Disciplinary reporting affects the interpretation of climate change impacts in global oceans

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Abstract

Climate change is affecting marine ecosystems, but different investigative approaches in physical, chemical, and biological disciplines may influence interpretations of climate-driven changes in the ocean. Here, we review the ocean change literature from 2007 to 2012 based on 461 of the most highly cited studies in physical and chemical oceanography and three biological subdisciplines. Using highly cited studies, we focus on research that has shaped recent discourse on climate-driven ocean change. Our review identified significant differences in spatial and temporal scales of investigation among disciplines. Physical/chemical studies had a median duration of 29 years (n = 150) and covered the greatest study areas (median 1.41 × 10^7 km^2, n = 148). Few biological studies were conducted over similar spatial and temporal scales (median 8 years, n = 215; median 302 km^2, n = 196), suggesting a more limited ability to separate climate-related responses from natural variability. We linked physical/chemical and biological disciplines by tracking studies examining biological responses to changing ocean conditions. Of the 545 biological responses recorded, a single physical or chemical stressor was usually implicated as the cause (59%), with temperature as the most common primary stressor (44%). The most frequently studied biological responses were changes in physiology (31%) and population abundance (30%). Differences in disciplinary studies, as identified in this review, can ultimately influence how researchers interpret climate-related impacts in marine systems. We identified research gaps and the need for more discourse in (1) the Indian and other Southern Hemisphere ocean basins; (2) research themes such as archaea, bacteria, viruses, mangroves, turtles, and ocean acidification; (3) physical and chemical stressors such as dissolved oxygen, salinity, and upwelling; and (4) adaptive responses of marine organisms to climate-driven ocean change. Our findings reveal that highly cited biological studies are rarely conducted on scales that match those of physical and chemical studies. Rather, we suggest a need for measuring responses at biologically relevant scales.

Keywords: baseline data, biological responses, climate change, interdisciplinary, marine ecosystems, observation bias, spatial and temporal scale

Introduction

Physical signals and biological responses of climate change are pervasive in marine ecosystems (Harley et al., 2006; Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2013; Rhein et al., 2013; Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). Anthropogenic climate change has altered global ocean temperatures and acidity, which influence other critical oceanographic properties, including global sea level, polar sea ice coverage, ocean circulation and stratification, and oxygen concentrations (reviewed in Doney et al., 2012). Diverse biological responses are associated with these physical and chemical changes. Responses such as shifts in species distribution, community composition, phenology, and abundance are largely consistent with climate change predictions (Poloczanska et al., 2013). However, the rates and magnitude of physical or chemical changes, and their associated biological impacts, are not identical across marine ecosystems (Burrows et al., 2011; Pinsky et al., 2013).

Understanding the scope of climate change impacts on marine environments requires integration of empirical observations, theory, and models across disciplines. Nevertheless, specific marine disciplines often apply distinct methodologies that operate at disparate scales,
influencing interpretations of global responses to climate (Parmesan, 2007). Studies of climate-driven change in marine environments may be impeded by spatially limited or generally short ocean time series, which are often inadequate to establish the necessary baselines upon which to assess change (Rosenzweig et al., 2008; Brown et al., 2011). The highest confidence in attribution of biological impacts to climate change occurs at the scale of ocean basins or larger (Parmesan et al., 2011). Long-term marine biological datasets are particularly lacking compared to key physical records (Brierley & Kingsford, 2009; Edwards et al., 2010; Koslow & Couture, 2015), yet they are necessary to understand how physical and chemical environmental changes may drive biological change. Mismatches in spatial and temporal sampling of biological responses compared to physical processes complicate climate change studies that require separation of complex natural cycles from climate change impacts (Hobday & Evans, 2013; Parmesan et al., 2013).

Studies on climate-driven ocean change rarely involve simultaneous sampling across physical, chemical, and biological systems over extended temporal or spatial scales, nor do they commonly incorporate natural climate variability (Edwards et al., 2010). Incompatible datasets, scale issues, and inappropriate statistical tests can limit inference in assessing broad effects across disciplines in marine climate change studies (Brown et al., 2011; O’Connor et al., 2015). Interactions among multiple climate and nonclimate stressors (e.g., fishing, pollution, habitat change), translation of controlled laboratory findings to real-world dynamics, and geographic biases persist in ocean change research (Wernberg et al., 2012), presenting additional challenges when comparing and integrating discipline-specific studies. The multitude of cross-discipline challenges associated with ocean change research raises fundamental questions, such as how sampling approaches for identification of ocean change vary across disciplines and what this variation means to our interpretations of climate change impacts in marine systems.

Our goal was to address these questions by reviewing the types of data available to detect changing ocean conditions across multiple marine disciplines, identifying disciplinary trends, and detecting areas where discourse on marine climate change has been lacking. We reviewed highly cited, contemporary literature on ocean change to provide a comprehensive assessment of the current discourse on climate change in marine environments. Specifically, we considered the following: (1) geographic scope of ocean change studies, (2) the spatial and temporal scales used to describe ocean change, (3) the oceanographic stressors implicated in biological responses, (4) the types of biological responses reported, and (5) field observations vs. laboratory manipulations. Our review encompasses hundreds of physical, chemical, and biological observations representing 19 specific research foci, or ‘themes’. We believe that enhanced recognition and understanding of discipline-specific differences and data limitations in ocean change research, as revealed by this review, will improve interpretation and communication of contemporary changes in marine ecosystems. No previous syntheses of marine climate impacts, to our knowledge, have examined in similar detail such a wide range of research foci among several marine disciplines. In particular, our comparison across biological and physical/chemical realms is a novel approach that helps identify key disciplinary differences that may affect interpretation of ocean change research. Our interdisciplinary approach reveals research areas worthy of expansion. For example, we suggest geographic regions that provide unique opportunities for more integrated studies considering multiple stressors, standardization of biologically meaningful metrics when synthesizing spatial and temporal scales of ocean change, and expanded support for interdisciplinary training and efforts.

Materials and methods

Disciplinary categorization

We focused our review among disciplines by classifying papers into two major groups: (1) those that addressed changes in the abiotic domain, consisting of papers on aspects of physical or chemical oceanography (referred to here as the ‘physical/chemical’ discipline), and (2) those that addressed changes in the biotic domain. We further divided the biotic domain into three subdisciplines, based on differences in process, species composition, and scale: (1) plankton communities, (2) benthic communities (specifically, macroalgae, seagrasses, mangroves, and invertebrates), and (3) vertebrates. We then subdivided the abiotic and biotic groups into 19 specific research ‘themes’ (see Table 1) for more thorough examination: 5 within the physical/chemical discipline and 14 within the three biological subdisciplines to span the range of marine taxonomic groups from the smallest (viruses) to the largest (mammals).

We selected our themes to represent a broad range of taxa and several lines of inquiry in physical/chemical oceanography, aiming to capture the most highly cited literature shaping contemporary scientific discourse on ocean change. Ocean acidity, temperature, sea level, sea ice, and dissolved oxygen are signals of climate change in global oceans (Doney et al., 2012) and as a result were the focus of our research themes in the physical/chemical discipline. Our categorizations of biological subdisciplines aimed to broadly define useful taxonomic groups and ecological distinctions. We focused on the smallest-bodied organisms at the lowest trophic levels (i.e.,
‘plankton communities’) as well as the largest-bodied organisms at the highest trophic levels (i.e., ‘vertebrates’) in pelagic systems. Our ‘benthic communities’ subdiscipline focused on organisms intermediate in size and trophic level, as well as ecological communities typically studied in coastal environments.

**Search criteria**

We searched the peer-reviewed ocean change literature using Web of Science, Google Scholar, citation lists, seminal review papers, and relevant journals (e.g., *Global Change Biology*, *Global Ecology and Biogeography*, *Geophysical Research Letters*, *Journal of Physical Oceanography*, *Marine Ecology Progress Series*). We used the number of citations in Google Scholar to identify the five most cited papers published per year from 2007 to 2012 for each theme, yielding a maximum of 30 papers per theme (see Appendix S1). We selected the 2007–2012 time frame as a pragmatic way to confine our searches, to assure that at least 1 year had elapsed to estimate number of citations, and to roughly coincide with the literature used in the most recent release of the Intergovernmental Panel on Climate Change (IPCC) Assessment Reports. Our search terms included combinations of ‘change’, ‘marine’, ‘climate change’, specific biological themes, and/or specific physical or chemical themes (e.g., ‘coral reef change’ or ‘coral reef ocean acidification’). We excluded review papers and projections of future change in an effort to strictly assess recent and direct observations of climate-related changes in marine environments, taken in both field and laboratory settings. Finally, at least one (and up to three) expert for each theme reviewed our list of highly cited studies to identify any influential studies that we potentially missed.

**Region and scale of investigation**

For each study, we recorded the temporal scale (i.e., study duration in years or fractions of years), spatial scale (i.e., approximate study area in km²), and geographic region of the study site or the field origin of laboratory organisms (see Table S1). We incorporated studies with continuous, periodic, or snapshot sampling, as done in other syntheses (e.g., Poloczanska *et al.*, 2013). If the exact study area was not provided, we used inset maps or geographic descriptions to determine approximate latitude and longitude for estimating study area. In the spatial and temporal analysis, we did not analyze

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**Table 1.** Number of highly cited studies reviewed within each research theme from marine biological subdisciplines and the physical/chemical discipline, from 2007 to 2012. Up to 30 papers (five per year) were reviewed for each theme, although <30 papers were reviewed if fewer than five papers were found within a year of a given theme.

| Discipline/subdiscipline and theme | No. of papers | No. of citations* (min – max) | No. of responses reported | Proportion of responses based on laboratory studies |
|-----------------------------------|---------------|------------------------------|---------------------------|---------------------------------------------|
| Benthic communities               |               |                              |                           |                                             |
| Coral reef                        | 30            | 32–448                       | 63                       | 0.29                                        |
| Kelp forest                       | 28            | 4–85                         | 48                       | 0.42                                        |
| Mangroves                         | 14            | 5–62                         | 20                       | –                                           |
| Rocky/sandy bottom                | 30            | 21–456                       | 69                       | 0.39                                        |
| Seagrass                          | 28            | 4–322                        | 57                       | 0.28                                        |
| Vertebrates                       |               |                              |                           |                                             |
| Bird                              | 30            | 6–79                         | 51                       | –                                           |
| Fish                              | 30            | 24–509                       | 50                       | 0.56                                        |
| Mammal                            | 27            | 1–130                        | 40                       | –                                           |
| Turtle                            | 18            | 1–130                        | 32                       | 0.03                                        |
| Plankton communities              |               |                              |                           |                                             |
| Archaeoplankton                   | 3             | 26–41                        | 4                        | 0.75                                        |
| Bacterioplankton                  | 17            | 7–220                        | 22                       | 0.64                                        |
| Phytoplankton                     | 26            | 15–274                       | 41                       | 0.54                                        |
| Virioplankton                     | 6             | 5–75                         | 6                        | 0.33                                        |
| Zooplankton                       | 24            | 18–306                       | 42                       | 0.12                                        |
| Physical/chemical oceanography    |               |                              |                           |                                             |
| Ocean acidity                     | 30            | 9–564                        | NA                       | NA                                          |
| Oxygen                            | 30            | 13–454                       | NA                       | NA                                          |
| Sea ice                           | 30            | 13–1128                      | NA                       | NA                                          |
| Sea level height                  | 30            | 27–848                       | NA                       | NA                                          |
| Sea surface temperature           | 30            | 5–1084                       | NA                       | NA                                          |
| Total                             | 461           | 1–1128                       | 545                      | 0.29                                        |

*Number of citations reported in Google Scholar during literature searches conducted March–April 2014.
studies that lacked adequate information to estimate temporal or spatial scale, or those that were conducted exclusively in the laboratory. In a few cases \((n = 9)\) papers, multiple spatial and temporal scales were described \(\text{e.g., when a laboratory study and field study were reported in the same study}\). In these cases, we used the maximum field study area or duration reported. We performed a two-step cluster analysis \textit{(IBM SPSS STATISTICS for Windows, version 19.0., IBM Corporation, Armonk, NY, USA)}, using study area and duration as clustering criteria to identify natural ‘study scale’ groupings \(\text{i.e., clusters}\) in the data. We specified the log-likelihood distance measure and the Bayesian information criterion \(\text{(BIC)}\) to construct the clusters and compared distributions of the cluster outputs using a nonparametric Kolmogorov–Smirnov test.

**Biological responses**

Ocean change studies addressing the biological effects of physical or chemical changes \(\text{i.e., those in the benthic, vertebrate, and plankton subdisciplines}\) often measured multiple biological response variables or included responses for more than one species. Therefore, we also cataloged each biological response reported. For each biological response, we recorded the number of stressors examined in each study, categorical data on the physical or chemical factor(s) driving the response \(\text{referred to here as a ‘stressor’}\) and type of biological response examined \(\text{(see Table S1)}\). In cases where multiple stressors were examined, we focused on the primary stressor identified by the author(s). We grouped stressors and responses into categories typically considered in studies of marine ecological responses to climate change \(\text{e.g., Brierley & Kingsford, 2009; Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012; Poloczanska et al., 2013)}\).

**Results**

We reviewed a total of 461 ocean change peer-reviewed papers, including 311 papers from biological subdisciplines \(\text{i.e., ‘benthic communities’, ‘vertebrates’, and ‘plankton communities’}\) and 150 from the physical/chemical oceanographic discipline. There were not always five papers available within each year for all designated themes, resulting in the review of fewer than 30 papers for some themes. In such instances, these papers were not only the most highly cited in that year, but also the only papers found. There was complete coverage \(\text{i.e., 30 papers per theme}\) of the physical/chemical discipline, but incomplete coverage of ocean change studies for all plankton themes, some benthic themes, and some vertebrate themes \(\text{(Table 1)}\). Number of citations per paper ranged among disciplines and themes, with the physical/chemical discipline attracting up to 1128 citations \(\text{i.e., for the ‘sea ice’ theme}\) compared to a maximum of 306 citations for the ‘zooplankton’ theme in the plankton communities subdiscipline \(\text{(Table 1)}\).

Geographically, we identified biases in the global distribution of highly cited ocean change studies that were not proportional to regional ocean surface area \(\text{(Eakins & Sharman, 2010)}\). For example, the North and South Pacific basins cover the greatest proportion of the Earth’s ocean surface \(\text{(21% and 25%, respectively)}\), yet did not represent the most frequently studied regions in our review \(\text{(Fig. 1)}\). Instead, the North Atlantic basin \(\text{(12% of the global ocean surface)}\) accounted for the greatest number \(\text{(n = 96, 21%)}\) of highly cited ocean change studies, followed by the Arctic basin \(\text{(area} = 4.3%; n = 67, 15\%\)}\). The Mediterranean Sea, making up <1% of the ocean surface, was also frequently studied \(\text{(n = 26, 6% of studies)}\) relative to its total surface area. Arctic studies were dominated by physical \(\text{(sea ice)}\) and vertebrate \(\text{(primarily marine mammal)}\) studies, whereas there was a more equal representation of all physical/chemical and biological disciplines among highly cited studies performed in the North Atlantic. The dominance of benthic studies in the Mediterranean was due to the abundance of shallow, coastal volcanic carbon dioxide vents providing natural sites to study the effects of acidification on benthic communities \(\text{e.g., Hall-Spencer et al., 2008; Rodolfo-Metalpa et al., 2011)}\). Relative to their expansive spatial coverage, the Indian \(\text{(20% surface area)}\) and South Pacific basins \(\text{(25% surface area)}\) were studied less frequently \(\text{(n = 14, 3% and n = 59, 13%, respectively)}\) and studies in those regions were primarily focused on coastal benthic communities. The South Atlantic \(\text{(11% surface area)}\) and Southern Ocean \(\text{(6% surface area)}\) were also poorly represented among the papers we reviewed \(\text{(n = 11, 2% and n = 20, 4%, respectively)}\), but had more equal representation from the four physical/chemical and biological disciplines, with the exception of the benthic communities subdiscipline in the Southern Ocean. Benthic studies were nearly absent from the highly cited ocean change research in polar regions.

Few highly cited studies \(\text{(~1%)}\) involved organisms exclusively grown and monitored in laboratory settings \(\text{(n = 5)}\) or studies that looked broadly over the extent of the entire tropical region \(\text{(n = 7)}\). Highly cited studies spanning the tropical ocean region were primarily physical/chemical, but a couple of benthic coral reef meta-analyses were also represented at this scale \(\text{(e.g., Carpenter et al., 2008; McCulloch et al., 2012)}\). A number of studies, primarily physical/chemical and plankton communities, were conducted in multiple regions \(\text{(n = 48, 10%)}\) or explored global patterns \(\text{(n = 55, 12%)}\). The physical/chemical discipline was particularly well represented at a global scale because authors used statistics to interpolate discrete samples from a cruise, buoy, or remote sensing to be representative of the
broad ocean basin (e.g., Reynolds et al., 2007; Domingues et al., 2008; Takahashi et al., 2009). Spatial and temporal scales of 377 highly cited ocean change studies were examined after laboratory studies were removed. Both spatial and temporal scales varied greatly among the physical/chemical discipline and biological subdisciplines, making it difficult to detect trends in the data beyond the predominance of physical and chemical studies at the largest spatial scales (Fig. 2a, Table 2). Nonparametric analysis indicated a significant difference in the distributions of both spatial (Kruskal–Wallis test, $P < 0.001$) and temporal (Kruskal–Wallis test, $P < 0.001$) scales across disciplines. A cluster analysis revealed two distinct clusters based on both the temporal and spatial scale factors shown in Fig. 2a. These two clusters were statistically different in terms of study area and duration (Kolmogorov–Smirnov test, $P < 0.001$; Fig. 2b). The ‘small-scale’ cluster ($n = 195$) was primarily comprised of ocean change studies that occurred at smaller spatial scales (median = 100 km$^2$) and over shorter durations (median = 7 years). The ‘large-scale’ cluster ($n = 163$) was comprised of studies that occurred at larger spatial scales (median = $1.4 \times 10^7$ km$^2$) and over longer durations (median = 31 years). Nearly three quarters of studies in the large-scale cluster were from the physical/chemical discipline, while the remaining one-quarter was predominately comprised of vertebrate studies (18%). In contrast, 84% of the studies in the small-scale cluster were from the biological subdisciplines: benthic communities (33%), vertebrates (31%), and plankton communities (20%). Considerable variation in both study duration and area was observed across the abiotic and biotic groups and among themes within each discipline or subdiscipline (Fig. 3, Table 2). Temporal scales ranged from studies lasting <1 day (e.g., kelp, phytoplankton, and seagrass in Staehr & Wernberg, 2009; Hopkinson et al.,...
Table 2  Number of ocean change studies (n), excluding laboratory studies, that reported the spatial and/or temporal scales of the study, with medians of the study area (km²) and duration (years) for each discipline or subdiscipline and research theme

| Discipline/subdiscipline and theme | n | n temporal | Median spatial scale (km²) | Median temporal scale (years) |
|-----------------------------------|---|------------|---------------------------|------------------------------|
| Benthic communities                |   |            |                           |                              |
| Coral reef                        | 18 | 17         | 2.4 × 10³                  | 9.0                          |
| Kelp forest                       | 15 | 18         | 125.0                     | 4.0                          |
| Mangroves                         | 13 | 12         | 7.30                      | 6.50                         |
| Rocky/sandy bottom                | 14 | 15         | 5.0                       | 8.0                          |
| Seagrass                          | 17 | 17         | 13.0                      | 2.0                          |
| Vertebrates                       | 88 | 89         | 1.45 × 10³                | 20.0                         |
| Bird                              | 29 | 30         | 160.0                     | 24.0                         |
| Fish                              | 14 | 14         | 1.61 × 10⁵                | 24.5                         |
| Mammal                            | 27 | 27         | 1.0 × 10⁵                 | 14.0                         |
| Turtle                            | 18 | 18         | 20.0                      | 17.50                        |
| Plankton                          | 31 | 47         | 512.0                     | 1.20                         |
| Archaeoplankton                   | 1  | 1          | 1.0                       | 1.0                          |
| Bacterioplankton                  | 6  | 6          | 1.0                       | 1.60                         |
| Phytoplankton                     | 14 | 15         | 1.0                       | 1.0                          |
| Virioplankton                     | 4  | 4          | 3.15 × 10⁵                | 1.16                         |
| Zooplankton                       | 6  | 21         | 3.80 × 10⁵                | 4.0                          |
| Physical/Chemical oceanography    | 148| 150        | 1.41 × 10⁷                | 29.0                         |
| Ocean acidity                      | 30 | 30         | 1.18 × 10⁴                | 10.50                        |
| Oxygen                            | 29 | 30         | 1.9 × 10⁵                 | 38.0                         |
| Sea ice                           | 29 | 30         | 1.41 × 10⁷                | 29.0                         |
| Sea level                         | 30 | 30         | 3.61 × 10⁸                | 44.50                        |
| height                            | 30 | 30         | 3.27 × 10⁸                | 51.0                         |

Total 344 365

2011; Arnold et al., 2012) to 301 years (in a sea level study, Jevrejeva et al., 2008). Highly cited plankton studies were conducted over the shortest temporal scales with a median duration of approximately 1 year. While study durations were primarily ≤1 year for archaeo- and bacterioplankton, durations were often several years for phyto-, viri- and zooplankton studies. For benthic communities, seagrass studies were of the shortest duration and coral reef studies were the longest, with nearly half of the coral reef studies lasting a decade or more. Vertebrate studies were typically of longer duration than studies of plankton or benthos and exhibited relatively less variation. The longest temporal scales occurred among the physical/chemical oceanography themes, with studies of oxygen, sea level height, and sea surface temperature (SST) often lasting several decades. Approximate study areas ranged from the smallest (0.002 km²) for a seagrass study in an outdoor mesocosm (Massa et al., 2009) to global-scale studies (~361 million km²), including two proxy studies of viral and phytoplankton abundance (i.e., Martinez et al., 2009; Danovaro et al., 2011) and several studies of SST and sea level height (e.g., Willis et al., 2008; Lyman et al., 2010; Church & White, 2011). For plankton communities, studies on archaea and bacteria were typically conducted under small spatial scales of around 1 km², but a few studies of viruses were conducted over the largest spatial scales (multiregional to global). Zooplankton studies incorporated large-scale continuously sampled plankton studies. With the exception of coral reef and some kelp forest studies, benthic communities papers tended to cover the smallest study areas. Marine vertebrate studies were of intermediate spatial scales. Studies of mammals and fish were of similarly large spatial scales and averaged two orders of magnitude larger than studies on marine birds and turtles. Consistent with the temporal data, physical/chemical studies typically had the largest spatial scales, often spanning areas more than an order of magnitude larger than other studies in other subdisciplines.

Biological response studies

We examined 545 biological responses from the 311 highly cited studies investigating potential biological changes (Table 1). Nearly 30% of these responses were measured in laboratory settings, but this varied greatly among biological subdisciplines and themes. For example, >50% of the biological responses among fish, archaeo-, bacterio-, and phytoplankton were measured in the laboratory compared to ≤5% for mangroves, birds, mammals, and turtles, clearly reflecting differences in tractability of experimental manipulations. For 85% of the biological changes examined in our database, the authors concluded that their results could be attributed to physical or chemical changes in the marine environment. Other factors, such as anthropogenic activities (e.g., fishing) or habitat degradation, were sometimes considered. It was not the goal of this review to assess confidence in the attribution of climate change impacts on marine systems, although other studies have addressed this issue extensively (e.g., Ploceanska et al., 2013; Hoegh-Guldberg et al., 2014; Hansen & Cramer, 2015).

We identified 11 categories of primary physical and chemical stressors among the biological response studies: atmospheric carbon dioxide, climate indices (e.g., Pacific decadal oscillation), dissolved oxygen, ocean...
acidification (e.g., pH, alkalinity, pCO₂), salinity, sea ice, sea level height, storms and precipitation, temperature (including SST, bottom temperature, or occasionally air temperature), upwelling processes, and secondary effects of physical changes (e.g., changes in physical habitat due to changes in temperature and chemistry). Most studies examined a response to a single stressor (59%; Fig. 4). Two stressors were occasionally studied (30%), and three or more were rarely studied (11%). Vertebrate studies examined multiple stressors more frequently than the other two biological subdisciplines. There was no association between the number of stressors examined and year of publication (Fig. 4).

The most frequent primary stressor considered among all three biological subdisciplines was temperature (44%; Fig. 5a), as found in Poloczanska et al. (2013). Ocean acidification (‘OA’) was the second most common primary stressor studied (36%). While the effects of OA were studied across all three biological subdisciplines, it was primarily examined in studies of benthic communities. Studies considering the effects of sea ice were largely focused on vertebrates. The other eight primary stressors constituted <10% of the biological response studies with salinity, upwelling, and dissolved oxygen being the least studied stressors.

Laboratory studies were used to examine the biological responses of a variety of stressors, including climate indices, dissolved oxygen, acidification, salinity, and temperature. Laboratory experiments involving OA were particularly common (65% of laboratory studies), followed by temperature (28%).

Primary stressors associated with each biological theme varied considerably (Fig. 5b). Temperature was the main stressor examined in plankton communities (61%) and was commonly examined across all benthic communities (35%) and vertebrate (45%) themes. Within benthic communities, the mangrove theme was unique in largely focusing on the effects of sea level height. Moreover, mangroves were the only theme for

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which atmospheric carbon dioxide was considered; this could be because they are directly vulnerable to both marine and atmospheric stressors. With the exception of mangroves, OA was the main stressor examined in benthic communities (52%). In particular, more than 50% of the rocky/sandy bottom and coral reef studies examined biological responses to OA. In contrast, fish studies were the only vertebrate theme investigating OA, all of which were conducted in the laboratory. With the exception of sea turtles, all vertebrate themes examined sea ice as a stressor, with mammal studies in particular having a strong focus on sea ice impacts (88% of mammal studies).

A variety of responses were examined across each of the biological themes within eight general categories: reproductive fitness (e.g., number of offspring produced), physiological effects (e.g., calcification rate, stress hormone response), phenological shifts, changes in distribution or range shift, dietary effects (e.g., body condition, diet, foraging preferences), changes in community structure (e.g., species composition), behavioral effects (e.g., antipredator response), or changes in population abundance and demography (e.g., recruitment rate, number of individuals). A single study examined evolutionary adaptation as a function of change in population growth (i.e., Lohbeck et al., 2012), which was included as a demographic response. Physiological changes (31%) and changes in abundance (30%) were most frequently reported (Fig. 6), followed by shifts in reproductive fitness (12%). The remaining five categories each constituted <10% of the responses reported. Physiological responses were most frequently measured in benthic communities, and nearly half (47%) were measured in the laboratory. Abundance studies were more evenly divided among the biological subdisciplines (Fig. 6a) and were examined by all themes, but
with varying frequency (Fig. 6b). Notably, changes in abundance were the main response studied by all themes in plankton communities. Dietary effects were not considered in any of the benthic communities studies included in this review, yet nearly all plankton and vertebrate studies examined dietary effects. Vertebrate studies exhibited the greatest diversity of biological response types, with turtle and bird studies often focusing on reproductive success and phenology more than any other themes.

Conclusions

Recent discussions on the state of global oceans are often marked with mounting concerns for the fate of marine species and communities (e.g., McCauley et al., 2015). However, Duarte et al. (2015) argue for increased scrutiny of the available evidence for “ocean calamities” and suggest that several observation and citation biases may lead to an unsupported perception of ocean condition. The goal of our study was to examine the current discourse on changing ocean conditions across multiple marine disciplines, identify disciplinary trends, and determine areas where discourse on marine climate change has been lacking. We provided a novel cross-disciplinary approach and reviewed a wider breadth of topics than previous syntheses, examining the nuanced intricacies of physical and chemical processes as well as biological impacts across research foci.

Our comprehensive review of highly cited literature revealed that current discourse on ocean change is shaped by potential research biases, disciplinary differences in research scope, and numerous research gaps. We identify several regions, taxa, physical and chemical stressors, types of biological responses, and scale issues warranting increased investigation and reporting to better inform ecosystem-based and interdisciplinary research, and to improve interpretation of climate change in marine systems (Table 3). Our synthesis suggests certain taxa are relatively understudied, such as archaea, bacteria, and viruses that serve critical roles in marine ecosystems and will likely be affected by climate change in unknown ways (Pörtner et al., 2014). While other studies have also diagnosed regional biases and mismatches in scales for marine biological responses (e.g., Poloczanska et al., 2013; Hoegh-Guldberg et al., 2014), our review is distinctive by simultaneously comparing and contrasting both abiotic and biotic ocean change studies. It is our intent that the findings of this review will be used to inform future directions of ocean change research. For example, our review and others (e.g., Hoegh-Guldberg et al., 2014) illustrate that some geographic regions have been extensively studied by several disciplines (e.g., North Atlantic and North Pacific), often for extended durations. We suggest these regions are fertile grounds for integrative studies that extend beyond single-species examinations of climate change and incorporate potential effects of multiple stressors (e.g., Large et al., 2015), ultimately improving our ability to understand climate-related ecosystem-level changes (Pörtner et al.,
Fig. 5 Primary physical or chemical stressor examined for 545 biological responses measured by 311 highly cited biological ocean change studies by subdiscipline in laboratory (a) and nonlaboratory (e.g., field, population modeling, paleobiology) settings (b), and specific theme (c). Number of biological responses are indicated in parentheses. Note ‘OA’ refers to ocean acidification studies.
Fig. 6 Type of biological response examined in a total of 545 biological responses measured in 311 highly cited biological ocean change studies by subdiscipline in laboratory (a) and nonlaboratory (e.g., field, population modeling, paleobiology) settings (b), and specific theme (c). Number of biological responses are indicated in parentheses. A single study examined evolutionary adaptation via population growth in the laboratory (i.e., Lohbeck et al., 2012), categorized as a response in abundance here.
Table 3 Critical research gaps in contemporary, highly cited ocean change literature and examples of potential effects on interpretation of climate impacts in marine systems

| Ocean change component | Research gaps | Effect on interpretation of climate impacts |
|------------------------|--------------|-------------------------------------------|
| Geographic examination (regional biases) | Lack of research in Indian, South Pacific, and South Atlantic basins | Local climate measures vary globally, resulting in geographically distinct impacts (Garcia et al., 2014). Regional over- or undersampling can bias an integrated interpretation of ocean change across the global ocean. Greater focus and broader disciplinary coverage in the North Atlantic and Pacific basins suggests these regions are more likely to foster cross-disciplinary or ecosystem-scale investigations. |
| Geographic examination (disciplinary biases) | Incomplete representation among disciplines within regions | A limited representation of studies among the suite of taxa within a region can affect a comprehensive assessment of climate impacts. For example, organisms in polar regions adapted to extreme, yet relatively stable conditions, are considered at high risk to changing ocean conditions (e.g., Laidre et al., 2008). Limited research on many biological systems in polar regions inhibits our ability to form a comprehensive understanding of climate change impacts on global marine ecosystems. |
| Spatial and temporal scales | Scaling biological response studies from laboratory to natural settings | Small-scale, controlled studies conducted at the individual level are difficult to translate to regional or global impacts at the population or ecosystem level (Wahl et al., 2015) and poorly replicate covariation among physical parameters or natural variability (Hofmann et al., 2011; Reum et al., 2014). |
| Spatial & temporal scale | Biological studies of long duration and large spatial scale | Long-term, large-scale, and high-resolution biological response studies have greater ability and more statistical power to attribute biological responses to climate-mediated physical/chemical changes (Brown et al., 2011; Parmesan et al., 2011; O’Connor et al., 2015) vs. natural variability (Doney & Sailley, 2013). |
| Spatial and temporal scales | Lack of standardization in biologically relevant spatial and temporal scales | The number of generations (temporal) or proportion of the home range examined (spatial) may be more biologically relevant than typical study scale measures, like study duration (years) or area (km²). Standardization of biologically relevant scales will improve the capacity to detect change when comparing and synthesizing biological responses among diverse marine species. |
| Biological themes | Archaea, bacteria, viruses, turtles, mangroves | Sensitivities to physical and chemical environmental changes are highly species specific (Poloczanska et al., 2013; Pörtner et al., 2014). Focus on particular taxa or ‘model’ organisms and a lack of study of others can obstruct a more comprehensive, ecosystem-based understanding of ocean change impacts, especially when underrepresented species play critical roles in marine ecosystems. |
| Physical/chemical oceanography themes | Acidity, dissolved oxygen | Physical/chemical themes were generally sampled over longer durations and greater study areas than biological themes. However, studies of OA and dissolved oxygen lagged behind other abiotic themes despite the need for high-resolution physical time series in biological response studies (Hoegh-Guldberg et al., 2014). |
| Physical/chemical stressors affecting biological responses | Dissolved oxygen, salinity, upwelling | Dissolved oxygen plays an important role in the ecophysiological response of many organisms to climate change (e.g., Pörtner & Knust, 2007), and widespread changes in salinity and upwelling can alter abundance and distributions of marine species (Hays et al., 2005; Doney et al., 2012). Enhanced examination of the responses of these understudied stressors to climate change and their impacts on marine populations will improve an ecosystem-wide understanding of ocean change. |
| Biological responses | Evolutionary adaptations | Adaptation is one of the four categories of biological response to climate change (O’Connor et al., 2012). Research is needed on adaptive responses of marine organisms to fully understand the impact of changing ocean conditions. |
| Number of stressors examined | Incorporating multiple and nonclimate stressors | Multiple environmental factors covary in time and space (Rhein et al., 2013). These synergistic stressors and other anthropogenic activities (e.g., fishing, pollution) may have difficult to predict interaction effects on biological responses (Doney et al., 2012; Hoegh-Guldberg et al., 2014). Studies that test for multiple alternative stressors have greater ability to attribute biological responses to physical/chemical changes (O’Connor et al., 2015). |

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communities were notably absent from the highly cited and a few marine bird species. Studies on benthic communities largely focused on polar bears, ice-associated seals, and the area covered by each taxonomic group. Some taxa and systems are limited by their biogeographic distribution (e.g., tropical coral reefs) or associations with localized physical phenomena (e.g., polar bears, Ursus marinus, associated with Arctic sea ice). For example, the Arctic is home to some of the most rapidly and drastically transforming marine ecosystems on the planet (e.g., Serreze et al., 2007; Grebmeier, 2012), as reflected by the relatively high number of Arctic ocean change studies. However, research on Arctic biological change studies remains primarily limited to vertebrate studies largely focused on polar bears, ice-associated seals, and a few marine bird species. Studies on benthic communities were notably absent from the highly cited Arctic studies. Wassmann et al. (2011) found similar biases toward biological response studies focused on vertebrates in the Arctic and argued for increased effort at lower trophic levels. Some physical parameters also have geographic limits. For example, monitoring of sea ice extent is geographically restricted to the poles, which contributed the majority of the physical measurements in polar regions.

We show observation biases concerning the regions where highly cited ocean change research is conducted and how this varies among disciplines. In particular, Southern Hemisphere ocean basins (e.g., the South Atlantic and Pacific, Indian, and Southern Ocean) were characterized by a general lack of ocean change research, especially relative to their large proportional surface area of the global ocean. Human development (which “remains a composite index that measures progress in three basic dimensions – health, knowledge and income”, 2014 UN Human Development Reports: http://hdr.undp.org/en/countries) and technological capacity are highest in Western Europe, North America, and Australia and may partially explain geographic biases of greater research focus (by nearly 3×) in the Northern Hemisphere. Greater human development in Australia and parts of South America (e.g., Chile) may contribute to the relatively high prevalence of benthic studies, focused on coral reefs and kelp forests, in the South Pacific. Additionally, we focused on the most frequently cited papers, which may impose geographic biases due to citation patterns. There may be higher citation potential in areas where there are more researchers, such as the North Atlantic or Mediterranean. However, similar geographic biases have been described elsewhere in the biological impacts literature, such as the predominance of biological change studies in more temperate (Wernberg et al., 2012) and Northern Hemisphere (Poloczanska et al., 2013) waters, especially the northeast Atlantic basin (Hoegh-Guldberg et al., 2014). Lenoir & Svenning (2015) note that a geographic bias in the Northern Hemisphere was not as prominent in a review of the marine compared to terrestrial range shift literature. Our study highlights finer regional and thematic biases than previous studies and also offers direct comparisons between studies with abiotic and biological focus. For example, we show that the proportion of studies from each discipline was more similar in the North and South Atlantic and Pacific basins than other regions. The more representative coverage among disciplines, in addition to an overall greater geographic focus, suggests that studies in the North Atlantic and Pacific basin may have more power for ecosystem-wide or cross-disciplinary investigations than elsewhere.

In addition to basin-specific patterns, we found that approximately 20% of the highly cited ocean change studies were multiregional or global in scale, providing the potential for a more representative view of ocean change (Parmesan et al., 2011). However, we also observed a trade-off between geographic scale and sampling resolution (data not shown) for a number of studies in this review. Smaller-scale environmental studies (<10 km²) often had increased sampling frequency (hourly–weekly) compared to studies that covered a greater geographic extent (greater than monthly or discrete sampling). Hence, while more localized studies may not be able to extrapolate findings to the basin or global scale (appropriate for ecosystem-wide assessments), they may be better suited to estimate rates of change on more localized scales (e.g., discrete populations). There is also the potential for citation biases for large-scale studies, where such studies may be cited more frequently due to their broad geographic representation and therefore more represented in our analyses. Indeed, multiregional and global papers had a mean number of 149.4 citations compared to 82.2 citations for all other smaller-scale papers included in this review. The potential citation bias associated with large-scale papers may be explained by uncritical or superficial citations (Banobi et al., 2011) when used in
introductory sentences rather than more substantive citations used to augment interpretations and discussion of research findings.

Studies covering physical/chemical signals of ocean change were typically the longest running and covered the largest study areas. A relatively small number of biological ocean change studies were conducted on similarly broad scales. The emerging field of ocean acidification (examining a suite of changes in OA including pH, aragonite saturation, and pCO₂) was often conducted on smaller scales and had a much shorter temporal record (median = 10.5 year) relative to other physical/chemical studies with median durations ranging from 2× (sea ice) to nearly 5× (SST) longer. Physical records like SST, sea level height, and sea ice are largely drawn from worldwide networks of autonomous sensors (e.g., Argo floats), interpolation of data from cruises, or derived from satellite measurements over particular geographic regions (global oceans in the former and polar regions in the latter). Such approaches allow data to be collected across wide areas and over extended durations. Long-term physical and chemical records are essential to understanding climate variability, especially when detecting and attributing biological responses to climate change (Hoegh-Guldberg et al., 2014).

Studies conducted over shorter time periods or lacking historical baselines have limited statistical power to demonstrate conclusively impacts due to climate (Edwards et al., 2010; Brown et al., 2011). Therefore, physical records, particularly the long duration and large spatial scale records for SST and sea level height, may ultimately have more statistical power to detect when a climate-driven change has occurred. However, relating biological responses to physical changes is often complicated by mismatches in scale, sampling frequencies, or proximity of samples. The problem of pattern and scale (Levin, 1992) is thus a key issue in attributing observed biological changes to climate (Rosenzweig et al., 2008). Biological responses are measured at local, regional, and global scales relative to an assortment of climate measures (García et al., 2014), and confidence in the assessment of climate impacts on marine taxa is greatest for long-term studies with fine-resolution data (O’Connor et al., 2015) or those conducted on the scale of entire ocean basins or greater (Parmesan et al., 2011).

Life-history characteristics of biological taxa also complicate a straightforward interpretation of differences in scale among disciplines. Climate responses are species specific (Poloczanska et al., 2013; Pörtner et al., 2014), and standardizing for the dispersal abilities and productivity of a given organism could provide a more comprehensive understanding of whether biological studies are conducted at scales and sampling frequencies necessary to assess change adequately. For example, marine mammal studies tended to incorporate relatively large spatial scales, but many of these species migrate over vast areas. Thus, sampling a single or relatively large study area may still only investigate a small portion of their overall home range, ultimately leading to an inadequate estimation of changes like shifts in distribution (Przeslawski et al., 2012). Similarly, long study durations, such as those for coral reefs, may still be inadequate for species that have extended generation times (e.g., ~100 year for Porites spp.; Veron, 1985). On the other hand, plankton, that often have short generation times of days to months and limited motility, may actually be some of the best sampled marine organisms with respect to understanding baselines of population dynamics that are needed in assessing natural variability (on daily, seasonal, and interannual time-scales) from climate-mediated change. The number of generations studied ultimately may be a more relevant metric for biological responses than study duration and useful for standardization when comparing among species. For example, a zooplankton (e.g., calanoid copepod) study with a 1- to 2-year duration, examining 1–10 generations, may be more comparable to a 10- to 15-year study of marine mammals (e.g., phocid seals) that surveys one generation. While noting information on generation time and home range size may not be available for each species or population examined, we suggest a different impression of how completely taxonomic groups are sampled (in terms of scale and frequency) may emerge if standardization for home ranges and generation times were available for organisms studied in these ocean change studies. For example, the literature examining species range shifts in terrestrial systems uses km/decade as a common metric to compare responses among taxa, which have recently been applied to marine taxa (e.g., Pinsky et al., 2013) and is a standardization that has historically been lacking for marine climate impact studies (Richardson & Poloczanska, 2008).

**Biological responses to physical and chemical stressors**

Our review indicates a strong reliance on laboratory experimentation to estimate biological responses to physical and chemical marine changes that occur in the field. This is particularly true for plankton and benthic invertebrates that are more easily cultivated and maintained in laboratory settings compared to large or highly mobile vertebrates. Laboratory studies typically are performed at small spatial and temporal scales and under controlled conditions that are not capable of mimicking the complexity of natural environments. For
instance, over half of the biological papers considering OA effects on organisms were conducted in the laboratory because seawater chemistry can be manipulated more easily in a controlled environment. However, OA expresses complicated natural patterns of variability (Hofmann et al., 2011) and is poorly replicated in experimental biological response studies due to covariance with factors like temperature, oxygen, and salinity (Reum et al., 2014). Short-term controlled studies of biological responses to chemical changes can provide direct measures of organismal responses; however, these studies are not easily scaled up or extrapolated to long-term or ecosystem-level effects (Wahl et al., 2015), and there is generally low-to-medium confidence in assessing the tolerance of many marine taxa to future CO2 levels (Pörtner et al., 2014).

Temperature was also frequently studied as a stressor under laboratory examination: 19% of biological responses considered temperature a primary stressor. Temperature in the ocean has been sampled widely for extended durations, and our results suggest that it is a readily available covariate in biological response studies. Despite being easy to sample, temperature may not always be the most ecologically meaningful stressor affecting a given marine species (Robinson et al., 2011). Instead, the physical or chemical factors most relevant to an organism or system of interest may be the best focus of examination. For example, changing temperature regimes may have little direct impact on warm-blooded marine mammals, seabirds, and fish (e.g., tuna and some sharks) that maintain body temperatures above ambient conditions. On the other hand, marine reptiles like sea turtles have temperature-dependent sex determination, such that increased nesting temperatures could bias sex ratios within populations (Hawkes et al., 2009). Thus, temperature was not surprisingly the most frequently studied stressor and, most appropriate, for marine turtle reproductive studies.

Temperature may be a key factor interacting with other important abiotic mechanisms that warrant simultaneous investigation. Sensitivity to changing thermal regimes may set the physiological limits for responses by some marine species, but other factors like oxygen, acidity, upwelling, and salinity can also complicate predictions of climate impacts (Pörtner et al., 2014). For example, a recent study demonstrated the importance of modeling interacting forces of acidification, temperature, and deoxygenation in understanding impacts on aerobic metabolic rates for teleost fishes (Del Raye & Weng, 2015). Dissolved oxygen was rarely studied as a primary stressor in biological response studies despite being an important ecophysiological factor affecting many marine organisms (e.g., Dodds et al., 2007; Pörtner & Knust, 2007; Froehlich et al., 2015) that is susceptible to climate variations (Deutsch et al., 2011). Hoegh-Guldberg et al. (2014) suggest that understanding the effects of declining oxygen concentrations is an emerging research need. Our study indicates that long-term, high-resolution data on dissolved oxygen are less available to researchers compared to data on temperature, which may contribute to the apparent lack of dissolved oxygen as a stressor in biological response studies. Similarly, climate-related changes in salinity and upwelling can strongly influence primary productivity, as well as the abundance and distributions of marine organisms (Hays et al., 2005; Doney et al., 2012). Understanding changes in surface winds may be critical to understanding regional upwelling processes and how upwelling contributes to hypoxia at varying depths or other important ecosystem effects of ocean–atmosphere interactions (Hoegh-Guldberg et al., 2014). Despite their regulatory influence on marine biota, salinity and upwelling were also poorly represented as primary stressors in our review of biological responses.

There is wide recognition in the literature of the importance of studying climate-related responses to multiple stressors and their cumulative or synergistic impacts (e.g., Richardson & Poloczanska, 2008; Hoegh-Guldberg et al., 2014; Pörtner et al., 2014). Nonetheless, few biological response studies considered the effects of more than two stressors, even though several environmental factors may covary in time or space. In addition, several nonclimate factors (e.g., commercial fishing, anthropogenic disturbance, pollution) may interact with and compound the effects of climate stressors. Distinguishing climate impacts from inherent variability and other drivers of change in marine systems can be complicated (Brown et al., 2011; Doney & Sailley, 2013), especially in the absence of long-term records of physical or chemical variability (Hoegh-Guldberg et al., 2014). Biological researchers should carefully consider other potential nonclimate factors (Brown et al., 2011; Doney et al., 2012). Incorporation of alternative mechanisms can also improve confidence in the attribution of climate impacts on biological responses in marine environments (O’Connor et al., 2015). Despite increasing interest in ecosystem-based management addressing interactions among multiple factors (e.g., Lester et al., 2010; Lubchenco & Sutley, 2010), our findings suggest that, to date, the most highly cited ocean change research does not address multiple interacting stressors.

Range and phenological shifts are among the most commonly cited effects of climate change on global biodiversity (e.g., Parmesan & Yohe, 2003; Root et al., 2003; Chen et al., 2011), but our review indicates that these types of biological responses are less frequently cited for the marine environment. Instead, our review
of the highly cited contemporary literature and those of others (e.g., Wassmann et al., 2011; Poloczanska et al., 2013) found that researchers most frequently studied changes in abundance or demography. Studies of marine range and phenological shifts have historically been disregarded and received lesser funding than those in terrestrial systems, the effects of which were amplified because marine ecologists did not always adopt the principles and standardizations used by terrestrial ecologists (Richardson & Poloczanska, 2008). Our current understanding of marine range shifts is largely consistent with climate change (e.g., Pinsky et al., 2013; Poloczanska et al., 2013; Wisz et al., 2015), but uncertainty remains regarding which species are shifting and the resulting impacts to ecosystems and communities (Hoegh-Guldberg et al., 2014). Strict selection criteria, such as the exclusion of single-species studies that could impose positive publication bias, can also impact the strength of conclusions about marine range shifts and changes in phenology (Parmesan, 2007; Przeslawski et al., 2012). Range shifts must also be put into the context of localized climate changes, which may not necessarily be consistent with global patterns and could be multidimensional (e.g., latitude and depth), to consider overall species persistence (Lenoir & Svenning, 2015). Although projections for future distributions of marine species exist (e.g., Cheung et al., 2009; Hazen et al., 2013; Jones & Cheung, 2014), long-term, corroborating observations necessary to detect contemporary shifts in species distribution appear to be rare in marine ecosystems.

Physiological responses were also frequently studied by the papers in our review, often in the laboratory and particularly for benthic communities. Of the 168 articles considering physiological responses, 63% investigated how OA was affecting processes like nutrient uptake or metabolism (phytoplankton, fish, seagrasses, kelp), tissue damage (fish), and calcification (rocky shore invertebrates, corals). Our findings suggest this focus on physiological effects is related to the recent proliferation of research on the effects of OA on marine species, especially calcifying organisms or those reliant on calcifiers (Orr et al., 2005; Hoegh-Guldborg et al., 2007; Fabry et al., 2008; Doney et al., 2009). Despite this focus on physiological responses, research on how other stressors interact with OA and potentially nonlinear biological responses is still needed (Hoegh-Guldborg et al., 2014).

Our review of highly cited marine biological responses yielded only one paper (i.e., Lohbeck et al., 2012) explicitly studying evolutionary implications of ocean change. Changes in gene frequency, via processes such as evolutionary or genetic rescue, are an increasingly recognized response to climate change (Carlson et al., 2014). The persistence of populations experiencing environmental change has been linked to individual performance regarding phenotypic plasticity, dispersal, and/or adaptive evolution (Merilä & Hendry, 2014), which can be categorized as acclimatization, colonization, adaptation, or extinction (O'Connor et al., 2012). We documented population-level responses corresponding to acclimatization (i.e., physiological, behavioral, diet, and physiological responses), colonization (i.e., distribution shifts), and avoidance of extinction (i.e., via reproductive or demographic responses) in the highly cited marine literature. In contrast, we found a general lack of studies on adaptations (i.e., changes in gene frequency), except for a selection study conducted on multiple generations of a coccolithophore in the laboratory (Lohbeck et al., 2012). However, we reviewed no studies confirming adaptive evolution in the wild. Attribution of genetic changes to climate forcing requires intensive common-garden experiments or genetic time series that are rarely done or available, especially for long-lived or large-bodied species. The evidence for adaptive evolution in response to climate change, whether marine or terrestrial, is actually quite rare (Gienapp et al., 2008). Rather, phenotypic plasticity is more apparent than adaptation (Hendry et al., 2008) and has been investigated for marine species (e.g., Reed et al., 2009; Kelly et al., 2011a).

Ultimately, future marine research could more acutely focus on the adaptive abilities of marine species to cope with changing conditions in order to better understand future population viability.

Social science disciplines also warrant focus in studies of ocean change and are highly relevant to considerations of current and future changes in the marine environment. Although beyond the scope of our review, marine climate change clearly affects social systems and how individuals and communities are responding to ocean change (e.g., McCay et al., 2011; Pinsky & Fogarty, 2012; Lauer et al., 2013). A growing body of literature is developing to assess the effects of ocean changes on social-ecological systems. Like the other papers reviewed here, this literature varies greatly in terms of temporal and spatial scales and themes addressed. A notable difference between the social-ecological literature and the papers reviewed in this study is that the former tends to focus on projected responses and how ocean change will influence human society in the future (e.g., Cooley & Doney, 2009; Kelly et al., 2011b), whereas the latter tends to address changes that have already occurred. Thus, these social-ecological studies introduce another set of spatial and temporal scales as well as levels of complexity, moving beyond climate change impacts to marine biodiversity but also to human societies associated with the ocean.
Advancing ocean change research

The study of ocean change is a rapidly growing field. We set out to review differences in approaches across marine disciplines that affect the collective interpretation of climate-associated changes in the ocean. Our review specifically focuses on literature that is most frequently cited to identify research that shapes the current discourse on ocean change. We highlight a rich body of literature that indicates a suite of biological responses accompany several signals of physical and chemical changes occurring in the global ocean. By looking across disciplinary distinctions in sampling approaches for ocean change, we simultaneously emphasize previously identified issues as well as distinguish avenues for future research in both abiotic and biological realms. Our key results suggest that the current discourse on ocean change is sparser for: Southern Hemisphere ocean basins (notably the Indian, South Pacific, and South Atlantic basins), understudied marine taxa (archaea, bacteria, viruses, mangroves and turtles) and oceanographic properties (OA and dissolved oxygen, especially outside of laboratory manipulations), specific physical and chemical stressor effects on biota (dissolved oxygen, salinity, and upwelling), and biological responses of climate-driven ocean change (evolutionary adaptation). We have shown that it is imperative to consider the statistical limitations associated with relatively short duration, small-scale, and low-resolution datasets when inferring broadscale signals of change, but also which datasets are applicable to the life history and population dynamics of target species. We invite future ocean change researchers studying biological systems to consider carefully the temporal (sampling duration and frequency) and spatial scales (study area) required to detect change beyond the level of an individual and establish critical baseline data. While broader-scale studies are expected to have greater statistical power and confidence, we also urge biological researchers to consider and standardize measures of species generation times and proportion of the home range studied to enable comparable investigations at biologically relevant scales. Identification of disciplinary distinctions, similarities, and areas lacking scientific research with respect to climate-mediated ocean change should facilitate cohesive research approaches and syntheses of observed impacts on the global ocean as well as more accurate forecasts for the future.

Calls for adaptive, ecosystem-based, and interdisciplinary approaches in marine sciences are now commonplace (e.g., Edwards et al., 2010; Lester et al., 2010; Lubchenco & Sutley, 2010), yet best practices for integrative studies have been elusive (Samhouri et al., 2013). The comparative cross-disciplinary approach taken in this paper and our ability to identify the associated effects on the interpretation of climate impacts in marine systems were possible because of an interdisciplinary early-career training program. Syntheses, such as this one, that consider biotic and abiotic marine disciplines in concert are rare. The institutional structure to train interdisciplinary students in the conduct and design of crosscutting studies remains deficient and requires increased, continuing support (Christie, 2011). As noted in Hoegh-Guldberg et al. (2014), we have yet to fully understand how single-species or ocean processes will reorganize ecosystems and communities under climate change. Concerted efforts to improve interdisciplinary education at early-career stages will provide future researchers with a necessary foundation for integrating and comparing disciplinary differences, and funding of early-career interdisciplinary training should be continued and strengthened. Our study provides a novel example of how cross-disciplinary research allowed for a comprehensive assessment of contemporary ocean change research that highlighted new research gaps and recommendations for future comparative research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Highly-cited literature reviewed for each theme across physical, chemical, and biological disciplines.

Table S1. Database fields and attributes collected from marine science articles listed in Appendix S1, noting data fields additionally recorded only for biological response studies.