vergés et al., 2014a), and polar ecosystems (Quartino et al., 2013).

Tropical fisheries

The biophysical impacts of climate change and ocean acidification on tropical marine ecosystems, with particular attention to coral reefs, were addressed with great detail in AR5 (Gattuso et al., 2014b). In particular, AR5 expressed high confidence that warming and acidification would lead to coral bleaching, mortality and decreased constructional ability, indicating that coral reefs were therefore the most vulnerable ecosystem to ocean warming and acidification, with little scope for adaptation (Wong et al., 2014). Having reached general consensus regarding the impacts of individual climate-related drivers on coral reefs (Chan and Connolly, 2012; Ateweberhan et al., 2013), studies have since sought to understand the synergistic effects of multiple stressors on coral reef resilience (Mumby et al., 2013; Ban et al., 2014; McClanahan et al., 2014) and the processes that influence reef adaptation and recovery (Dixson et al., 2014; Palumbi et al., 2014; Roff et al., 2014).

Studies have now discovered that some species of coral have the capacity to acquire heat resistance through acclimatization (Palumbi et al., 2014) and to recover from bleaching events (Roff et al., 2014). For example, changes in symbiotic communities from stress-sensitive to stress-tolerant symbionts following bleaching events can lead to increased thermo-tolerance among corals (Silverstein et al., 2014). This has been supported by modeling studies that have indicated that some adaptive responses have already resulted in higher thermal tolerances in some corals (Logan et al., 2013). Recent studies have also suggested that biogeochemical responses of coral reef communities to ocean acidification could partially offset changes in seawater pH (12–24%) and the aragonite saturation state (15–31%) (Andersson et al., 2013). In other cases, biofilm-induced larval settlement for coral reef sponges was found to exhibit higher settlement success among biofilm communities developed at higher seawater temperatures (e.g., *Rhopaloeides odorabile* in the Great Barrier Reef), suggesting groups that may be more resilient to increased temperatures under climate change (Whalan and Webster, 2014).

However, the capacity for recovery or adaptation has been shown to be less certain if multiple anthropogenic and environmental stressors act in concert (Palumbi et al., 2014), with taxon-specific responses (Whalan and Webster, 2014). For instance, changes in water quality through nutrient loading and sedimentation can increase the severity of coral disease and bleaching (Vega Thurber et al., 2013), while improved water quality management can aid reef resilience and recovery (Gurney et al., 2013). Ocean acidification can also decrease calcification and increase reef erosion, making reefs increasingly susceptible to storm damage and SLR (Silbiger et al., 2014). Scientists have noted that observed changes in net ecosystem calcification could, in fact, be primarily due to increased dissolution of $CaCO_3$ rather than decreased calcification (Eyre et al., 2014). Other documented responses have noted that cumulative impacts of repeated bleaching events could lead corals with little or no phenotypic plasticity to become increasingly sensitive to bleaching, with responses to singular bleaching events being insufficient to gauge subsequent resilience (Grottoli et al., 2014). The inclusion of such adaptive responses (e.g., directional genetic selection, symbiont shuffling) and management strategies in models is important for accurately predicting how ocean warming and acidification may affect coral reefs, with one such example reducing the frequency of mass bleaching events by 20–80% (scenario-dependent) by 2100, compared with "no adaptive response" projections (Logan et al., 2013).

The accompanying impacts on tropical coastal communities and fisheries have increasingly been explored, with evidence supporting AR5's hypothesis that there will be "winners" and "losers" under climate change. AR5 estimated that a reduction in coral cover and associated fisheries production would likely lead to net revenue losses as early as 2015 in the Caribbean (Wong et al., 2014), and projections have since suggested that greater instances of declines in fisheries catch potential are likely to occur in tropical regions (Barange et al., 2014). Modeled estimates suggest that the diversity of exploited species is likely to decrease under both RCP 8.5 and 2.6 due to a decrease in habitat suitability, with the magnitude of the decline positively correlating with the level of emissions (Jones and Cheung, 2015). There are likely to be variable impacts within tropical regions: for example, eastward range shifts in response to climate-related drivers are expected for skipjack tuna by 2050, leading to increased catches for Pacific Island countries to the east of 170°E and decreased catches for those to the west (Bell J. D. et al., 2013). Fewer catches in the western EEZs of Papua New Guinea (−11%) and the Solomon Islands (−5%) are expected to translate to a 0.1 to 0.4% decline in GDP because of the large size of their economies (Bell J. et al., 2013). In Bangladesh, prawn postlarvae fishers have been impacted indirectly by increased intrusion of saline water into agricultural land, which has increased fishing pressure from displaced farmers, while climate-related drivers have and are expected to lead to a net loss in revenue, food security, and livelihood sustainability (Ahmed et al., 2013).

Marine taxa in tropical regions are also likely to lose critical habitats such as coral reefs, mangroves, and seagrasses through phase shifts toward other habitats (e.g., macroalgae; Kroeker et al., 2012; Ainsworth and Mumby, 2014), with corresponding declines in fisheries productivity (Bell J. D. et al., 2013). While phase shifts could lead to new or increased fishing opportunities, such as increased shrimp biomass and landings through a reduction in carnivorous macrobenthos, it is likely that local communities will need to abandon traditional harvests in lieu of less valuable but more abundant species (Ainsworth and Mumby, 2014). Reduced fitness of commercially important species, such as coral trout (*Plectropomus leopardus*; Johansen et al., 2013), could also have implications for the sustainability of coral reef fisheries.

The interdependence between different tropical marine habitats has been highlighted recently, suggesting cascading effects across ecosystems through habitat loss (Saunders et al., 2014). Coastal vegetative habitats such as seagrasses function as nurseries for the early life-stages of reef fishes and are, in turn, sheltered from incoming waves by coral reefs (Saunders et al., 2014). This suggests that a climate- and CO_2- driven loss of coral reefs or other critical habitats may therefore have large-scale implications across ecosystems (Saunders et al., 2014) and the sectors that depend on them. The importance of coastal lagoon ecosystems to fishing, aquaculture, tourism, and industrial sectors, particularly within the Mediterranean Sea, demonstrates how biophysical changes could yield detrimental socioeconomic impacts across sectors, thereby reducing local food and economic security (Marques et al., 2014).

Temperate and subtropical fisheries

Overfishing has been shown to be the major driver of catch declines in heavily exploited ecosystems globally (Pauly and Zeller, 2016), although warming-driven changes in species composition are also affecting fisheries (Pinsky and Fogarty, 2012; Cheung et al., 2013b). For instance, total catch decline in the Mediterranean has been primarily linked to overexploitation (Vasilakopoulos et al., 2014; Tsikliras et al., 2015), with fewer instances of changes in the abundance of individual species having been linked primarily to changes in climate (Milazzo et al., 2012; Teixeira et al., 2014; Gamito et al., 2015).

Moving forward, anthropogenic pressures such as these are likely to be exacerbated under climate change, with climate-induced declines in catch projected for fisheries in the Northeast Pacific (Ainsworth et al., 2011; Barange et al., 2014), Northwest Atlantic (20–22% declines; (Guenette et al., 2014), and Northeast Atlantic (8.3% decrease in maximum catch potential; (Jones et al., 2014). An ecosystem-based assessment of synergistic climate change effects on the Nova Scotian shelf of eastern

Canada projected a 19% (optimistic scenario) to 29% (pessimistic scenario) reduction in biomass with accompanying declines in fisheries catch potential (–20 to 22%, respectively; Guenette et al., 2014). Likewise, declines in seafloor biomass have been projected for more than 80% of deep-sea biodiversity hotspots around the world by the end of the century (2091–2100), with up to a 38% decrease in benthic biomass in parts of the Northeast Atlantic (Jones et al., 2013).

Over the last few years, studies have demonstrated the link between sea surface temperatures (SST) and fisheries landings in temperate and subtropical regions (Tzanatos et al., 2013; Teixeira et al., 2014; Gamito et al., 2015). Portuguese fisheries have experienced declines in landings of temperate fish and increased landings of subtropical and tropical species between 1970 and 2011, which have been statistically linked to changes in SST; since the latter species are often of greater commercial importance, increased SST under climate change may offer opportunities for fishers in the Mediterranean (Teixeira et al., 2014). Conversely, culturally-important sponge fisheries in the Mediterranean Sea have been threatened by climatic and anthropogenic stressors such as ocean warming, overfishing, and species invasions (Pérez and Vacelet, 2014), all of which are likely to continue under climate change. Likewise, the loss of economically valuable and endangered corals as a result of ocean acidification could lead to considerable losses in revenue, with values of 230–300 US$ kg^{-1} for thin juvenile branches of red coral (*Corallium rubrum*) and up to 50,000 US$ kg^{-1} for Pacific Corallium sp. colonies with a diameter greater than 4 cm (Bramanti et al., 2013).

A recent study projected that climate-induced changes in relative environmental suitability and fisheries catch potential would translate to a 10% loss in net present value within the UK's exclusive economic zone by 2050, without accounting for the additional fuel and gear costs that might be incurred (Jones et al., 2014). Economic impacts are also likely to extend to seaports where fisheries' landings are taken through increased maintenance costs associated with corrosion from ocean acidification, disruption of transport, and damage to infrastructure through storm surges, SLR, and flooding (Becker et al., 2013; Nursey-Bray et al., 2013).

Polar Fisheries

Discernible impacts attributed to climate change have been recorded in polar marine ecosystems, but studies evaluating these impacts remain scarce and primarily focus on species of economic importance, such as cod and shrimp, or on marine mammals (Wassmann et al., 2011; McBride et al., 2014). Recently, polar ecosystems and corresponding fisheries have experienced a marine "Klondike," or the expansion of industrial exploration polewards in response to a reduction in the spatial extent of sea ice, with industrial fisheries and aquaculture alike increasingly finding new commercial opportunities at higher latitudes (Christiansen et al., 2013). Moving forward, declines in the temporal and spatial extent of sea ice cover are likely to provide finfish fisheries with greater access to stocks, thereby offering new opportunities (Constable et al., 2014). In particular, the Antarctic krill fishery has been suggested as a significant opportunity for expansion under climate change through changes in sea-ice extent, but the opportunities and losses with respect to this fishery remain ambiguous (Constable et al., 2014). For instance, projections have suggested that climate change could have a negative effect on Antarctic krill growth habitat (Hill et al., 2013), with krill embryos and larvae exhibiting enhanced energetic requirements and delayed development in response to elevated CO_2 levels (Kawaguchi et al., 2013). Likewise, while recent observations suggest that invertebrate species may be invading deep-sea and benthic habitats in the Southern Ocean, the potential for highly productive pelagic finfish to invade this region appears low due to minimal projected changes in the thermal gradient (McBride et al., 2014). However, the opening of trans-Arctic trade routes through reduced sea ice cover has been discussed as a potential driver of species invasions through ship-mediated transport and natural dispersal, which will likely alter the dynamics and structure of Arctic ecosystems (Ware et al., 2013; Miller and Ruiz, 2014). To date, there is accumulating evidence of species that have shifted into polar regions in response to warmer temperatures (Astthorsson et al., 2012; MacKenzie et al., 2014),

Recent studies project that a loss of critical habitat, including sea ice, is likely to lead to an increase in genetic connectivity and disease transfer between previously isolated populations of marine fauna (Post et al., 2013; Wisz et al., 2015), while a longer open-water season through decreased sea-ice cover could increase coastal erosion and storm impacts (Barnhart et al., 2014). A recent study projected an Atlantic-Pacific fish interchange, with up to 41 species entering the Pacific and 44 species entering the Atlantic by 2100 via the Northwest and Northeast Passages (Wisz et al., 2015). This interchange would alter the composition and predator-prey dynamics of ecosystems, with corresponding changes to existing fisheries yields and potential new opportunities within the Northwest Passage (Wisz et al., 2015). Recent research has also provided new insight regarding the susceptibility of polar marine ecosystems to light-driven tipping points emerging from changes in ice loss and solar irradiance. Areas without ice and snow following the summer solstice are particularly vulnerable to abrupt changes resulting from increased solar exposure through earlier ice loss; for this reason, future ice loss could lead to autotroph-dominated polar ecosystems with higher productivity, but lower regional biodiversity (Clark et al., 2013).

The geopolitical consequences associated with an increasingly ice-free Arctic are of critical concern not only with respect to maintaining the ecological structure and function of polar ecosystems, but also to the local communities that depend on marine resources for a range of ecosystem services (Christiansen et al., 2013). Increased marine access through sea-ice loss is likely to lead to increased industrial development, resource extraction, and shipping opportunities (Miller and Ruiz, 2014), with the accessibility of near-coastal and remote marine zones of all eight Arctic nations anticipated to increase by up to 28% by 2050 (Post et al., 2013).

Small-scale fishing communities in polar regions are likely to be detrimentally affected by temperature- and pH-induced changes in fisheries due to a large dependence on local harvests for food and economic security (AMAP, 2013). However, community-based assessments of socioeconomic impacts on rural and Indigenous coastal populations risk undervaluing the importance of marine harvests to Arctic cultures given their role in forming cultural identity and providing essential nutritional requirements (AMAP, 2013). Thus, while the broad range of species harvested by indigenous communities offers opportunities for adaptation through alternative harvests, they may be accompanied by seasonal or cultural losses (AMAP, 2013). Moreover, despite the projected increases in the relative abundance of fish stocks, increased competition over new resources and reduced availability of traditionally harvested species may severely inhibit fishing opportunities, while limited management offers few precautionary controls to ensure sustainable fisheries management under climate change (AMAP, 2013; Lam et al., 2014). Moreover, the growing presence of industrial fisheries under climate change may lead to intensified bottom trawling and unprecedented bycatch, affecting ecosystem function and structure and the availability of indigenous peoples' traditional foods (Christiansen et al., 2013).

A recent estimate projected that total fisheries revenue in the Arctic region may increase by 39% (14–59%) by 2050 relative to 2000 under the Special Reports on Emission Scenario (SRES) A2, while ocean acidification is expected to reduce the potential increases in fisheries catch and revenues (Lam et al., 2014). On the other hand, while increased anthropogenic activity in the Arctic has been linked to economic opportunities and ecological concerns (Larsen et al., 2014), Whiteman et al. (2013) argue that the global economic implications associated with climatic change in the Arctic have been ignored. For instance, the release of methane from thawing permafrost off northern Russia alone has been valued at $60 trillion in the absence of mitigation (Whiteman et al., 2013). After accounting for global changes in sea level, economic and non-economic sectors, and the melting of ice sheets, the mean projected cost of climate-related impacts fell between $82 trillion ("low-emissions" scenario) and $400 trillion ("business-as-usual" scenario), of which the majority of the projected cost (80%) is expected to be borne by developing nations in Africa, Asia and South America (Whiteman et al., 2013).

Aquaculture

Projected Impacts on Future Shellfish and Fish Aquaculture Production

Aquaculture production formed 90.4 million tonnes, (live weight equivalent) as of 2012, contributing approximately US$144.4 billion to the global economy in food products and an additional US$222.4 million in non-food products, such as pearls and seashells (FAO, 2014). While few studies have provided quantitative estimates of economic impacts associated with climate-induced changes in aquaculture production, studies have offered assessments of the likelihood of regional losses or gains.

Climate- and acidification-related impacts on aquaculture are expected to vary by location, species, and method of aquaculture. Latitudinal and taxon-specific trends have been identified, with the farming of higher trophic level species (e.g., trout farming in northern Mediterranean countries) expected to exhibit higher mortality rates and lower productivity under warming (Rosa et al., 2014). Conversely, inland production in southern countries tends to be based on more resilient species (e.g., carp and tilapia farming in Egypt), and may therefore experience increased metabolic rates, growth rates, and overall production (Rosa et al., 2014). The projected resilience of freshwater species is attributed to faster growth rates associated with warming and an increase in the availability of freshwater through increased precipitation (Bell J. D. et al., 2013).

Despite the capacity to control for conditions, recent studies suggest that aquaculture is likely to be both negatively and positively affected by changes in precipitation, temperature, drought, storms, and floods, all of which would have socioeconomic implications (Bell J. D. et al., 2013; FAO, 2014; Li et al., 2014). For instance, aquaculture facilities in the Caribbean and Latin American regions are likely to be vulnerable to ocean acidification and extreme weather events, with the potential for flooding in the Caribbean to affect local facilities (FAO, 2014). Similarly, the economically valuable black pearl industry in Polynesia is expected to be vulnerable to increased SST and ocean acidification, which—given its role in employing thousands of people on remote atolls—is expected to lead to a loss in local revenue and employment (Bell J. D. et al., 2013).

SLR is further expected to impact aquaculture production through increased intrusion of saline water into deltas and estuaries, where aquaculture commonly occurs (e.g., Mekong and Red River deltas in Viet Nam and the Ganges-Brahamputra Delta in Bangladesh) (De Silva, 2012). In Bangladesh, where fish cultivation and agriculture are the main occupations in coastal regions, fish cultivators have already reported production problems associated with increased salinity and disease prevalence (Garai, 2014). As the greatest producers of aquaculture, small-scale Asian practices in coastal bays are at high risk from storms, wave surges, and high winds, with the potential for significant losses for local livelihoods (De Silva, 2012). Li et al. (2014) estimated both positive and negative economic impacts for Chinese aquaculture, with lower latitudes likely to experience predominantly negative impacts as a result of increased water temperatures and reduced primary production, leading to significant impacts on food security and employment. In particular, increased precipitation yielded significant benefits to profit, while increased weather variability was associated with lower profit, highlighting the sensitivity of aquaculture production to sudden, extreme weather events (Li et al., 2014). However, these impacts may be reduced by selecting more saline-tolerant and brackish-water species for aquaculture operations (Rosa et al., 2014).

The increased threat of infectious disease to aquaculture under climate change has been explored more recently, with shellfish larval dispersal having been implicated in the transport of disease (Rowley et al., 2014). The susceptibility of molluscs and crabs to diseases such as vibriosis has been linked to SST, and temperature-driven poleward range shifts are expected from an influx of new pathogens in temperate regions (Rowley et al., 2014). These may pose an increased threat to human health through the consumption of contaminated seafood and water-borne pathogens (Rosa et al., 2014). The toxicity of common pollutants to fish can increase with higher temperatures, while a decrease in salinity has been shown to increase toxicity for some species by altering the chemical speciation of metals (Fabbri and Dinelli, 2014). As reported in AR5, studies have continued to warn that increased ocean temperatures and eutrophication under climate change may lead to a greater occurrence of toxic tides, such as more frequent HABs in the Mediterranean Sea, and thereby detrimentally affect aquaculture production and human health (Himes-Cornell et al., 2013; Rosa et al., 2014). From a global perspective, cumulative mortality from disease was found to be relatively higher in tropical aquaculture than in temperate aquaculture (88 vs. 34%, respectively), with juvenile invertebrates exhibiting greater vulnerability in comparison with adult finfish (Leung and Bates, 2013). This evidence highlights a management concern for developing nations at subtropical and tropical latitudes that would otherwise benefit from increased food security through aquaculture.

Overall, with decreased dependence on wild-caught stocks for fishmeal and farming combined with technological developments, recent research suggests that aquaculture could significantly contribute to global food security under climate change (Barange et al., 2014), but highlights the trade-offs between coastal sectors that are likely to occur (Ruckelshaus et al., 2013). Longer growing seasons, faster growth rates, and lower winter mortality arising from increased temperatures could yield positive effects at mid- to high-latitudes (e.g., extended breeding periods for Indian carps in fish farm hatcheries in West Bengal; De Silva, 2012; Li et al., 2014). However, trade-offs are expected to occur as aquaculture industries compete with other sectors (e.g., wild-caught fisheries, coastal tourism) for different ecosystem services derived from coastal and wetland habitats that are sensitive to climate change (Ruckelshaus et al., 2013), and tropical and subtropical aquaculture may encounter challenges associated with SLR and an increased risk of disease susceptibility.

Coastal Tourism and Local Economies

Tourism is one of the largest sectors in the global economy, with coastal tourism comprising a significant part of global revenue derived from the tourism sector. Climate-induced impacts on tourism have considerable ramifications for local, national, and regional economies, including the transportation, fishing, and agricultural sectors. Drivers such as ocean warming and acidification are likely to lead to changes in SST, the composition and abundance of marine biodiversity, and sea levels (Pörtner H. O. et al., 2014; Howes et al., 2015). In addition, extreme and abrupt climatic events such as storms and cyclones will impact coastal environments and communities. Collectively, these drivers will lead to changes in the basic conditions for coastal tourism, including climatic parameters (air temperature, precipitations, wind speed, etc.), underwater parameters (SST, invasive species such as jellyfishes, etc.), and coastal hazards (erosion, marine flooding, etc.). Such changes will affect the main components of the tourism industry—such as tourists' preferences, tourism operators' strategies, and the transportation market—and thus the tourism supply and demand balance at the global scale.

Ocean Warming and Acidification Impacts on Tourism Flows

As documented in AR5, changes in the quality and abundance of coral reef cover are expected to cause socio-economic and environmental concerns for small island developing states (SIDS) and developing countries, with particular relevance to the tropics (Wong et al., 2014). Coral reefs draw significant tourism each year, supporting recreational activities, such as diving and snorkeling, and supporting coastal communities and auxiliary sectors.

Tropical coastal areas are unlikely to be the only areas affected. In Europe, Spain's coastal tourism is expected to face water shortages, reduced opportunities for different tourism modalities, and, in turn, fewer job opportunities in the tourism industry (Saurí et al., 2013). In particular, new findings suggest that there may be "winners" and "losers" in coastal tourism as a result of higher temperatures that discourage southward tourism flows in Europe while reinforcing northwards flows (DiSegni and Shechter, 2014).

Recent studies provide additional evidence that species range shifts are likely to alter tourism flows. For instance, poleward range shifts in the United States could yield new opportunities for recreational fishing in temperate regions, while warmer conditions could benefit some species purposively introduced for recreational fishing (Nelson et al., 2013). Conversely, increases in the prevalence of tropical box jellyfish through climate-induced poleward range shifts could detrimentally affect coastal tourism and water-related activities in subtropical and temperate regions. In particular, a recent study found that irukandjii jellyfish (*Alatina* nr *mordens*) polyps were resilient to the combined effects of ocean acidification and warming, suggesting that these polyps would be able to colonize new areas under climate change and thereby increase socioeconomic losses and hospitalization events (Klein et al., 2013). Increased prevalence and transmission of diseases are also likely to occur under warmer ocean temperatures, with empirical evidence of poleward shifts in disease outbreaks under warmer conditions (Burge et al., 2014). Importantly, adverse publicity accompanying an increased risk of disease transmission in tropical and subtropical regions could further have deleterious impacts on coastal tourism (DiSegni and Shechter, 2014).

Impact of Ocean Warming and Acidification on Tourism Operators' Infrastructure, Strategies, and Revenue

Key impacts arising from warming and SLR are likely to include degradation of coastal infrastructure through coastal erosion, marine flooding, high winds, and/or inundation of rivers, as well as changes in the attractiveness of destinations due to changes in air and sea temperatures, landscapes, and swimming conditions. Coastal flooding is increasingly a concern both for developed and developing cities, with coastal populations expected to grow by 25% by 2050 (Aerts et al., 2014).

Ocean warming and acidification is therefore expected to not only affect tourism in SIDS and developing countries, but also in developed areas such as Europe and the United States. Consequently, the economic implications of coastal tourism are expected to be significant for most of the destinations around the world, and especially at the local scale. In the United States, 7.52 million jobs and $1.11 trillion in sales are supported by tourism, with the majority of tourism occurring in coastal regions that are expected to experience changes in weather conditions and extreme events, such as typhoons and hurricanes (Himes-Cornell et al., 2013). Beach recreation values are also expected to decline in response to narrower beaches resulting from SLR and erosion, with considerable losses for local economies (e.g., $1 billion loss between 2006 and 2080 in North Carolina Whitehead et al., 2009; Nelson et al., 2013). As principal assets of coastal tourism, the loss of beaches could significantly impact local economies in subtropical and topical regions, and could incur additional costs associated with coastal protection and infrastructure repairs (DiSegni and Shechter, 2014).

Human Health and Food Security

Knowledge regarding the impacts of climate change on human health in coastal regions has departed little from that outlined in AR5 (Pörtner H. O. et al., 2014; Wong et al., 2014). While the future consequences of ocean warming and acidification on food security derived from aquaculture and capture fisheries are difficult to estimate (Portner J. R. et al., 2014), regional trends illustrate the particular vulnerability of developing nations and the rural and indigenous communities that depend on tropical and polar marine ecosystems for food security (Larsen et al., 2014; Portner J. R. et al., 2014; Pörtner H. O. et al., 2014).

Declines in fisheries catch potential are expected to detrimentally impact food security in tropical nations—predominantly those in South and Southeast Asia and SIDS—through reduced access to nutrition (Barange et al., 2014), while recent studies suggest that competition over resources and ocean acidification may offset some of the gains in fisheries catch potential projected for polar regions (Lam et al., 2014; Larsen et al., 2014; Miller and Ruiz, 2014). For instance, a 20% reduction in coral reef fish production by 2050 is expected to detrimentally affect food security for Pacific Islanders, with even well-managed fisheries failing to meet nutritional requirements of a growing population (Bell J. D. et al., 2013). Recent shifts in anchovy and sardine regimes in the Pacific Ocean also demonstrate altered patterns of food availability (Wheeler and von Braun, 2013). However, while acidification and warming-related declines in fisheries productivity in South and Southeast Asia are expected to reduce food security, opportunities have been identified through the regions' growing aquaculture production (Barange et al., 2014). Although range shifts have been projected to increase the availability of fish stocks in polar regions, these projections are uncertain (AMAP, 2013; Larsen et al., 2014), and studies have suggested that ocean acidification and increased competition arising from increased accessibility through reduced ice cover (Lam et al., 2014; Miller and Ruiz, 2014). Likewise, SLR is expected to increase the risk of loss of agricultural land in coastal regions through flooding, with further detriment to food security (Wheeler and von Braun, 2013).

Recent research has demonstrated that Indigenous fishing communities that depend on traditional marine resources for food and economic security are particularly vulnerable to climate change through a reduced capacity to conduct traditional harvests because of limited access to, or availability of, resources (Larsen et al., 2014; Weatherdon et al., 2016). For instance, shellfish and traditional clam beds—which form an integral part of the culture, economy and diet of many Indigenous communities situated along the Pacific Coast of North America—may be affected detrimentally by increased SST, SLR, and changes in ocean chemistry and circulation patterns (Lynn et al., 2013). This has critical implications for the food and economic security of coastal Indigenous communities, the preservation and transfer of their traditional knowledge, and the legal upholding of their rights to access traditional resources (Lynn et al., 2013).

Hosts and parasites are likely to accompany species poleward range shifts under climate change, with disease outbreaks having been witnessed under warmer conditions (e.g., faster replication of disease among corals in the Caribbean) (Altizer et al., 2013). Such diseases can lead to community shifts and trophic cascades through the loss of habitat or keystone species (Altizer et al., 2013). For instance, Arctic warming has been projected to facilitate disease transmission between eastern and western Arctic species (Post et al., 2013). While these impacts predominantly focus on ecological systems, such changes are likely to affect human health through declines in food security (e.g., disease propagation in crops or traditional foods) and increased opportunities for pathogen transfer between hosts (Altizer et al., 2013).

Supporting AR5's findings, research continues to suggest that human exposure to diseases is likely to increase under climate change through storm surges and SLR, each leading to an expansion of the geographical and seasonal ranges of bacteria (Burge et al., 2014). For instance, a poleward range shift of outbreaks of *Vibrio* has been witnessed as far north as the Baltic Sea and Alaska (Burge et al., 2014). Sub-Saharan Africa is projected to experience a southern climate-induced shift in malaria incidences, while additional health concerns include food insecurity, hunger and malnutrition, natural disasters, air pollution, communicable, and non-communicable diseases, high-injury burden, mental health, and occupational health (e.g., heat stress) (Ziervogel et al., 2014). Similarly, SIDS have been framed as "canaries in the coal mine" with respect to climate change and health given their dependence on marine resources for nutrition and the prevalence of infectious diseases, each of which are expected to be affected detrimentally by climate change (Hanna and McIver, 2014). Despite these concerns, data supporting causal pathways between climatic variables and human health outcomes through marine ecosystems are still limited (Ziervogel et al., 2014).

Finally, HABs and toxins associated with climate change have continued to be identified as priority areas for research (Fleming L. E. et al., 2014). HABs are expected to increase in frequency through higher coastal eutrophication, and are likely to have detrimental effects on coastal productivity, nursery grounds, biodiversity, and human health through the consumption of contaminated seafood (Himes-Cornell et al., 2013; Marques et al., 2014).

Brief Insights on Coastal Adaptation Across Sectors

Adaptation in Fisheries, Aquaculture, and Auxiliary Sectors

The capacity for fisheries to mitigate and adapt to climate change has been increasingly studied in different regional contexts. Some examples of adaptation strategies to climate change effects on fisheries include changing targeted species (e.g., Cheung et al., 2013a) and establishing multi-lateral fisheries agreements (e.g., Miller et al., 2013). In one context, three-fleet dynamic models were used to investigate the effects of climate change on the ecological, economic, and social viability of the Tasmanian rock lobster fishery in southern Australia, highlighting the importance of dynamic adaptation in response to environmental conditions and stock abundance (Hamon et al., 2013). While it remains uncertain whether small-scale fisheries will have the mobility to follow target species, those with access to multiple gears may be able to adapt more easily to climate-related changes in stock composition (Gamito et al., 2013, 2015; Teixeira et al., 2014).

Livelihood diversification continues to be supported within the literature as a viable adaptation strategy in response to reduced production in some fisheries and aquaculture operations (Bell J. D. et al., 2013; Ruckelshaus et al., 2013). For example, poleward range shifts may provide opportunities for fisheries to redirect fishing effort toward emerging fisheries; however, the capacity for fisheries to capitalize on these shifts would depend on the adaptive capacity of local economic, cultural, and regulatory institutions (Nelson et al., 2013; Ruckelshaus et al., 2013).

Adaptation options for aquaculture production have also been suggested. Livelihoods based on pearl production may be supported through deeper-water cultivation, selective breeding, and selection of suitable sites for production (Bell J. D. et al., 2013). Richards et al. (2015) concluded that aquaculture is likely to be more viable in the future than wild fisheries because of the capacity to monitor and modify conditions to avoid excessive stressors arising from ocean acidification and other climate-related drivers. After accounting for different life stages, they further gauged that prawns would likely be more resilient to ocean acidification than scallops in Queensland, Australia, due to a greater diversity of species across a larger geographical distribution (Richards et al., 2015). The capacity for aquaculture stocks to be more resilient to climate change than wild stocks is further supported through selective breeding and vaccination, which provide means of increasing stock resilience and reducing the frequency of disease transmission (Himes-Cornell et al., 2013). Intertidal oyster reefs have also demonstrated resilience by exhibiting the capacity to outpace SLR, and can function as buffers to help preserve vegetated estuarine ecosystems and coastal structures from erosion (Rodriguez et al., 2014).

Recent studies exploring climate-related impacts on seafood supply chains have found that there is a limited understanding of how these impacts will affect other parts of the supply chain, despite a comprehensive understanding of impacts at the harvest stage (Fleming A. et al., 2014). Increased stakeholder awareness in the Australian seafood industry regarding potential impacts of climate change on supply chains has led participants to highlight adaptation options within their respective sectors, including improved fuel efficiency, breeding programs, altered industry structure, simplified regulations, and improved public awareness (Fleming A. et al., 2014).

Adaptation in the Tourism Sector

The tourism sector is sensitive to both gradual changes in climatic and oceanic conditions, and to extreme and abrupt weather events. Historically, the tourism industry has exhibited high adaptive capacity in response to shocks (e.g., financial crises, natural disasters, and disease), strongly suggesting the capacity to respond to future climate-induced variability through dynamic adaptation (Scott, 2014). For instance, recreational fishers in the Arctic appear to be willing to target alternative species, suggesting a future change in the relative composition of recreational catches under climate change (AMAP, 2013).

The capacity for stakeholders to respond to long-term changes, such as increased mean seasonal temperatures and beach erosion, is less understood. Destinations may benefit from or lose opportunities as a result of changes in observed or perceived attractiveness (Ciscar et al., 2011; Magnan et al., 2012; Arent et al., 2014). This indicates that various strategies must be evaluated when considering the diversity of tourist operators' responses, which are influenced by their level of dependence on local environmental conditions. Schematically, while it may be feasible for international companies to relocate their investments, small business owners may face limitations when endeavoring to protect local resort infrastructure. With respect to location attractiveness, a study evaluating perceptions of climate-related impacts along the Balearic coasts of Spain noted that a lack of concern indicated by citizens could lead to a higher degree of vulnerability since adaptive measures could be seen as unnecessary, and therefore not implemented (March et al., 2013). This could, in turn, affect the feasibility of coastal tourism markets given increased vulnerability of local real estate. Forecasting stakeholders' responses to ocean warming and acidification is challenging as stakeholders are not equal in terms of their risk perception, interests, and adaptive capacities, and thus they will adopt different strategies. Here again, there will inevitably be winners and losers (Arent et al., 2014), both among international tourism companies and small enterprises.

While it is very complex to forecast changes in tourists' preferences, companies' adaptation strategies, and transportation companies' responses to changes in a destination's attractiveness, models have begun to emerge in the past decade and, although encountering limitations (Arent et al., 2014), have started identifying key questions related to tourism flows, tourism operators' adaptation strategies, and economic impacts at the local scale.

Ecosystem-Based Adaptation for Coastal Communities

Adaptation strategies suggested in AR5 included the restoration or ecosystem engineering of marine vegetative habitats to assist with buffering climate-related impacts and to provide shelter for fish nurseries and important coastal habitats (Wong et al., 2014). Studies have continued to suggest the capacity for coastal ecosystems, including intertidal wetlands and reefs, to protect coastlines by reducing wave energy, minimizing impacts from storm surges, increasing sedimentation, and/or reducing erosion (Spalding et al., 2014).

While promising, ecosystem-based coastal adaptation approaches are still emerging, and require an improved understanding of key ecosystem services and values for coastal communities in order to assess risk, aid coastal development planning, and build decision support systems (e.g., Spalding et al., 2014). Managing realignment of coastal ecosystems as they migrate landwards or polewards can aid in proactively planning for future conditions, while hybrid engineering structures can provide an integrated way of conserving ecosystems and ecosystem services (e.g., carbon storage and sequestration; regulating nutrient fluxes; maintaining species biodiversity). This could in turn increase coastal protection (Duarte et al., 2013; Spalding et al., 2014). Proposed mechanisms for protecting these ecosystems include strategic zoning that anticipates habitat migration and minimizes climate-related impacts (e.g., Wetland Buffer Guidelines implemented by the Queensland government) and the use of predictive models to situate reserves (e.g., landscape and SLR models) (Shoo et al., 2014). Evidence that the preservation of coastal vegetative habitats and wetlands can yield a net uptake of atmospheric CO_2 has continued to emerge, with examples found for boreal, temperate, and subtropical seagrasses (Tokoro et al., 2014), and agreement that coastal wetlands aid in regulating GHG emissions continues to accumulate (Ross and Adam, 2013). Importantly, recent research has suggested that the magnitude of carbon storage can vary greatly by location (i.e., depth or latitude) and species (e.g., temperate and subtropical seagrasses in coastal Australia) (Lavery et al., 2013). Given this potential to mitigate anthropogenic emissions, some authors argue that the expansion of the current REDD+ (Reducing Emissions from Deforestation and Forest Degradation) scheme to include vegetative coastal ecosystems could provide opportunities for SIDS and other developing states to mitigate climate change, while promoting restoration of coastal habitats that have been degraded or removed for development (Duarte et al., 2013).

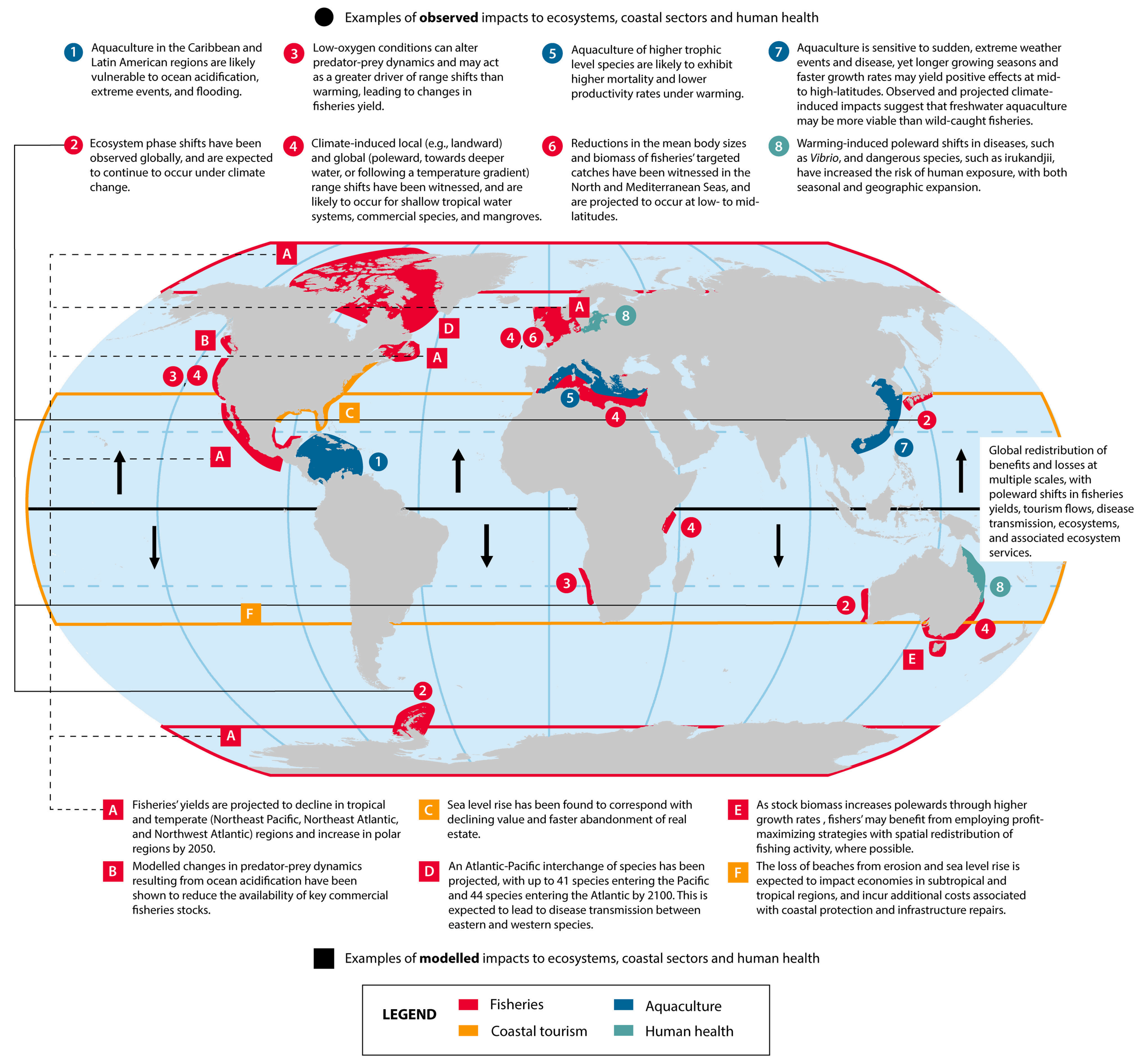
Recent studies have also highlighted the economic feasibility of restoring and maintaining coastal habitats, which offer a cost-effective measure of increasing coastal protection and ecosystem services when compared with "hard" engineering solutions, such as seawalls (Nelson et al., 2013). Coastal habitats can also yield profit for commercial and recreational activities occurring on the coast, with the potential for the benefit-to-cost ratio of such eco-engineering solutions to exceed that of "hard" solutions (Nelson et al., 2013). From another perspective, the loss of ecosystem services accompanying SLR-induced coastal erosion in Europe is estimated at €2.9 billion per year by 2050, resulting in an almost 15% decrease in coastal ecosystem service values compared to 1975 (Roebeling et al., 2013). In South America, the coastal lagoon ecosystems in Uruguay provide a range of ecosystem services, including food, fuel and fiber, flood and storm protection, erosion control, and carbon sequestration (Fanning, 2014). In particular, climate-induced impacts on ecosystem service values in a coastal lagoon, Laguna de Rocha, were calculated for carbon sequestration services (annual revenue of €178,487 to €290,540 between 2008 and 2011 in the Laguna de Rocha) and habitat maintenance and cultural values (damage costs avoided method yielded an inferred value of US $300,000 between 1986 and 2012) (Fanning, 2014). Thus, maintenance of coastal habitats functions both as a cost-effective measure for protecting coastal infrastructure and as a method of preserving economically important ecosystem services.

While examples of coastal habitat recovery exist (e.g., recovery of cordgrass in New England following die-off), the capacity for habitats to fully recover to their previous state is less certain and subsequent trophic cascades can further reduce habitat resilience (e.g., loss of ribbed mussel beds in New England without cordgrass habitats, which in turn limits cordgrass production) (Brisson et al., 2014). In the context of coral reefs, Rogers et al. (2014) used a scenario-based approach to evaluate the sensitivity of 14 ecosystem services to different climate-related drivers and management strategies. While their research suggests that reserves will remain effective for reefs with high structural complexity, maximizing ecosystem services in degraded reefs would require a portfolio of management strategies (e.g., provision of artificial complexity, coral restoration, fish aggregation devices, herbivore management) (Rogers et al., 2014). Yet, it may be possible for full ecosystem services to be restored without fully recovering the original ecosystem structure (Brisson et al., 2014).

AGREEMENT AND POINTS OF DEPARTURE FROM AR5

In agreement with the findings of AR5, strong evidence continues to indicate that climate change will lead to a redistribution of benefits and losses at multiple scales, and across human and ecological systems (Barange et al., 2014). For instance, tourism flows, diseases, and species are projected to shift polewards under warmer temperatures (Magnan et al., 2012; Cheung et al., 2013a; Burge et al., 2014; DiSegni and Shechter, 2014). Latitudinal trends suggest benefits accruing in polar regions for commercial sectors (e.g., new fishing and extraction opportunities, increased shipping access) (Post et al., 2013; Miller and Ruiz, 2014), while losses are projected for tropical and subtropical regions through reductions in fisheries catch potential and reduced food and economic security (Barange et al., 2014). Ecologically, "winners" and "losers" are also expected to arise from community phase shifts and trophic cascades (Bell J. et al., 2013; Inoue et al., 2013; Ainsworth and Mumby, 2014), with some species outcompeting others under multiple stressors (Brown and Thatje, 2014) (**Figure 1**; **Table 2**).

Empirical and theoretical evidence continues to support the occurrence of climate-induced range shifts of species and coastal marine ecosystems, which were reported with very high confidence in AR5 (Pörtner H. O. et al., 2014). Shallow tropical water systems and coastal mangroves are expected to shift polewards, with species richness increasing at higher latitudes (Ross and Adam, 2013). While projections suggest the capacity for some coastal vegetative ecosystems to shift landward in response to sea level rise, adaptive capacity and growth rates may



● Examples of **observed** impacts to ecosystems, coastal sectors and human health

1. Aquaculture in the Caribbean and Latin American regions are likely vulnerable to ocean acidification, extreme events, and flooding.
2. Ecosystem phase shifts have been observed globally, and are expected to continue to occur under climate change.
3. Low-oxygen conditions can alter predator-prey dynamics and may act as a greater driver of range shifts than warming, leading to changes in fisheries yield.
4. Climate-induced local (e.g., landward) and global (poleward, towards deeper water, or following a temperature gradient) range shifts have been witnessed, and are likely to occur for shallow tropical water systems, commercial species, and mangroves.
5. Aquaculture of higher trophic level species are likely to exhibit higher mortality and lower productivity rates under warming.
6. Reductions in the mean body sizes and biomass of fisheries' targeted catches have been witnessed in the North and Mediterranean Seas, and are projected to occur at low- to mid-latitudes.
7. Aquaculture is sensitive to sudden, extreme weather events and disease, yet longer growing seasons and faster growth rates may yield positive effects at mid- to high-latitudes. Observed and projected climate-induced impacts suggest that freshwater aquaculture may be more viable than wild-caught fisheries.
8. Warming-induced poleward shifts in diseases, such as *Vibrio*, and dangerous species, such as irukandjii, have increased the risk of human exposure, with both seasonal and geographic expansion.

Global redistribution of benefits and losses at multiple scales, with poleward shifts in fisheries yields, tourism flows, disease transmission, ecosystems, and associated ecosystem services.

A Fisheries' yields are projected to decline in tropical and temperate (Northeast Pacific, Northeast Atlantic, and Northwest Atlantic) regions and increase in polar regions by 2050.

B Modelled changes in predator-prey dynamics resulting from ocean acidification have been shown to reduce the availability of key commercial fisheries stocks.

C Sea level rise has been found to correspond with declining value and faster abandonment of real estate.

D An Atlantic-Pacific interchange of species has been projected, with up to 41 species entering the Pacific and 44 species entering the Atlantic by 2100. This is expected to lead to disease transmission between eastern and western species.

E As stock biomass increases polewards through higher growth rates , fishers' may benefit from employing profit-maximizing strategies with spatial redistribution of fishing activity, where possible.

F The loss of beaches from erosion and sea level rise is expected to impact economies in subtropical and tropical regions, and incur additional costs associated with coastal protection and infrastructure repairs.

■ Examples of **modelled** impacts to ecosystems, coastal sectors and human health

FIGURE 1 | Geography of modeled and observed impacts of climate change on marine and coastal ecosystems, sectors, and human health. This figure, inspired by Figure 3 from Gattuso et al. (2015), shows examples of modeled and observed impacts of climate change, and is not meant to be exhaustive.

be reduced under higher levels of salinity (Mitra, 2013; Di Nitto et al., 2014). Furthermore, the capacity for coastal habitats to shift landwards may be inhibited by the construction of storm-resilient infrastructure or coastal development (Lynn et al., 2013). Ecosystem phase shifts and trophic cascades have been observed and projected across multiple ecosystems and latitudes, including tropical coral reefs (Bell J. J. et al., 2013; Inoue et al., 2013; Ainsworth and Mumby, 2014), tidal marshes (Langley et al., 2013), subtropical ecosystems (Milazzo et al., 2012), temperate ecosystems (Wernberg et al., 2012; Thomson et al., 2014; Vergés et al., 2014a), and polar ecosystems (Quartino et al., 2013). These indicate a corresponding poleward shift in the distribution of ecosystem services derived from these species and ecosystems, with diverse outcomes for all coastal sectors and communities.

Noted as an uncertainty in AR5, new research suggests that a species' capacity to track climate velocity may be hindered geographically by "climate sinks," where local climatic conditions differ from the temperature gradients tracked by migrating species (Burrows et al., 2014), and that some species may be unable to keep pace with climate velocity (Hiddink et al., 2014). Other recent issues that have been highlighted include the physiological plasticity to adapt to climate change (Seebacher et al., 2015), potential for genetic bottlenecks to arise in situations where dispersal is constrained (Knutsen et al., 2013),

TABLE 2 | Examples of modeled and observed impacts of climate change on marine and coastal sectors and human health.

Topic			**References**
Fisheries and auxiliary sectors	Fisheries' yield and catch quality	Poleward range shifts and ecosystem phase shifts to occur globally, altering the availability, and composition of fisheries' landings; shifts observed in tropical, subtropical, temperate, and polar regions. Increase in mean body size and biomass of landings at high latitudes; strong decrease at low- to mid-latitudes. Poleward redistribution of fishing effort	**[1]**; 2, 4; 6
		Negative effect of OA on the survival, calcification, growth, development, and abundance of marine taxa; synergistic impacts with increased temperatures leading to reduced species tolerance; resilience to OA varies strong across species and functional groups	**[2]**; B
	Tropical fisheries	Declining fisheries yields and species diversity in tropical regions; ecosystem phase shifts, leading to declines in fisheries productivity; habitat interdependence leading to cascading ecosystem effects	**[3]**; A, 2
	Temperate and subtropical fisheries	Declining catch projected for the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic. Seafloor biomass projected to decline for more than 80% of deep-sea biodiversity hotspots by the end of the century; observed changes in landings composition in the Mediterranean, with subtropical and tropical species replacing temperate species. Expected 10% loss in net present value within the UK's EEZ	**[4]**; A
	Polar fisheries	Invertebrate species may invade deep-sea and benthic habitats, but pelagic finfish may not due to minimal changes in the temperature gradient. Loss of sea ice leading to increased genetic connectivity, disease transfer, access to fisheries stocks, and ship-mediated transport, altering the composition and predator-prey dynamics of ecosystems, and corresponding yields. Higher productivity, but lower regional biodiversity. Increased competition over resources; total fisheries revenue in the Arctic may increase by 39% (14–59%) by 2050, yet OA is expected to reduce this potential increase by 15%	**[5]**; A, D
Shellfish and fish aquaculture		Higher trophic-level species to experience higher mortality rates and lower productivity. Longer growing seasons, faster growth rates, and lower winter mortality from increased temperatures could positively affect production. Caribbean and Latin American aquaculture likely to be vulnerable to OA and extreme weather events; Chinese and small-scale Asian aquaculture operations likely to encounter both positive and negative impacts. Cumulative mortality from disease found to be greater in tropical aquaculture than temperate aquaculture; juvenile invertebrates exhibit greater vulnerability than adult finfish	**[6]**; 1, 5, 7
		Decreased dependence on wild-caught stocks for fishmeal and farming and selection of more resilient species could contribute to global food security. Trade-offs from competition with other sectors for different ecosystem services derived from sensitive habitats	**[7]**
Coastal tourism flows and economic impacts		Likely "winners" and "losers" in coastal tourism, with poleward tourism flows. Poleward range shifts of diseases and dangerous species could detrimentally impact tourism. Range shifts could lead to new opportunities for recreational activities (e.g., fishing). Economic implications are expected to be significant for most destinations around the world. Beach recreation values expected to decline from SLR and erosion. Developing and developed countries alike to be impacted by ocean warming and acidification, with degradation of coastal infrastructure, coastal erosion, flooding, and extreme weather. Property owners likely to invest in defensive expenditures before abandoning real estate, leading to price volatility	**[8]**, C, F
Impacts of climate-related drivers on human health		Reduction in fisheries-derived food security in tropical nations, particularly for South and Southeast Asia and SIDS. New opportunities from aquaculture production. SLR expected to detrimentally impact agricultural land in coastal regions. Increased likelihood of disease outbreaks through poleward range shifts and warmer temperatures. Natural disasters, harmful algal blooms, air pollution, and heat stress are expected to detrimentally affect human health	**[9]**; 8

References in bold (i.e., ***[1]****) refer to references at the bottom of the table, while the other references (e.g., A, 2) are linked to* ***Figure 1****.*

[1] *Bates et al., 2013;Bell J. J. et al., 2013; Cheung et al., 2013b; Hamon et al., 2013; Ainsworth and Mumby, 2014; Baudron et al., 2014; Lefort et al., 2014; Montero-Serra et al., 2014; Sumaila et al., 2014; Thomson et al., 2014; Vergés et al., 2014a,b; Bennett et al., 2015; Quartino et al., 2013.*

[2] *Branch et al., 2013; Kroeker et al., 2013; Range et al., 2013; Wittmann and Pörtner, 2013.*

[3] *Kroeker et al., 2012; Bell J. D. et al., 2013; Ainsworth and Mumby, 2014; Barange et al., 2014; Saunders et al., 2014; Jones and Cheung, 2015.*

[4] *Ainsworth et al., 2011; Becker et al., 2013; Jones et al., 2013, 2014; Nursey-Bray et al., 2013; Tzanatos et al., 2013; Barange et al., 2014; Guenette et al., 2014; Teixeira et al., 2014; Gamito et al., 2015.*

[5] *AMAP, 2013; Christiansen et al., 2013; Clark et al., 2013; Hill et al., 2013; Kawaguchi et al., 2013; Post et al., 2013; Ware et al., 2013; Lam et al., 2014; McBride et al., 2014; Miller and Ruiz, 2014; Wisz et al., 2015.*

[6] *Bell J. D. et al., 2013; Leung and Bates, 2013; De Silva, 2012; Garai, 2014; Li et al., 2014; Rosa et al., 2014; Rowley et al., 2014.*

[7] *Ruckelshaus et al., 2013; Barange et al., 2014.*

[8] *Whitehead et al., 2009; Himes-Cornell et al., 2013; Klein et al., 2013; Nelson et al., 2013; Aerts et al., 2014; Burge et al., 2014; DiSegni and Shechter, 2014.*

[9] *Altizer et al., 2013; Bell J. D. et al., 2013; Himes-Cornell et al., 2013; Wheeler and von Braun, 2013; Barange et al., 2014; Fleming L. E. et al., 2014; Hanna and McIver, 2014; Marques et al., 2014; Ziervogel et al., 2014.*

and species' thresholds to hypoxia, temperature and pressure, which may constrain their capacity to migrate in response to climate change (Brown and Thatje, 2014). These findings inform our understanding of how regional compositions of fisheries' landings are likely to change as climate change progresses, and of how these changes are likely to affect local economies and food security.

While recent studies continue to emphasize the vulnerability of tropical communities to climate change, new research suggests the capacity and conditions of the coral reef ecosystems upon which they depend to acquire tolerance to warmer temperatures (Logan et al., 2013; Palumbi et al., 2014) and to recover from bleaching events (Roff et al., 2014). However, this capacity is less certain under cumulative pressures, with taxon-specific responses (Vega Thurber et al., 2013; Palumbi et al., 2014; Silbiger et al., 2014; Whalan and Webster, 2014).

New research on observed and projected climate-induced impacts suggest that sustainable freshwater aquaculture may be more viable than wild-caught fisheries under climate change (Bell J. D. et al., 2013; Rosa et al., 2014; Richards et al., 2015), thereby contributing to global food security (Barange et al., 2014). Increased temperatures are expected to lead to higher growth rates among some cultivated species (e.g., tilapia, carp), while the capacity to control for environmental variables and the likelihood of increased rainfall may yield greater resilience and opportunities for tropical and subtropical aquaculture production (Rosa et al., 2014; Richards et al., 2015). However, changes in the efficiency of aquaculture production associated with an increased prevalence of disease under warmer temperatures are uncertain, and may detrimentally affect human health (Himes-Cornell et al., 2013; Leung and Bates, 2013; Rosa et al., 2014; Rowley et al., 2014). Moreover, new research highlights the potential for trade-offs to occur as coastal sectors compete for different ecosystem services derived from habitats that are sensitive to climate change (Ruckelshaus et al., 2013).

Since AR5, efforts to characterize and value ecosystem services in the context of climate change have been strengthened, with a specific focus on ecosystem-based adaptation (Lavery et al., 2013; Nelson et al., 2013; Roebeling et al., 2013; Fanning, 2014; Spalding et al., 2014). Coastal vegetative habitats have been highlighted as potential and economically efficient means of achieving multiple objectives by combining habitat restoration and climate change mitigation strategies (Nelson et al., 2013; Ross and Adam, 2013; Tokoro et al., 2014; Wong et al., 2014). Research continues to focus on the role of coastal habitats in carbon sequestration and storage, supporting the restoration and cultivation of such habitats to aid climate mitigation efforts (Duarte et al., 2013; Spalding et al., 2014).

Lastly, research continues to indicate that climate-induced changes in tourism flows are likely to create "winners" and "losers," with opportunities and losses arising from changes in environmental conditions and destinations' attractiveness. These changes could lead to substantial geospatial shifts in economic costs and benefits associated with tourism revenue and coastal infrastructure protection and repairs (Whitehead et al., 2009; Nelson et al., 2013; DiSegni and Shechter, 2014). Moreover, increased threat from invasive species (e.g., jellyfish), diseases, and extreme weather could reduce the attractiveness of destinations to tourists (Himes-Cornell et al., 2013; Klein et al., 2013; DiSegni and Shechter, 2014).

AUTHOR CONTRIBUTIONS

LW led the review and the development of the manuscript, and created **Figure 1**. WC designed and coordinated the review, contributed to the development of the manuscript, and provided feedback on all components of the manuscript. AM, AR, and US contributed to the development of the manuscript and provided feedback at various stages of its development.

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