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RESEARCH REVIEW

Biological responses to environmental heterogeneity under future ocean conditions

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Abstract

Organisms are projected to face unprecedented rates of change in future ocean conditions due to anthropogenic climate-change. At present, marine life encounters a wide range of environmental heterogeneity from natural fluctuations to mean climate change. Manipulation studies suggest that biota from more variable marine environments have more phenotypic plasticity to tolerate environmental heterogeneity. Here, we consider current strategies employed by a range of representative organisms across various habitats – from short-lived phytoplankton to long-lived corals - in response to environmental heterogeneity. We then discuss how, if and when organismal responses (acclimate/ migrate/adapt) may be altered by shifts in the magnitude of the mean climate-change signal relative to that for natural fluctuations projected for coming decades. The findings from both novel climate-change modelling simulations and prior biological manipulation studies, in which natural fluctuations are superimposed on those of mean change, provide valuable insights into organismal responses to environmental heterogeneity. Manipulations reveal that different experimental outcomes are evident between climate-change treatments which include natural fluctuations vs. those which do not. Modelling simulations project that the magnitude of climate variability, along with mean climate change, will increase in coming decades, and hence environmental heterogeneity will increase, illustrating the need for more realistic biological manipulation experiments that include natural fluctuations. However, simulations also strongly suggest that the timescales over which the mean climate-change signature will become dominant, relative to natural fluctuations, will vary for individual properties, being most rapid for CO₂ (~10 years from present day) to 4 decades for nutrients. We conclude that the strategies used by biota to respond to shifts in environmental heterogeneity may be complex, as they will have to physiologically straddle wide-ranging timescales in the alteration of ocean conditions, including the need to adapt to rapidly rising CO_2 and also acclimate to environmental heterogeneity in more slowly changing properties such as warming.

Keywords: climate variability, emergence, marine life, ocean climate change, phenotypic plasticity

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Introduction

The ocean covers ~70% of the planet, drives ~50% of global productivity (Field *et al.*, 1998), and is characterized by diverse environmental conditions comprising over 50 biogeographical provinces or biomes from tropical to polar waters (Longhurst, 2010). Each province exhibits spatial and temporal fluctuations in oceanic

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Correspondence: Philip W. Boyd, tel./fax 61 3 6226 8554, e-mail: philip.boyd@utas.edu.au properties ranging from millimetres (mm) to 100's of kilometres (km), and seconds to decades, which together influence ocean productivity and biogeochemistry (Behrenfeld, 2014; Barton *et al.*, 2015). Variability at the largest spatial (e.g. ocean gyre) and interannual to decadal temporal scales are mainly driven by natural variability of the coupled ocean-atmosphere system and are often associated with climate modes such as the El Nino-Southern Oscillation (ENSO). External forcing such as changes in solar irradiance or altered atmospheric composition come in to play on centennial and longer time-scales. At smaller spatial scales meteorological factors such as winds and storms play a pivotal role (Mann & Lazier, 2013). These physical factors, together

with biological processes (such as grazing and photosynthesis) contribute to spatial and temporal heterogeneity in ocean properties, defining the range of conditions that marine organisms encounter (Horne & Schneider (1994); Fig. 1).

The interplay between environmental heterogeneity and the environmental sensitivity of marine life will dictate biological responses. The sensitivity of marine biota to environmental conditions varies widely and is influenced by many factors which can be ordered by underlying physiological principles (Pörtner *et al.*, 2014). For example, thermal sensitivity increases with organismal complexity and also with body size (Pörtner, 2002). Hence, metazoans are more sensitive to temperature than eukaryotes, which in turn are more sensitive than prokaryotes (Pörtner *et al.*, 2014). In addition to allometry and complexity, the life history of organisms – from larval stages to spawners – is also characterized by changes in tolerances to temperature (Pörtner & Farrell, 2008) and pH (Sunday *et al.*, 2011) as they develop. Latitude also plays a role in setting thermal sensitivity, with the upper thermal tolerances of marine life being set close to the temperatures in the tropical oceans (Pörtner *et al.*, 2014), with major



Horizontal space length scale (m)

Fig. 1 Schematic of the time and space scales for different biological (yellow), physical (blue) and coupled physico-chemical and biological (red) processes. The cartoon is modified from the "Stommel" diagram in Dickey (2003).

ramifications for low latitude ectotherms which are already very close to their heat limits (Deutsch *et al.*, 2008). Other factors that influence environmental sensitivity include organismal response times to fluctuations in a range of environmental properties (defined as 1/growth rate), over and above temperature (Vasseur, 2007).

The wide ranging environmental sensitivity of marine life means that many different responses - from rapid for taxa with short generation times to slower for more complex life-forms - to climate-change mediated shifts in environmental heterogeneity are possible in the future. Environmental heterogeneity potentially exerts both beneficial and detrimental effects on marine biota. While it can offer organisms respite from extremes of physiological stress, the combined effect of environmental fluctuations and climate change may expose organisms to extremes that exceed their thresholds of tolerance long before mean climate change exerts such influence (Hollander & Butlin, 2010; Service, 2012; Flynn *et al.*, 2015a).

Climate change is already affecting many oceanic properties, altering both the mean state of the oceans and the variability about that mean (IPCC, 2014). However, most studies, such as numerical modelling experiments, examine the effects of changes in the mean state of the environment as a result of climate change, not the alteration of climate variability (IPCC, 2014). Hence, they may poorly reflect the full biological impact of a changing climate (Thornton *et al.*, 2014). Furthermore, few biological manipulation experiments consider the effects of both environmental fluctuations and climate-change alteration of the mean state (see below).

Three generic findings suggest that future responses of marine organisms to climate change may be fundamentally affected by natural heterogeneity in their environment. First, environmental heterogeneity differs markedly among marine provinces (Karl et al., 2003). Second, studies such as von Dassow et al. (2015) report that organisms from environments characterized by greater heterogeneity may have more phenotypic plasticity. Here, phenotypic plasticity is defined as 'the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions' (Pigliucci, 2006). Third, the inclusion of natural environmental fluctuations in climate-change manipulation experiments can result in different outcomes from perturbation studies that do not (Cornwall et al., 2013). Together, these findings question the extent to which climate-change experiments that exclude the combined effects of environmental heterogeneity are representative of biological responses in nature.

Here, we restrict our examination of the environmental sensitivity of marine life to taxa that form the base of

foodwebs (from microbes (generation time of hours) to corals (life-time of decades)). We explore how spatial and temporal variability, across a range of scales, defines environmental heterogeneity. Next we examine how life history, from asexually dividing single-cells to multicellular complex organisms, and modes of existence such as sessile vs. planktonic, intersect with natural fluctuations in oceanic properties. We then document the strategies organisms employ to tolerate environmental heterogeneity, and in particular the role of phenotypic plasticity in mitigating oceanic variability. We conclude by considering the implications of longer term (i.e., decadal) climate-change mediated shifts in both mean climate and climate variability on taxa. This analysis helps to appraise the degree to which the outcomes of climate-change manipulation experiments on marine organisms are altered when environmental heterogeneity is incorporated into their design.

Spatial and temporal variability in oceanic properties

The ocean is characterized by a similar range of scales of variability to the terrestrial environment (e.g. continental land masses vs. ocean basins), but some scales of variability differ between the ocean and the land. For example, Reusch & Boyd (2013), in a comparison of the environmental variability encountered by marine vs. terrestrial life (see also Clarke, 1985; Marquet et al., 1993), revealed that land (seed) plants (which have longer timescales of environmental interaction (months to years) than phytoplankton) were exposed to higher variability on the scale of mm to metres (m) for resources such as nutrients and irradiance, compared with marine plants (phytoplankton). Reusch and Boyd termed this higher variability on land as 'finer grained structuring of the distribution of resources than in the sea' and linked this comparison to the seminal study on patchiness and habitats by MacArthur & Levins (1964). Land plants are also subjected to higher thermal variability across all scales (mm to km, hours to years) than phytoplankton, whereas the latter encountered higher variability (relative to land plants) in nutrient availability, carbon dioxide and irradiance at temporal (hours to months) and spatial (m to >km) scales (Reusch & Boyd, 2013).

The heterogeneity of provinces is wide-ranging in the ocean, from highly variable in regions subjected to episodic events such as upwelling and sea ice cover (Massom & Stammerjohn, 2010; Padilla & Savedo, 2013) and energetic coastal and western boundary current regions with elevated submesoscale and mesoscale variability (Chelton *et al.*, 2007; Pfister *et al.*, 2014), to almost invariant in the deep ocean (Smith *et al.*, 2009).

Remote-sensing of marine sites, for example with moored sensors, confirms this range of heterogeneity. Hofmann *et al.* (2011, 2013) showed pH varied little in the open ocean but was highly heterogeneous in both productive coastal waters and at highly polluted near-shore sites. The lexicon of metrics to describe environmental heterogeneity, particularly under climate change, is growing and includes terms such as 'abruptness' to describe extreme events (Jentsch *et al.*, 2007); see Table 1).

Recent examples of extreme events include so-called marine heat waves (Olsson et al., 2014) recorded in Western Australia (Pearce et al., 2011), the Gulf of Maine (Petes et al., 2014) and the NE Pacific (Bond et al., 2015). Heat waves were characterized by sustained (i.e., weeks) warming of 1–3 °C of surface waters (relative to the long-term monthly regional average), and in some cases local warming of 5 °C (days) (Pearce et al., 2011). The magnitude of these transient warming events is comparable to projected (mean) warming from global climate change models for 2100 (Moore et al., 2013). Other examples of episodic events, associated with climate variability as opposed to climate change, include upwelling of corrosive low pH waters off the Oregon coast (Feely et al., 2008). Similar to 'heat waves', shifts in pH during upwelling events (weeks) are comparable to those projected for changes in ocean acidification by 2100 (Moore et al., 2013). Only a subset of modelling studies is presently focussing on simulating such extreme events and how their dynamics will change in the coming decades (Kowch & Emanuel, 2015).

Temporal and spatial fluctuations are modulated by diverse processes including physical (Fig. 1), chemical (e.g. nutrient speciation, Raven *et al.*, 2005) and biological (photosynthetic- and respiration-driven environmental modifications (Hurd *et al.*, 2011; Flynn *et al.*, 2012)), and their combined effects. These environmental fluctuations have distinct characteristics for each bio-

Table 1 Metrics commonly used to define the components of environmental time series – such as the annual cycle of temperature at an ocean site (Karl *et al.,* 2003) that comprise its environmental heterogeneity

Metric	Analogous or inclusive terms
Average state	Mean, Median, Mode
Variability	Standard deviation, Variance
Magnitude of	Range or amplitude, Minimum value,
events	Maximum value
Rate of change	Abruptness, Sustained, Progressive,
	Step-wise
Duration of events	Prolonged, Transient
Frequency of events	Periodicity, Intermittency, Stochastic,
	Cyclic

logically influential property. For example, underwater irradiance varies by >3 orders of magnitude over the diurnal cycle (Mann and Lazier, 2013), whereas nutrient variability is most conspicuous on timescales of days to weeks (Table S1). Distinctive clusters of environmental properties will shape the physiology, morphology and life history of different organisms (Boyd et al., 2010). For example, the physiological performance of phytoplankton is set by the combined effects of chemical (e.g. nutrients, CO₂), physical (e.g. hydrodynamics, temperature, light) and biological (e.g. light attenuation by phytoplankton) properties. The environmental cluster that influences phytoplankton differs with that for microbes, corals or coralline algae (Table S1). In summary, multiple environmental factors, across nested suites of scales (Fig. 1), for each biologically influential property (Table S1), interact with the environmental sensitivity of organisms to dictate biological responses to marine environmental heterogeneity.

Life histories and modes of existence

Marine taxa encompass wide-ranging life histories from planktonic microbes with fast turnover times (hours to days) to more complex longer-lived sessile corals (decades to centuries) and coralline algae (months to years). Many organisms (e.g. shellfish, corals) have planktonic larvae and settled or benthic adult stages. These various developmental stages occupy different environments and have inherently different environmental sensitivities (Kawaguchi et al., 2013). For example, krill in the Southern Ocean have a life cycle of >10 stages (over several years) which straddle surface waters to those >700 m deep. Thus, krill encounter a range of gradients in environmental heterogeneity such as in pH from high (surface ocean 8.0) to lower pH values (7.7, deep water), which may influence their vulnerability to increasing ocean acidification (Kawaguchi et al., 2013). Different life histories and modes of existence integrate environmental heterogeneity over wide-ranging scales, and may influence the degree to which spatial (e.g. planktonic organisms) vs. temporal (e.g. sessile taxa) variability sets the cumulative environmental heterogeneity.

Longer-lived organisms may encounter and thus integrate a greater range of fluctuations relative to short-lived organisms, but this will depend upon the heterogeneity of their environment (Table S1). Other characteristics of marine life include the relative abundances and turnover times of organisms, which determine if they need to be viewed primarily as a community or as individuals. For example, microbes are often considered as a community characterized by high genetic diversity and generation times of hours, relative to slower growing individuals which have lower genetic diversity (Collins, 2013). All of these factors must be considered when examining the relationship between scales of organismal response and environmental heterogeneity (Hoffmann & Sgrò, 2011). In many cases, biota has developed strategies to manage differing scales of fluctuating oceanic conditions (Padilla & Savedo, 2013).

Environmental heterogeneity: organismal strategies to survive

Over evolutionary timescales, organisms have developed many approaches to modulate the effects of environmental heterogeneity across different scales. Examples of such approaches are provided below for photoautotrophs that underpin coastal and offshore food webs. For phytoplankton, physiological flexibility (e.g. photoacclimation, Falkowski & LaRoche, 1991; Dimier et al., 2009) enables them to deal with rapid changes in light as they are mixed vertically. Timescales of mixing of hours in surface waters set irradiance gradients that may span >3 orders of magnitude (Denman & Gargett, 1983). In contrast polar phytoplankton have devised strategies to survive during months of complete darkness in the austral winter (McMinn & Martin, 2013). Similar physiological flexibility enables cells to survive the physiological stress imposed by conditions characterized by fluctuating nutrient supply via plastic stoichiometry (Arrigo, 2005; Diehl et al., 2005), alteration of cell size (Marchetti & Harrison, 2007), colony formation (Beardall et al., 2009) or vertical migration by dinoflagellates (Ross & Sharples, 2007). These flexible strategies come at an energetic cost. For example, the enhanced costs for cellular upkeep and repair associated with phytoplankton photo-acclimation under high variability in the underwater light climate may limit energy allocation to other cellular processes (Dimier et al., 2009). The energy required to sustain tolerance may restrict the duration and/or magnitude of environmental stress that an organism can survive (Frieder et al., 2014).

Phytoplankton and macroalgae can tolerate changes in CO_2 or pH by employing carbon concentrating mechanisms (Hepburn *et al.*, 2011; Raven *et al.*, 2011) and proton pumps (Taylor *et al.*, 2012), respectively. Many phytoplankton, such as dinoflagellates, can alter their trophic mode (mixotrophy) if conditions such as low nutrient supply dictate a shift in nutritional strategy (Béjà & Suzuki, 2008; Ward *et al.*, 2011) with implications for the representation of energy transfer in foodweb modelling (Mitra *et al.*, 2014). Macroalgae have developed morphological strategies to withstand high water motion in energetic nearshore environments where they are characterized by streamlined shapes (Hurd, 2000; Koehl *et al.*, 2008; Hurd *et al.*, 2014). Some macroalgae alter their physiology during their growth season (for example to modify reproductive condition) by using an endogenous clock (Kain, 1989; Luning, 1991).

Other responses employed by organisms to tolerate environmental heterogeneity include behavioural flexibility for marine invertebrates, such as modified feeding behaviour as prey characteristics are altered (Padilla & Savedo, 2013). Heterotrophic bacteria have many mechanisms to respond to fluctuating environments such as alteration of their surface:volume ratio by modification of cell shape (Young, 2006). Bacteria also respond to shifts in temperature through environmentally mediated shifts in community structure (Chow *et al.*, 2013), and/or increasing the rate of synthesis of heat shock proteins which repair or eliminate proteins damaged by heat stress and are important for growth (Yura *et al.*, 1993).

Two of the most commonly reported survival strategies for environmental heterogeneity are the resource acquisition generalist (often termed r-species and prevalent in unstable (i.e. more heterogeneous) environments) vs. the resource acquisition specialist, termed K-species which dominate in relatively stable environments (Chevin et al., 2010; Murren et al., 2015). In marine phytoplankton, the specialist and generalist can be distinguished by their different modes of physiological optimization (sensu Klausmeier et al., 2004). These modes are characterized by an emphasis on cellular 'growth machinery' for the r species, whereas the K species is typified by large amounts of "resourceacquisition machinery" to subsist under stable conditions where resources such as nutrients limit growth (Arrigo, 2005). Over the seasonal cycle, the flexible responses to a range of environmental heterogeneity, such as for nutrient supply, imparted by the strategies of the generalist vs. the specialist lead to niche specialization. Characteristic patterns of phytoplankton succession result in r species (e.g. diatoms) dominating under conditions of high environmental heterogeneity early in the growth season, and K species (e.g., dinoflagellates, which can also exhibit mixotrophy) dominating in the mid-summer (less environmentally variable) part of this cycle (Barton et al., 2015).

Phenotypic Plasticity

Organismal responses to pronounced changes to the environment are grouped into four general categories - migrate, die, acclimate or adapt (Davis *et al.*, 2005; Gienapp *et al.*, 2008). The response(s) of an organism to pronounced environmental fluctuations (such as episodic events, Table 1) depend on a range of factors including its ability to migrate, its capacity to tolerate higher temperatures (Huey *et al.*, 2009) and the relationship between an organism's physiological limits and environmental fluctuations (Hoffmann & Sgrò, 2011; Edwards *et al.*, 2013) (Fig. 2). Hence, an organism's phenotypic plasticity defines to what extent it can tolerate altered conditions, until it reaches its physiological limit (Litchman *et al.*, 2012). An example of such limits being exceeded comes from the deaths and/or migrations observed during marine 'heat waves' off Western Australia (Pearce *et al.*, 2011). Here, we focus on phenotypic plasticity in relation to environmental heterogeneity.

Phenotypic plasticity has for many years been viewed as a short-term (hours to days) response to environmental heterogeneity in which *'individuals of the same genotype develop alternative phenotypes'* (Stearns, 1989, 1992). However, more recently phenotypic plasticity has also been considered as a potent response to more stressful environmental conditions (Brakefield, 1997) in which fluctuations are increased. Phenotypic plasticity is viewed as very important in environments with high variability over short time scales and/or in spatially patchy environments (Miner et al., 2005). Hence, it may be viewed as the most flexible response mechanism to respond to environmental heterogeneity and is ubiquitous among marine organisms (Padilla & Savedo, 2013). The wide range of recent studies and reviews testify to the growth of research into phenotypic plasticity in the context of a changing climate. These include organismal resilience to change (Seebacher et al., 2015) and limits to the utility of plasticity for organisms (such as tropical ectotherms) close to their upper thermal tolerance (Deutsch et al., 2008; Tewksbury et al., 2008). There has also been targeted research into evolutionary constraints, the limits and costs of plasticity (Murren et al., 2015), and the relationship between plasticity and variable environments (Schaum & Collins, 2014).

Terrestrial studies show that heterogeneous environments contain plants with greater phenotypic plasticity



Present

Fig. 2 Relationship between the four organismal responses to changing environmental conditions – migrate, acclimate, adapt or die (from Gienapp *et al.*, 2008; for definitions see Flynn *et al.*, 2015b Table 1) and future climate change. Short-term (days to months) responses include acclimatization, migration or death. Adaptation is a longer term response (months to years). Further acclimatization may be required after migration (for example, poleward migration by calcifiers to colder temperatures may require subsequent acclimatization to more acidic conditions, Pfister *et al.*, 2014). The dashed circle denotes uncertainties that surround the transition from acclimatization (Ghalambor *et al.*, 2015) to adaptation, and three alternatives are provided beneath the downwards arrow. Label 'a' denotes that microevolution on a timescale of months has been observed for phytoplankton (Lohbeck *et al.*, 2013). Label 'b' denotes that nonmotile organisms such as passively drifting phytoplankton seldom are reported to migrate but are often rapidly dispersed for example by ocean currents.

Future

than stable environments (Van Kleunen & Fischer, 2005); an observation consistent with the Climatic Variability Hypothesis (CVH) of Janzen (1967). Subsequent studies, along latitudinal gradient in marine and terrestrial environments in South America have confirmed this assertion. For example Molina-Montenegro & Nava (2012) reported a positive relationship between phenotypic plasticity of plants and environmental variability. Gaitán-Espitia et al. (2014) reported the influence of greater thermal variability at higher latitudes on the plasticity of responses in thermal physiology of porcelain crabs. Molina-Montenegro & Naya (2012) advocated that the CVH could be a powerful conceptual framework with which to view the impact of future climate change on species persistence and phenotypic plasticity.

Other marine studies have also pointed to enhanced phenotypic plasticity in populations from sites with greater environmental heterogeneity. Schaum *et al.* (2013) reported such an outcome during an ocean acidification perturbation experiment in which they manipulated different populations of a globally ubiquitous picoeukaryote (*Ostreococcus tauri*), to explore the role of Trans Generational Plasticity (TGP, i.e., enhanced tolerance to changing conditions in offspring, see (Reusch, 2013)) on the evolution of plasticity in this picoeukaryote. Schaum & Collins (2014) found that exposure of *O. tauri* to fluctuating environments for 400 generations led to the descendants being more plastic than their ancestor. They concluded that these fast growing microbes have large genetically diverse populations that initially (i.e., hundreds of generations) may become more plastic in a future ocean.

Schaum & Collins (2014) contrasted and compared O. tauri grown under either constant or fluctuating environments, and their study provides insights into organismal responses in the coming decades when mean climate change may reach a threshold or inflection point in which mean climate change breaks outside the natural climate variability window (Fig. 3). They noted that some of these plastic responses (such as elevated growth rates of O. tauri) may eventually be curtailed by natural selection, to redress the increased physiological stresses associated with fast growth rates. Such an inflection may mark a transition which favours directional selection (see Discussion in Seebacher et al. (2015)) as opposed to phenotypic plasticity which is presently dominant in highly fluctuating environments (Reusch, 2013). In the next sections the possibility of such a threshold (termed 'the Emergence', Hauri et al., 2013; Mora et al., 2013) and its ramifications are discussed in more detail.



Fig. 3 Insights into the rate of change of mean climate change vs. natural climate variability from the Community Earth System Model (CESM). Changes in temperature (left) and salinity (right) for polar (upper panels) and subpolar (lower panels) Southern Ocean surface waters for three IPCC climate change scenarios (A2, A2-2X, A2-4X (highest CO_2 emissions trajectory)) vs. the control run from Boyd *et al.* (2008). Estimates of climate variability are provided by the control, and are contrasted with changes in mean temperature and salinity between the years 2000 and 2100. Vertical arrows and question marks indicate a qualitative estimate of the potential threshold (estimated from the range of natural variability) around 2050 when the magnitude of environmental heterogeneity is superseded by anthropogenic climate change, i.e. the Emergence (*sensu* Mora *et al.*, 2013). See Hauri *et al.* (2013) for a discussion about the range of methods that can be applied to compute this threshold ranging from when the mean for some time period is outside the natural range (mean ± 1 sigma or two sigma) to when the range (mean \pm sigma) at some new point in time is outside the natural variability range.

Alteration of environmental heterogeneity in a future ocean

An assessment of shifts in environmental heterogeneity requires accurate projections of both mean climate change and natural climate variability. In 2012, the IPCC released a special report on "Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation" (Field et al., 2012). It offers valuable insights into how a changing climate will alter many of the metrics summarized in Table 1 but provided no estimate of their cumulative effect on environmental heterogeneity. A critique of this report by Thornton et al. (2014) concluded that projections of changes in mean climate by 2100 are currently more robust than those for climate variability in terrestrial systems, with implications for our ability to assess changes in environmental heterogeneity.

In marine systems, recent analysis of modes of environmental heterogeneity have been conducted for the multi-decadal Continuous Plankton Recorder zooplankton time-series in the NE Atlantic (Edwards et al., 2013). A Principal Component Analysis (PCA) revealed that natural climate variability explained ~18% of the observed fluctuations, whereas mean climate change explained >30%. These findings point to no sustained trend over the last five decades (1960-2010), and thus neither climate variability nor mean climate change are dominating shifts in environmental heterogeneity. Sexton & Harris (2015) in an appraisal of regional modelling assessments of shifts in mean climate change vs. climate variability also advocate the inclusion of more detailed (i.e., year-to-year) projections of future climate variability to capture more information on potential trends in extremes.

Insights into the nature of the relationship between alteration of mean climate change and natural climate variability in a future ocean have been obtained from modelling studies. Coupled ocean-atmosphere (Boyd et al., 2008) and/or Earth system (Moore et al., 2013) models enabled an intercomparison of projected trends in mean climate with that of changes in climate variability by 2100. For example, Boyd et al. (2008) generated estimates of the Root Mean Square (RMS) climate variability (decadal average from 2000-2100) vs. that of climate change with the decadal climate variability signal removed (Fig. 3). In our Review, this analysis has been advanced for polar and subpolar Southern Ocean waters providing illustrative regional estimates of the monthly anomalies from the mean annual cycle, the rate of change per decade from linear or quadratic regressions in a suite of oceanic properties that are each biologically influential, and the number of years needed to detect a trend in mean climate change relative to natural climate variability (sensu Henson et al., 2010).

This comparison for the Southern Ocean reveals four interesting climate-induced trends with implications for alteration of environmental heterogeneity in a future ocean (Table S2, Fig. 4). The variability of some factors (e.g. temperature and salinity) has projected shifts in decadal mean climate change that are comparable to or larger than the range of natural variability, indicating that climate thresholds (sensu Mora et al., 2013) will occur relatively soon compared to other properties with smaller ratios of climate change to natural variability e.g. mixed layer depth (Table S2). Second, other factors (e.g. pCO₂) have even larger relative projected decadal rates of change up to 30-fold higher than the range in natural variability. Third, trends in the mean state relative to the range of natural variability of oceanic properties such as temperature become more conspicuous as the CO₂ emission scenarios become more extreme (Fig. 3). Fourth, natural variability and decadal rates of change of some factors (e.g. iron supply) can differ substantially among ocean regions (e.g. polar vs. subpolar waters, Fig. 3).

Fig. 4 (a) The rate of change in biologically influential oceanic properties – temperature (SST), salinity (SSS), mixed layer depth (MLD), phosphate (PO₄), dissolved iron (Fe),, carbon dioxide (pCO₂), irradiance (SHF) and ice fraction (ifrac). Blue symbols denote the monthly anomalies from the mean annual cycle using the CESM1 RCP 8.5 run (Moore *et al.*, 2013) for the polar Southern Ocean. In all cases except temperature and pCO₂, a linear regression is used to estimate the long-term rate of change in each property per decade (m*, i.e., annual regression slope times 10 years). For temperature and pCO₂, a quadratic fit was employed. n* is the number of years required to detect a long-term secular trend at some specified probability level. Following Henson *et al.* (2010), n* is computed from model simulations from the residual or noise after removing the low frequency trend. n* scales proportional to the standard deviation of the residual time-series. (b) Comparison of simulated grid-scale (~1 degree) surface ocean time-space variability in the polar Southern Ocean for the beginning (blue) and end (red) of the 21st Century. Each panel displays 20-year binned histograms (relative frequency) created from model grid point monthly mean anomalies from regional average for Southern Ocean polar waters; model output has been de-seasonalized and corrected for the long-term regional climate change trend over the 21st Century. Histograms capture both spatial and subannual to decadal temporal variability for temperature (abbreviations are as for panel a), salinity, mixed layer depth, phosphate, dissolved iron, carbon dioxide, irradiance and ice fraction. Model output is from CESM1 (BGC) RCP8.5 simulation (Moore *et al.*, 2013).



In Fig. 4a the metric n* is the number of years needed to detect a mean climate-change mediated trend from the natural variability background; it provides

useful quantification that enables future trends to be intercompared between oceanic properties. For example, the oceanic uptake of anthropogenic CO_2 emissions



Fig. 4 Continued

results in the mean climate change being the dominant signature relative to variability, and hence changes in surface pCO_2 have a short detection threshold of <11 years. Temperature, salinity and ice extent have longer detection thresholds of 20–30 years, whereas other biologically influential ocean properties are much noisier requiring from >40 (phosphate) to >80 (iron) years of data for detection, indicative of a much more complex inter-relationship between climate variability and change (Fig. 4a).

There is also evidence of projected changes in natural variability over the decades from present day to year 2100 that must be taken into consideration when estimating n* (Fig. 4b). For polar waters there is support from modelling simulations (Moore et al., 2013) of an increased variability range for surface ocean temperatures and pCO_2 , and to a lesser extent for mixed layer depth, nutrients and ice fraction. In contrast, there may be a small decrease in the range of natural variability observed in coming decades for surface ocean irradiance (Fig. 4b). As was apparent in Fig. 3, there is evidence of inter-regional differences in these climatic trends (range of natural variability) between oceanic provinces (Fig. S2). A comparison of polar and subpolar regions of the Southern Ocean points to less conspicuous trends for subpolar waters, with an increased variability range for pCO₂, smaller projected increases for iron, and in contrast with polar waters a small decrease in the range of natural variability for surface ocean temperature.

Future transitions during the Emergence: from phenotypic plasticity to directional selection?

Model projections point to mean climate change becoming the dominant driver of future shifts in environmental heterogeneity (Fig. 4). How will the biota respond in the coming decades to such altered oceanic conditions? The findings from the lab study of Schaum & Collins (2014), using a fast-growing microbe (400 generations in \sim 1 year, i.e. not readily applied to other slower growing more complex taxa) hinted at the possibility of a future transition for microbes from the dominance of phenotypic plasticity to that of directional selection as the mode of response to changing environmental conditions. The issue of the predominance of phenotypic plasticity vs. directional selection/adaptation in coming decades has also been raised by Seebacher et al. (2015) and Botero et al. (2015). For example, Botero et al. (2015) conceptually modelled organismal responses to more rapid and less predictable environmental heterogeneity due to anthropogenic change, and discussed a range of strategies to such changes (including both reversible and irreversible phenotypic plasticity). Notably, Botero et al. (2015) found that the nature of the variability (random vs. trending over time) was less important evolutionarily than the ability of organisms to 'anticipate' (i.e., adaptive alteration based on responses to environmental cues) such variability. The trends for projected changes to oceanic conditions by 2100, from Figs 3 and 4, help to inform this debate about the biological ramifications of joint changes to climate variability and mean climate change in the coming decades.

For oceanic phytoplankton, the decadal rate of change of some biologically influential properties is comparable to that of natural climate variability (e.g. phosphate or dissolved iron), whereas for other properties, such as CO_2 or temperature the decadal rate of change greatly exceeds that of natural climate variability (Fig. 4). Thus, for oceanic properties such as nutrients, acclimatization is likely to be the strategy that dominates phytoplankton responses to a changing oceanic environment (also see Fig. 3 in Flynn *et al.*, 2015b), whereas for factors like CO_2 (and potentially warming) it is likely that genetic adaptation will be the dominant mode of response by phytoplankton to future ocean conditions.

It is becoming increasingly apparent from laboratory and field manipulation studies that the response of phytoplankton to multistressors, such as nutrients, temperature, and CO₂, is complex since it may involve interactions (i.e., synergisms and antagonisms) between these changing properties (Boyd & Hutchins, 2012; Breitburg et al., 2015). Hence, it is probably simplistic to state that the biota will use acclimatization to respond to changes in one ocean property, but genetic adaptation to others. A major unknown is whether organisms can accommodate these diverse strategies to tolerate exposure to multistressors (Boyd et al., 2015). The projected rate of change in oceanic conditions is unprecedented in the last 300 million years (Field et al., 2014), raising questions about how readily individuals can respond to myriad (i.e., local, regional and global stressors) and shifting patterns in climate variability and / or mean climate change.

Boyd *et al.* (2008) in their modelling study recognized that "secular climate change will only induce significant biological effects when the magnitude of environmental perturbations exceed background natural variability on seasonal to interannual timescales", and also the need for "a clear and sustained change in environmental conditions" to enable adaptation to occur. Other studies have used multiyear satellite records of ocean chlorophyll to test whether a mean climate change trend can be detected against climate variability (Henson *et al.*, 2010; Beaulieu *et al.*, 2013; Keller *et al.*, 2014). Figures 3 and 4 indicate that the strategies organisms adopt in response to environmental change will vary between oceanic provinces. Such strategies, across a spectrum of short- to long-lived taxa, will be mediated by environmental sensitivity (Pörtner *et al.*, 2014), life history and modes of existence (e.g., zooplankton and latitudinal migration, Edwards *et al.*, 2013). Clearly, given these unknowns, and their potentially confounding interplay, environmental heterogeneity must be better represented when studying organismal responses to a changing ocean.

Inclusion of environmental heterogeneity in biological manipulation experiments

It is long-established that the nature and magnitude of biotic responses is dictated by the duration of the exposure to stress (Bender et al., 1984; Helmuth, 2009). Environmental perturbation studies have traditionally been divided into 'press' or 'pulse' experiments (Bender et al., 1984), where 'press' denotes a sustained or permanent perturbation and 'pulse' is a brief or transient change. Incorporating long-term change and short-term heterogeneity into experiments demands that future manipulations must incorporate both aspects of 'press' and 'pulse' perturbations (Thornton et al., 2014). Schaum & Collins (2014) have asserted that because most lab-based experimental evolution studies have been performed using constant environments, they may underestimate the ability of microbial populations to adapt to changing conditions in which both variability and mean change are altered concurrently. Moreover, natural fluctuations in some properties may already exceed the change in the mean state predicted by the end of 2100 due to mean climate change, for example the pH of upwelled coastal waters (Feely et al., 2008). This trend of high environmental heterogeneity can also be biologically mediated, as reported for micro-layers where the resident biota largely drives shifts in carbonate chemistry (Hurd et al., 2011; Flynn et al., 2012).

Here, we report the outcomes of a small subset of experiments that have included environmental fluctuations as part of the design of biological manipulations. We critique these studies and in particular the need to inform the experimental design with observations of environmental heterogeneity on the appropriate scales. We conclude by summarizing suggestions for metrics to include in the design of such experiments to enhance the (multi-faceted) interpretation of their outcome(s) (Table 2).

The central hypothesis that is tested in manipulation experiments that incorporate changes in both the mean environment and its variability (Table 2) is that: organisms from more environmentally heterogeneous environments, which regularly encounter large fluctuations in biologically influential properties, should be better able to withstand the changes in these properties that are projected for 2100. Although most lab ocean acidification experiments have studied the effects of variable pH (Table 2A), few have used full factorial experiments where the effects of changing mean climate change vs. variability can be examined.

Experiments with three treatments are commonly employed: a "low static pH" (e.g. pH 7.7), an "ambient static pH" (e.g. pH 8.0) and a "fluctuating" treatment with ambient seawater (pH 8.0) during the day and pH 7.7 at night (i.e., its mean pH does not reflect that of either the low or ambient pH treatment). Thus, a major unknown in these treatments is if they had constant pH (i.e., with the same mean as their fluctuating treatment, 7.85) whether such a manipulation would elicit different biological responses than the fluctuating treatment. In such studies it is difficult to determine whether the change in the mean state or the change in the variability influenced the responses of individuals to the "fluctuating" treatment. Here, we consider two different approaches to understand how pH variability may alter the response of coralline algae (life time of months to years) to acidification - a fully factorial experiment by Cornwall et al. (2013), and a study by Noisette et al. (2013) which compares the responses of species collected from habitats with different degrees of environmental variability.

Noisette et al. (2013) selected individual coralline algae from habitats ranging from the intertidal to subtidal, which were then grown under constant pCO_2 from 380 to 1000 ppmv. They reported no difference in the responses of species from habitats with greater heterogeneity than those from low variability sites. Cornwall et al. (2013) collected coralline algae from one subtidal site, within a kelp bed with 0.4 pH units of diurnal fluctuation, and grew them under lab conditions of static (present day, 8.05 and 2100, 7.65) and fluctuating (7.65 \pm 0.4 and 8.05 \pm 0.4) pH. The daytime pH in the fluctuating treatments was 0.4 units greater than the mean (either 8.05 or 7.65), and at night pH was 0.4 units lower than the means. Cornwall et al. predicted that the effects of fluctuating pH would be less severe than in the static treatments, because higher daytime pH would offer respite from low night-time pH. They found that treatments which fluctuated around the mean pH (both for present day or 2100), enhanced the effect of acidification by depressing growth rate.

The findings of both studies were opposite to their predictions on the responses of coralline algae to fluctuating pH, and they each provided potential explanations for the departures from the expected outcomes. Noisette *et al.* (2013) suggested that interspecific differences set the physiological responses to ocean acidification. They also noted a potentially confounding

Approach	Study organism(s)/ experiment(s)	Study site(s)	References
(A) In situ observations used to inform fluctuations	Temperate corallines/ lab-based CO ₂ manipulations*	Coastal ocean / subtidal kelp bed	Cornwall et al. (2013)
In situ observations used to inform fluctuations Samples from habitats with different degrees	Antarctic sea ice Temperate corallines/ lab-based CO. manimulatione	Sea ice brine algae Rockpool/rocky subtidal	McMinn <i>et al.</i> (2014) Noisette <i>et al.</i> (2013)
on neterogenerty Samples from habitats with different degrees of heterogeneity / <i>In situ</i>	CO2 maniputations Tropical corallines∕ lab-based CO2 manipulations†	Coral back-reef	Johnson et al. (2014)
observations used to inform fluctuations In situ observations used to inform fluctuations	Mesocosm with tropical corals and associated	Growth zone of	Dove et al. (2013)
Samples from habitats with different degrees	patch-reef organisms such as invertebrates Corals/ lab-based temperature manipulations	a coral reef Rockpool/subtidal coral reef	Schoepf et al. (2015)
of heterogeneity Samples from habitats with different degrees	Corals/ lab-based CO2 manipulations†	Coral back-reef	Comeau <i>et al.</i> (2014)
or neterogeneity/ <i>in suu</i> observations used to inform fluctuations			
Tested the effects of environmental variability	Corals/lab-based CO ₂ manipulations [†]	Subtidal coral reef	Dufault et al. (2012)
<i>In situ</i> observations used to inform fluctuations <i>In situ</i> observations used to inform fluctuations	Corals/ lab-based temperature manipulations‡ Isopods/ lab-based CO2 manipulations†	Subtidal coral reef Wharf	Putnam & Edmunds (2008) Alenius & Munguia (2012)
Tested the effects of environmental variability	Mussels/ lab-based CO ₂ manipulations*	Wharf	Frieder et al. (2014)§
t ranscriptomics to assess the inituence of upwelling events on pH folerance	Urchin larvae (<i>strongylocentrotus purpuratus</i>)	Interudal habitat	EVans et al. (2013)
Samples from habitats with different degrees of heterogeneity	Sea urchins / lab-based CO2 manipulations	Subtidal rocky shore	Kelly et al. (2013)
Longitudinal studies testing for genetic	Sheep / size	St. Kilda (island) Scotland	Ozgul et al. (2010)
changes in populations Comparison of mean niche vs. mean environment	Phytoplankton / temperature.	Tropical ocean multidecadal	Irwin et al. (2015)
1	light, nutrients	time series	
Experimental evolution in simulated environments	Phytoplankton/ CO ₂	Lab cultured phytoplankton	Collins & Bell (2004); Schaum et al. (2013); Schaum & Collins (2014)
Spatial studies across climatic gradients; space for time substitutions	Drosophila sp. / Alpine plants	Lab and field studies	Ayrinhac <i>et al.</i> (2004); Dunne <i>et al.</i> (2004)
Åssessment of the roles of novel environments and relaxed selection on the limits of plasticity	Campylobacter genome	Lab study	Sheppard et al. (2013)
DNA methylation signatures	Signatures of phenotype-environment mismatch	Lab studies	Gilbert & Epel (2009)

Summary of: (A) Approaches used to incorporate environmental heterogeneity into climate-change manipulation experiments. (B) Methodologies and assays that are reviews (Tahle 1 in Hoffmann & Sorò (2011): Tahle 1 in Murren eity (derived from prior od loto ç dontion 3 ç 1 - continue L- -LL 4+7 Table 2 - 7- -

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experimental artefact: that although they focussed on acidification using pCO_2 manipulations, they did not mimic the light climate (highly fluctuating, Table S1) which coralline alga from the high variability site encounter. This artefact (high irradiances in all treatments) probably caused bleaching which may have enhanced dissolution of the calcite structures, and altered energy allocation across a range of metabolic processes. In this case, an additional stressor (irradiance) was inadvertently included in their acidification study.

Cornwall *et al.* (2013) also alluded to confounding factors in their study – they mimicked fluctuating pH using a symmetrical 'step-wise' pCO_2 fluctuation. This rapid change in pH differs markedly from the gradual shifts in biologically modulated pH fluctuations within a kelp bed (Hofmann *et al.*, 2011, 2013). Despite, these artefacts, both studies, and others (Table 2), have demonstrated departures in organismal responses in experiments that include environmental fluctuations along with the representation of mean climate change conditions. Future studies must remove the potential for confounding artefacts which compromise the findings and interpretation of this new suite of manipulation experiments.

The Noisette et al. (2013) and Cornwall et al. (2013) studies represent targeted variations (selection of individuals that straddle different habitats; inclusion of environmentally valid fluctuations in treatments) on conventional single-stressor manipulation experiments. These designs could be further optimized by considering other approaches and/or adoption of other metrics proposed for biological studies of environmental heterogeneity. Merilä & Hendry (2014) synthesized six different approaches to investigating the relative roles of genetic vs. plastic responses to climate change (Table 2B), and Murren et al. (2015) compiled the range of 'omics' approaches that have the potential to investigate the evolution of phenotypic plasticity (Table 2B). Some approaches - such as space-for-time substitution studies - have been mainly deployed in terrestrial ecosystems (Dunne et al., 2004; but c.f. Wright et al., 2010) or in complex laboratory microbiology studies with yeasts (Hillenmayer et al., 2008) and so their utility for, and applicability to, marine studies will require careful scrutiny.

Conclusions: the need for interdisciplinary studies

This Review reveals that environmental heterogeneity can significantly influence the sensitivity of organisms to changing oceanic conditions. It is also clear that climate-change mediated shifts in environmental heterogeneity, projected from model simulations, may enhance the phenotypic plasticity of biota, which in turn will probably alter how they respond to climateinduced shifts in oceanic conditions. Multiple stressors, community level interactions and evolutionary rescue (i.e., relatively rapid rates of evolution that can mitigate climate-change mediated declines in organismal populations, Gonzalez et al., 2013), have all been proposed as important mediators of the response of organisms to climate change (Boyd & Hutchins, 2012; Brose et al., 2012; Gonzalez & Bell, 2012). We advocate that it is equally important to quantify the effects of environmental heterogeneity on the sensitivity of organisms to climate change (Fig. 5). Interdisciplinary studies are required to understand the effect of environmental heterogeneity and phenotypic plasticity on the tolerance of climate change by marine life. We conclude by outlining three key research questions that will benefit from a transdisciplinary approach.

Rate of change in climate variability vs. the ocean mean state

Few models currently predict rates of change in environmental heterogeneity - i.e., the cumulative effects of alteration of both the mean state and variability of environmental properties [see Fig. 4 This study; (Montalto et al., 2014)]. It is important to build this capability into model projections if we are to better predict the effects of climate change (Somero, 2010; Thornton et al., 2014). Model outputs of mean state and variability have been obtained to increase confidence in predicting the future state of ocean physics until the year 2100 and its effects on productivity (Doney et al., 2004; Bopp et al., 2013; Laepple & Huybers, 2014). Developing the capability to predict the biological ramifications of natural variability and changes in the mean state of the ocean will require the development of new models that incorporate metrics to represent the limits of phenotypic plasticity. Bounds can be set by a range of factors including physiological - such as biochemical constraints (Huey et al., 2012; Seebacher et al., 2015) - and ecological restrictions, including the effects of ecosystem-level interaction (Murren et al., 2015) and/or responses to altered species interactions (Cahill et al., 2013).

What are the energetic costs of tolerating environmental fluctuations, for individual vs. multiple properties?

Studies that straddle disciplines, ranging from physiological modelling (Geider *et al.*, 1998), acclimatization / physiological responses (Seebacher *et al.*, 2015), to the evolution of plasticity (Ghalambor *et al.*, 2015; Murren

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Fig. 5 The four main research themes that need to be developed to be able to better understand and predict biological responses to changing oceanic conditions. Each of these themes is interlinked, for example the climate-change mediated modification of multiple stressors and of environmental heterogeneity will both influence the tolerance strategies of organisms to changing ocean conditions.

et al., 2015) have each tackled aspects of the interplay between energetic costs and the physiological plasticity required to respond to environmental heterogeneity. However, none has yet investigated these interactions in a holistic manner. Modelling studies have been able to explore energetic costs and benefits in optimizing the physiological responses to coincident changes in several environmental properties such as light, temperature and nutrients (Flynn, 2001). In contrast, most detailed lab-based physiological studies have been forced to target acclimation to variability in a single environmental property, such as temperature (Seebacher et al., 2015). Such modelling studies should guide the design of a new generation of manipulation studies to better understand the energetic costs and trade-offs of acclimatization (or adaptation) in circumstances where organisms are exposed to coincident variation of several environmental drivers (each of which has a different relationship between mean change and variability, Fig. 4a). This would allow the implications of environmental heterogeneity for marine life to be more accurately assessed (Thornton et al., 2014).

Climate-induced changes in tolerance strategies of organisms

Schaum & Collins (2014) highlight the challenge of assessing the extent to which various responses by organisms can mitigate against changing climate (migration, acclimatization or adaptation). In their experimental evolution study on a green microalga they report that the initial plastic response to ocean acidification is to increase growth rates, followed by - after 400 generations - a slowing of growth that is indicative of a shift in its tolerance strategy. Their key finding can be contextualized using projections from ocean climate change models that examined the rate of change in both mean climate and its variability. Model simulations point to an inflection point, for some regions in the coming decades, when the rate and direction of secular climate change will exceed that of the noise of environmental heterogeneity. How will such a projected shift – that may take as little as a decade (for pCO_2) alter the capacities of biota to respond to these different modes of climate change? Again a transdisciplinary approach, from modelling to biological manipulation experiments, is essential to address this central issue in the debate about the relationship between environmental heterogeneity, marine life and climate change.

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Supporting Information

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

Figure S1. (a) The rate of change in biologically influential oceanic properties – temperature, salinity, mixed layer depth, phosphate, dissolved iron, irradiance and sea-ice fraction. Blue symbols denotes the monthly anomalies from the mean annual cycle using the CESM1 RCP 8.5 run (Moore *et al.*, 2013) for the subpolar region of the Southern Ocean. All terms are as described in the caption for Fig. 4b) Comparison of simulated grid-scale (~1 degree) surface ocean time-space variability in the subpolar Southern Ocean for the beginning and end of 20th century. All terms are as described in the caption for Figure 4.

Table S1. Fluctuations in biological influential environmental properties over a range of scales for (A) time and B) space.

Table S2. Regional illustration of the influence of decadal climate change vs. natural climate variability for biologically influential properties (reformatted from Boyd *et al.*, 2008).