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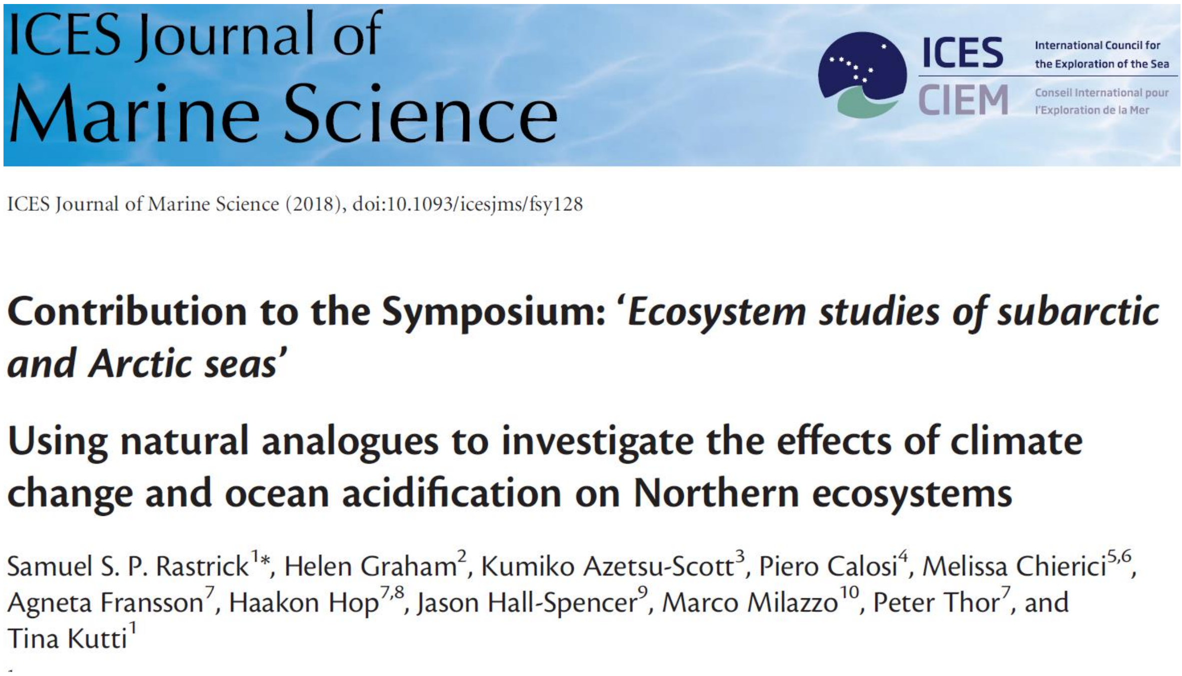

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Using natural analogues to investigate the effects of climate change and ocean acidification on Northern ecosystems

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Running Head: Analogues of climate change in northern ecosystems

Abstract

Northern oceans are in a state of rapid transition. Still, our knowledge on the likely effects of climate change and ocean acidification on key species in the food web, functionally important habitats and the structure of ~~polar~~ Arctic and sub-Arctic ecosystems is limited and based mainly on short-term ~~single-species~~ laboratory studies on single species. This review ~~demonstrates~~ discusses how tropical and temperate natural analogues to ~~ocean acidification~~carbonate chemistry drivers, such as CO_2 vents, have been used to ~~move~~ further our knowledge on the sensitivity of biological systems to predicted climate change, and thus assess the capacity of different ~~tropical and temperate~~ species to show long-term ~~acclimate~~ acclimation and adaptation to elevated levels of pCO_2. Natural analogues ~~and has~~ have also provided the means to scale-up from single-species responses to community and ecosystem level responses. However, to date the application of such approaches is limited in high latitude systems. A range of Arctic and sub-Arctic sites, including CO_2 vents, methane cold seeps, estuaries, up-welling areas and polar fronts, that encompass gradients of pH, carbonate saturation state and alkalinity, are suggested for future high latitude, *in-situ* ocean acidification research. It is recommended that combinations of monitoring of the chemical oceanography, ~~laboratory studies, monitoring of the chemical oceanography,~~ observational and experimental (*in situ* and laboratory) studies of organisms around these natural analogues be used to attain ~~good~~ better predictions of ~~future~~ the impacts~~effects~~ of ocean acidification and climate change on high latitude species and ecosystems.

Introduction

Rising levels of CO_2 in the atmosphere are causing worldwide modification of seawater carbonate chemistry, with gradual reductions in pH and carbonate ion (CO$_3$~~$_2$~~~~^{3}~~$^{2-}$) availability, in a process known as ocean acidification (OA) (Caldeira and Wickett, 2003;~~;~~ IPCC, 2014). The Arctic Ocean is particularly sensitive to OA, already having a naturally low pH and $CaCO_3$ saturation caused by the large freshwater content, which may increase due to warming and associated ocean and tundra ice melt and increased river runoff (Chierici and Fransson, 2009; Chierici et al., 2016). The relatively cold water in these regions also causes a high solubility of CO_2, which could exacerbate OA in the future. Increased ice melt and river runoff not only effects the solubility of CO_2 via alterations in salinity, but depending on the geology of the runoffs terrestrial catchment can also inference totlal alkalinity (e.g. McGrath et al., 2016). The northern Norwegian Sea is ~~a~~one region where a large part of the anthropogenic CO_2 has been absorbed during cooling of the warmer Atlantic water transported north along the Norwegian coast (e.g. Olsen et al., 2006). This has resulted in decreased pH and calcium carbonate ($CaCO_3$) saturation, as well as shoaling of the saturation horizon. In fact, recent observations show that the pH decrease in the Norwegian Sea is occuring~~s~~ at one of the highest rates globally (Chierici et al., 2017; Jones et al., 2018). ~~The Arctic Ocean is particularly sensitive for OA, since it already has a naturally low pH and $CaCO_3$ saturation caused by the large freshwater contentocean (Chierici and Fransson, 2009; Chierici et al., 2016). The relatively cold water in these regions causes a high solubility of CO_2 , which could progress OA in the future.~~ The Arctic ~~It~~ is one of the first ~~areas~~ regions ~~already~~ being affected by a rapid expansion in carbonate undersaturation (Olafsson et al., 2009; AMAP 2013; Qi et al., 2017)~~. The polar ocean~~ and is experiencing one of the most rapid shifts in biogeographic boundaries on the planet due to ~~polar and tundra~~ rapid warming ~~ice melt~~ coupled with ice melt ~~rapid warming~~ and ~~acidification~~s decrease in alkalinity.~~ — these all affecting the ecology of marine organisms~~. Whilst rapid adaptation and borealization of the benthic flora are expected (Brodie et al., 2014), some benthic animals in the region may ~~often~~ have limited physiological plasticity which ~~may~~ can reduce their chances of survival (e.g. Rastrick and Whiteley, 2011,~~;~~ 2013; Calosi et al., 2017).

Ocean acidification in Arctic and sub-Arctic seas may have negative effects on pelagic species such as the copepod *Calanus glacialis* (Thor et al., 2017) and the shell-bearing pteropod *Limacina helicina* (Bednarsek et al., 2017) that constitute the main prey items for a ~~large~~ variety of larger zooplankton, juvenile fish, baleen whales and seabirds. Acidified seawater has also been suggested to impact coralline algae (Brodie et al., 2014) and cold-water corals (Jackson et al., 2014), which ~~that~~ form extensive biogenic habitats around northern Norway~~,~~. To date our best predictions of habitat change in the North Atlantic are that warming will depleted kelp forests in the south and that ocean acidification will compromise maerl reefs in the north (Brodie et al., 2014). However, these predictions are based on a range of published laboratory experiments on signal species in isolation and so lack an understanding of the complex effects of interactions between species that can only be studied in naturally assembled systems. ~~Tthis is~~Such habitat change is expected to impact nursery and brood stock areas for commercially important molluscs and fish (Branch et al., 2013; Sunday et al., 2017). It is predicted that cephalopods and crustaceans will be mostly unaffected by elevated $p\text{CO}_2$ levels expected by the end of the century, in contrast to shelled molluscs will be negatively affected (Branch et al., 2013). However, again these predictions are based on studies that cannot comprehend how the responses of these key species to elevated $p\text{CO}_2$ may be modulated by and in turn modulate wider community level change.

Although a number of studies have shown adult fish to be relatively resistant to elevated $p\text{CO}_2$, they many suffer neurological impairment (Milazzo et al., 2016). ~~, and a~~A recent study showed increased mortality in Atlantic cod larvae exposed to elevated $p\text{CO}_2$, potentially resulting in reduced recruitment to the stock (Stiasny et al., 2016). Our current understanding of key processes driving the ~~response~~ responses of northern commercially important species and ecosystems to climate change is~~, however,~~ limited. In addition, ~~since~~ the majority of studies conducted so far have been ~~in vitro~~laboratory, short-term, rapid perturbation experiments on isolated elements of ~~the~~ ecosystems (e.g. Agnalt et al., 2013; Andersen et al., 2013; Bednarsek et al., 2017). Most studies have used set stable (but unrealistic) $p\text{CO}_2$ levels and focus on the responses of organisms that are separated from their natural suite of competitors, predators, parasites and facilitators, and experiment conducted are ~~ofte~~often too short-term to reveal how organisms may adapt/acclimatise. Thus, i~~I~~t is difficult to extrapolate from ~~such~~ individual level responses studies to larger ecological scales.~~,~~ ~~as these are generallysuch as~~ Population-level effects, ~~but this has also been~~ have to date been studied ~~done either~~ by applying laboratory rates (e.g. Stiasny et al., 2016) or with integrated models for effects of ocean warming and acidification (Koenigstein et al., 2018).~~the w~~ However it extremely difficult to validate such modals in a natural context. ~~too short-term to reveal how organisms may adapt/acclimatise~~, ~~have use in most cases often set stable (but unrealistic) eady $p\text{CO}_2$ levels (which are unrealistic) and use focus on the responses of organisms that are separated from their natural suite of competitors, predators, parasites and facilitators.~~

One approach to study ~~the~~ ecosystems' responses to ~~effects of predicted~~ future predicted chronic ~~elevations~~ increases in mean *p*CO$_2$~~-~~, as well as associated increases in acute fluctuations in carbonate chemistry due to freshwater run off, is to use natural analogues. Such analogues for future predicted OA have included so far volcanic vent sites (e.g. Hall-Spencer et al., 2008; Kroeker et al., 2011, 2013), up-welling of deep CO$_2$ rich water (Manzello et al., 2014) and temperate systems which present a mosaic of alkalinity and pH conditions (Thomsen et al., 2010).

These natural analogues provide an opportunity to simultaneously investigate changes in community structure (Hall-Spencer et al., 2008; Kroeker et al., 2011, 2013) and the capacity for physiological adaptation/acclimatisation of species in response~~s~~ to elevated *p*CO$_2$ and low CO_3^{2-} ~~carbonate ion~~ concentration (Calosi et al., 2013a; Harvey et al., 2016). In addition, broader evolutionary responses to past and future *p*CO$_2$ changes can be addressed (Garilli et al., 2015). They have also been used to investigate the importance of natural variability in carbonate chemistry on the mechanisms that set or limit the distribution of species (Small et al., 2015) and to investigate the effect of multiple stressors on the ecological performance and distribution of species -in naturally fluctuating environments (Thomsen et al., 2010; Kroeker et al., 2016). However, to date studies utilising natural analogues are limited to temperate and tropical systems.

Recent studies have identified how shifting boundaries of water and ice in a high-latitude ~~systems~~ glacial fjord create mosaics of seawater total alkalinity and pH conditions (Fransson et al., 2015~~;~~ , 2016), which could be used as natural analogues to investigate the effects of climate change and OA on the physiology, ecology and distribution of flora and fauna in northern ecosystems. However, to date, despite the potential for natural OA analogues at higher latitudes, such studies are limited to the Baltic (Thomsen et al., 2010).

Consequently, the aim of this ~~paper~~ review is to explores the possible use of natural analogues for investigating the effects of future changes in carbonate chemistry on northern species and ecosystems. ~~D~~Herein, we discuss~~ing~~: 1) the advantages and challenges of using natural analogues to investigate physiological, ecological and evolutionary effects of climate change and OA, drawing on temperate and tropical studies highlighting the arctic as an under-studied region ; 2) Challenges of using natural analogues in more studied ~~other ecosystems~~temperate and tropical ~~to explore both~~ regions, moving from studies of individual ~~and~~ to multiple carbonate chemistry drivers ~~stressors~~; 3) how such analogue approaches could be modified for ~~chemical oceanography and possible natural analogues that could be~~ use~~d~~ in Arctic and sub-Arctic ecosystems given the present understanding of chemical oceanography in this region; and 4) what key target habitats and species in northern ecosystems could be studied using such analogues.

The advantages and challenges of using natural analogues to investigate physiological, ~~evolutionary and~~ ecological and evolutionary effects of climate change

Our knowledge of the biological effects occurring under anticipated changes of ocean chemistry is primarily informed by laboratory experiments. Such studies are informative, as they enable us to identify the effect of one or a few variables on many processes such as reproduction, development, physiology and behaviour of different organisms. However, most laboratory studies are carried out on a single generation of species in isolation and during short-term exposure to stress, neglecting many processes involving species in the wild, such as intra- and interspecific interactions and trans-generational adaptation, or nutrition supply and fluctuations in environmental parameters ~~fluctuations~~ (Barry et al., 2010). Research using natural analogues allows the investigation of the chronic~~ally~~ exposure to ~~ed populations to~~ elevated levels ~~of dissolved~~ pCO$_2$~~,~~ in natural populations, thus providing a means by which to scale-up from physiological~~,~~ to ecological processes with further extrapolation~~,~~ -to evolutionary processes ~~that~~by which ~~what is known about the effects of~~ OA could structure and modify the community and ecosystem levels.

A shift in community structure and composition favouring algal assemblages over reef forming species, for example, is consistently documented for chronically exposed benthic species along natural pCO$_2$ gradients (Sunday et al., 2017). However, CO$_2$ seep sites used in such studies are not perfect analogues of future change. A challenge being that within volcanic seep gradients variability in carbonate chemistry is often more rapid and of a higher amplitude than is expected due to the effects of gradually rising atmospheric levels of CO$_2$ (Kerrison et al., 2011; Kroeker et al., 2011). This high rate of change in seawater chemistry is known to be especially detrimental to coralline algae, for example, which are less sensitive to gradual change (Kamenos et al., 2013). ~~Such~~ P~~p~~atterns in community structure across natural CO2 gradients are likely driven by a combination of direct physiological effects on habitat forming species (such as, elevated costs of maintaining homeostats and calcification) and indirect effects ~~such as~~involving changes in the energy available in feed, competition, predation and habitat structure. The natural distribution of ecosystem engineers, such as grazing sea urchins across volcanic pCO$_2$ gradients in Italy, is suggested to be controlled by the physiological capacity to maintain acid-base homeostasis (Calosi et al., 2013b; Small et al 2015). These species-specific responses will depend on both the physiological limits and energetic costs of the specific mechanisms employed (Small et al., 2015). Changes in the energetic costs of maintaining homeostasis across pCO$_2$ gradients can lead to energetic trade-offs that ~~effect~~ impact growth and reproduction affecting populations (Harvey et al., 2016). This demonstrates how natural analogue studies can be used to scale from direct physiological impacts at the individual level to population level responses that may have implications at the community level ~~implications~~ within naturally assembled systems. Fleshy non-reef forming macroalgae, for example, show marked increases under naturally elevated pCO_2 levels and appear capable of exploiting pCO_2 *via* photosynthesis (Cornwall et al., 2017a). This allows seaweed to out-compete calcifying reef species (e.g. corals and vermetids), whose performance is lowered by dissolution and increased energetic costs associated ~~to~~ with calcification (Milazzo et al., 2014). In addition to this, key groups (e.g., crustose coralline algae) that trigger the recruitment of reef forming species, can be out-competed or cannot survive (Diaz-Pulido et al., 2011; Milazzo et al., 2014). Overall such responses lead to ecosystem shifts from calcareous reefs to algal-~~-~~dominated habitats (Diaz-Pulido et al., 2011).

Carbon dioxide seep research carried out in temperate, sub-tropical and tropical regions has revealed that responses of benthic habitats vary regionally~~,~~ . ~~as no total coral cover reduction~~ Reduction ~~but~~ in species ~~composition~~ diversity of corals, but not in total cover of corals, has been c~~hanges~~ observed in Papua New Guinea and Palau (Fabricius et al., 2011; Barkley et al., 2015~~; Fabricius et al., 2011~~), while a shift from hard to soft corals has been documented in Japan (Inoue et al., 2013) and from corals to macroalgae in Northern Mariana Islands (Enochs et al., 2015). Hall-Spencer et al. (2008) and Linares et al. (2015) describe a transition from communities with abundant calcareous organisms to communities lacking scleractinian corals and a significant reduction in coralline algae off CO_2 vents in the Mediterranean Sea.

A common feature shared by biological systems~~-~~chronically exposed to elevated CO_2~~-~~, and demonstrated uniquely by the use of natural analogues, is the general loss of habitat complexity and ~~usually of~~ the associated diversity. ~~Acidification~~ Decreasing pH conditions also leads to ecological shifts, such as changes in competitive dominance and habitat provisioning (Sunday et al., 2017). For instance, when kelp/macroalgae and seagrass habitats shift to low-relief turf-algal habitats off CO_2 seeps in New Zealand and Italy, this causes loss of fish predators and increase in prey fish species ~~release~~, even though their antipredator responses were compromised (Nagelkerken et al., 2015). However, such patterns of response are species-specific (Cattano et al., 2017).

In addition to~~,~~ facilitating the investigation of the interaction between individual, population and community responses to chronic changes in carbonate chemistry within naturally assembled systems, natural analogues provide a suitable test bed for studies of adaptation to many different environmental drivers. While lab studies of adaptation require multi-generation incubation periods, which is impractical in longer lived species and species with complex life history patterns, the real strength of natural analogous approaches is the possibility of tests on populations pre-adapted through many generations. Thus, natural analogous ~~They~~ may be specifically used to test the potential for a species' adaptation to future environmental changes, and how such adaptation may potentially rescue species from local or global extinction. Evolutionary rescue from environmental changes may be facilitated ~~by either~~by mutation, evolutionary selection~~adaptation~~, or migration (Bell and Collins, 2008; Bell and Gonzalez, 2009). However, in long-lived multicellular organisms, mutations progress at rates much lower than what would be needed to facilitate adaptation to ~~Mutation rates are far slower than~~ present- day environmental changes. ~~in metazoans. However~~This said, genetically-~~-~~based phenotypic variation throughout a species' distribution range provides a constant supply of physiological alternatives or new possibilities upon which selection can operate to facilitate adaptation to the new set of conditions ~~to~~that occur (Foo et al., 2012; ~~Kelly and Hofmann, 2013;~~Munday et al., 2013~~ Ecology Letters~~; Reusch, 2014; Sunday et al., 2014; Calosi et al., 2016). Therefore, adaptation from selection in extant genetic diversity, as well as migration among locally adapted populations may effectively decrease the risk of extinction in the face of climate change and OA. Both of these processes can be tested using natural analogues, given certain conditions. The main prerequisite for differential adaptation among natural analogues is that populations should be genetically isolated. In addition, ~~The~~ rates of selection should not be matched by the rate of gene flow among populations (Kawecki and Ebert, 2004; Savolainen et al., 2013). Therefore, a potential challenge in using natural gradients is to establish possible connectivity patterns between experimental populations/sub-populations. Many benthic organisms proliferate in the larval stages and establishing models of larval dispersal may be important (Cowen et al. 2007). Genetic isolation may be obtained at a distance of 2-5 times the larval dispersal range (Palumbi 2003). However genetic differences may be compromised with the migration of only a few individuals per generation (Cowen and Sponaugle 2009, Slatkin 1993). Consequently, differences in physiological responses of individuals across natural analogues should be accompanied by an understanding of the phylogenetic relationship between populations/sub-populations (Hill and Bucklin 2001; Calosi et al., 2013) or if posable the allelic heterogeneity in genes related to the physiological processes. In addressing these challenges analogue selection is critical with many seep systems presently used showing localised steep gradients in carbonate chemistry over distances of 10s to 100s of meters, allowing organisms to move in or recruit from outside. This may hinder genetic adaptation (Calosi et al., 2013; Harvey et al., 2016~~5~~; Turner et al., 2016) and cause short-term physiological shocks to organisms that are suddenly exposed to hypercapnia (Small et al., 2015). ~~While our knowledge on the adaptation potential to climate change and OA has been very limited (Dam, 2013; Munday et al., 2013; Reusch, 2014; Sunday et al., 2014Kelly and Hofmann, 2013), recent studies have brought more insight (Calosi et al., 2016).~~ ~~In~~ Despite this in benthic animals, adaptation to ~~e.g.~~ OA has been recently demonstrated. For instance, the polychaete *Platynereis dumerilii* has been shown to adapt to chronic and elevated levels of $p\mathrm{CO}_2$. Populations occupying CO_2 vent sites on the Italian coast are physiologically and genetically different from nearby populations that experience low $p\mathrm{CO}_2$ (Calosi et al., 2013). However, no adaptation to high CO_2 conditions was found in the calcifying spirorbid worm *Simplaria* sp. following a putative multi--year exposure to high OA conditions ~~no evidence for adaptation to high CO2 conditions where found~~ (Turner et al., 2016). ~~In the sea urchin *Centrostephanus rodgersii*, the presence of tolerant genotypes indicates a potential to adapt to concurrent warming and acidification (Foo et al., 2012).~~ Thus ability to adapt to OA conditions does not appear ubiquitous in marine metazoans (~~see also~~e.g., Calosi et al. 2016). Using natural analogues to testing adaptation in planktonic species may be a specific challenge as ~~But even planktonic species may experience differential adaptation throughout their distribution range. While l~~ low genetic differentiation and efficient dispersal of ~~propagules~~ all life stages may ~~were previously thought to~~ hinder local adaption~~,~~. However, recent studies have shown pelagic copepods to be dispersed in distinct populations locally with little genetic interchange ~~throughout~~ around the Northern hemisphere (Nelson et al., 2009; Unal and Bucklin, 2010; Yebra et al., 2011; but see Weydmann et al., 2016), although some species have large oceanic distributions (Wassmann et al., 2015)~~.~~ ~~Coupled with~~Moreover large population sizes of planktonic organisms, as opposed to less abundant longer-lived benthic organisms, ~~this~~ can promote effective selection with an increased potential for local adaptation (Charlesworth, 2009; Peijnenburg and Goetze, 2013).

Reciprocal transplant tests between locations characterized by different environmental regimes should be employed to ascertain that differences in phenotypes among locations are not caused by phenotypic plasticity but occur as a result of adaptation (Niewiarowski and Roosenburg, 1993). Transplant individuals, once transferred to the new environment, should show the same phenotype ~~of~~as individuals found in the environment~~In such transplant tests, phenotypic plasticity results in transplant individuals attaining native individuals' phenotype~~. Any deviation from this outcome signals that differences stem~~s~~ from either ~~pure genetic~~ adaptation or ~~or~~ transgenerational effects ~~-~~caused by~~,~~ for instance reversible epigenetic or post-transcriptional changes (Bonduriansky et al., 2012). However, whilst evidence for phenotypic differences are essential, so is the a~~A~~nalyses of allelic differences between populations. This will ~~is needed to~~ in fact further ascertain that observed differences are indeed genetically based (Calosi et al., 2013; Pespeni et al., 2013; De Wit et al., 2015). Obviously most of genetic variation involved in adaptation to environmental changes lies within expressed sequences (Jones et al., 2012). Reverse transcription sequencing and transcriptomic treatment ~~is~~ are ~~a~~ powerful tools to assess the connection between physiological differences and allelic changes in expressed genes. Aligning allelic differences to observed differences in targeted physiological processes can be used for a hypothesis-testing strategy to detect cellular targets of adaptation to ocean acidification (De Wit et al., 2015; Thor and Dupont, 2015). This novel approach seems promising for future studies of effects of environmental change~~s~~ in ecologically important non-model organisms.

Use of natural analogues to explore both individual and multiple stressors

Hall-Spencer et al. (2008) initiated the use of volcanic CO_2 seeps as analogues for future OA off the Island of Ischia in the Mediterranean. More recently, similar volcanic sites ~~have been~~~~were~~have been investigated, for example, in Papua New Guinea (Lamare et al., 2016), in the subtropical North East Atlantic reefs (La Palma Island) (Hernández et al., 2016), in the temperate Pacific Ocean in Japan (Shikine Island) (Agostini et al., 2015), and Bay of Plenty, New Zealand (Burrell et al., 2015). A natural CO_2 seep was also found in Salt Dome Juist in the North Sea (McGinnis et al., 2011), although OA studies ~~are~~ have not yet been conducted there. Most ~~ocean acidification~~OA research using such sites has focused on sessile benthos~~,~~ to retain greater control over exposure elevated $p\mathrm{CO}_2$ conditions ~~to acidified conditions~~. Organisms in the water column can be exposed to abrupt changes in seawater carbonate chemistry as they move towards or away from the gas vents (Kerrison et al., 2011; Kroeker et al., 2011). That said, experiments and observations in the water column around CO_2 seeps have ~~shown~~ been useful in demonstrating shifts in naturally assembled plankton communities and greater sensitivity of calcifying plankton even if their exposure may be transitory (Johnson et al., 2013; Ziveri et al., 2014). For example, ~~that~~ large diatoms tend to grow well ~~in the acidified conditions~~ at sites with elevated pCO_2 with a significant increase in chlorophyll concentrations and diatom abundance observed, however cyanobacteria were reportedly uninfected (Johnson et al., 2013).~~,~~ In contrast ~~whereas~~ coccolithophores show a decrease in cell concentrations and diversity as calcite saturation decreased from 6.4 to <1, with malformed *Emilianía huxleyi* observed at the highest $p\mathrm{CO}_2$ levels ~~do not~~ (Ziveri et al., 2014). Such studies are not a perfect representation of future pelagic systems due to migration in and out of the vent system. However, they facilitate a greater understanding of how plankton communities that are critical to marine primary production and biogeochemical cycling naturally assemble under elevated pCO$_2$ conditions in a way not posable using laboratory experiments. In temperate and tropical conditions invertebrate recruitment to the benthos is severely disrupted in the ~~high~~ elevated pCO$_2$ conditions found at volcanic seeps, although these observations may overestimate the impact of ~~ocean acidification~~OA since drifting larvae from normal seawater conditions are suddenly exposed to ~~acidified waters~~waters characterised by elevated pCO$_2$ (Cigliano et al., 2010; Allen et al., 2016). More realistic, perhaps, are observed impacts of elevated pCO$_2$ ~~acidification~~ on pelagic organisms that spend long periods ~~of time~~ in areas with naturally acidified conditions. The reproductive behaviour of nesting fish is affected at CO$_2$ seeps (Milazzo et al., 2016). Zooplankton and fish that use coral habitat are also much less abundant in elevated pCO$_2$ ~~acidified~~ conditions, which ~~is thought to be due to the fact that~~ may be because~~acidification~~ elevated pCO$_2$ reduces coral reef complexity (Smith et al., 2016).

The steep gradients in pH and carbonate saturation that occur next to volcanic seeps consistently have marked effects on the abundance and distribution of sessile calcified organisms. Studies show how most coralline algae are highly susceptible to these naturally acidified conditions as their high-Mg calcite skeletons are easily corroded or damaged (Kamenos et al., 2013; Martin and Hall-Spencer, 2017). Although some species are less sensitive, ~~it has been shown that~~ very few survive where aragonite saturation levels fall below 1 for even brief periods of time (Martin et al., 2008; Fabricius et al., 2015), and in these acidified conditions they are easily outcompeted by fleshy algae (Kamenos et al., 2016~~7~~). The sensitivity of calcified organisms to ~~to acidifie~~ low pH~~d~~ conditions depends on how well they are able to protect their skeletons or shells. Vent studies have shown that some corals, for example, can calcify and grow well in ~~acidified~~ low pH conditions, if they have enough food, as their skeletons are covered in protective tissue (Rodolfo-Metalpa et al., 2011; 2015). The same is true of certain molluscs, whilst others grow in a dwarf form to more easily meet the metabolic costs of hypercapnia (Garilli et al., 2015). OA is in ~~its self~~itself a multiple stressor, with the effects or low carbonate saturation, low pH and increased DIC working together to shift the outcome of competition within marine communities, often to the benefit of~~r~~ weed-like or r-~~-~~selected species such as turf algae (Connell and Russell, 2010) and uncalcified polychatetes (Gambi et al., 2016).

Whilst a great deal has been learnt from CO_2 seeps worldwide about the likely long-term ecological effects of ~~acidification~~OA, these systems are not perfect analogues for the future. For example, acidification is happening alongside local or regional warming. One way to address this is to compare CO_2 seep systems in different ~~biogeographic~~ thermal regimes and regions~~zones~~ to ~~find out~~reveal whether related organisms show consistent responses to elevated CO_2 despite differences in temperature (Johnson et al., 2012). Another approach is to take advantage of marine heat waves to assess the combined stress of high CO_2 and elevated seawater temperature (Rodolfo-Metalpa et al., 2010; 2011). ~~A drawback with volcanic seep systems is that variability in carbonate chemistry is much more rapid and of a higher amplitude than is expected due to the effects of gradually rising atmospheric levels of CO_2 (Kerrison et al., 2011; Kroeker et al., 2011). This high rate of change in seawater chemistry is known to be especially detrimental to coralline algae, for example, which are less sensitive to gradual change (Kamenos et al., 2013).~~ Confounding factors may also be present at CO_2 seeps, so a great deal of care is needed to tease apart the effects of multiple stressors such as low oxygen or elevated metal toxicity (Vizzini et al., 2013). Consequently, seep sites are selected to reduce confounding factors and focus only on changes in pCO_2, with a major challenge being how to develop analogue studies from investigating single to multiple carbonate chemistry drivers.~~.~~ ~~Finally, seep systems are usually very localised with steep gradients in carbonate chemistry over distances of 10s to 100s of meters, so organisms may move in or recruit from outside, . This may hinder hindering genetic adaptation (Calosi et al., 2013;, Harvey et al., 2015; Lucey et al., 2016 Evol. APpl.) and causing causea short-term physiological shocks to organisms that are suddenly exposed to hypercapnia (Small et al., 2015).~~

Despite ~~drawbacks~~ challenges, data collected at CO_2 seeps currently provide us with the best window we have into the future for assessing the risks of acidification to marine communities, habitats and ecosystems. ~~Unfortunately, suitable CO_2 seeps sites are uncommon.~~ However ~~-~~other analogues for future conditions are available that retain the advantages of seep systems, i.e. ~~(~~chronic exposure of entire marine communities to low carbonate saturation and high DIC,~~)~~ but lack the disadvantages of rapid variations in carbonate saturation, steep gradients in pH and DIC.~~,~~ These analogues may also lack potentially confounding factors such as hypoxia or H_2S toxicity and the influx of organisms that are exposed to a sudden increase in CO_2 levels as they recruit, swim or drift through these open systems.

Sites where the biology affects the CO_2 of the environment could be used similarly to the seep sites. Due to carbonate production on coral reefs, some atolls, lagoons and barrier reefs can exhibit consistently higher surface pCO_2 values than those in offshore waters (Suzuki and Kawahata, 2004). Sea grass beds, on the other hand, can reduce CO_2 levels causing increases in pH and aragonite saturation (Unsworth et al., 2012). There are also natural CO_2 gradients formed in areas of large~~-~~scale seaweed culture (for example in China). These systems typically experience large temporal changes in carbonate chemistry due to water movement and diurnal photosynthesis patterns. These temporal shifts are even more pronounced in the intertidal environments, for example in tide pools, where pCO_2 can reach 1800 µatm due to the respiration of the inhabitants (Andersson et al., 2013). Similarly, mangrove environments ~~(~~in Bermuda~~)~~ ~~were~~have been shown to ~~can~~ experience large fluctuations in carbonate chemistry parameters (pH, pCO_2 and Ω_a,) over daily cycles (e.g. due to groundwater input) with pCO_2 levels varying from 500 to 4200 µatm (Andersson et al., 2013). It is still important to characterise these habitats because of the effects ~~the~~ that varying carbonate parameters can have on organisms. However, these large daily fluctuations may make it difficult to disentangle the effects of singular factors (e.g. salinity or temperature) as they may co-vary.

Carbonate chemistry gradients can produce a mosaic pattern where species and communities ~~are naturally~~may be adapted to diverse conditions, putatively, ~~-~~over multiple generations. This could allow for the study of the effects of multiple stressors, and allow work on natural analogues to move forward and encompass multiple drivers of climate change ~~drivers~~. Naturally overlapping carbonate chemistry gradients have been described in marine habitats throughout the world. One of the most common areas for them to occur in is coastal regions and estuaries, where several interacting biotic and abiotic stressors are occurring within the environment. Large estuaries may have limited gene flow between populations allowing for the investigation of the capacity for adaption. There are several examples of mosaics identified in estuarine environments globally. One such system of interacting gradients (total alkalinity, DIC and salinity) has been identified around the coast of Ireland. Due to the underlying limestone bedrock of river catchment areas, runoff to coastal and estuarine areas can have high total alkalinity (TA) values (2864 µmol Kg^{-1} TA at salinity 15.86, Shannon plumes) creating these TA gradients, which expand outwards from the rivers and estuaries (McGrath et al., 2015). Interacting gradients of salinity, with

O$_2$, DIC and pH, have been highlighted in the Strait of Georgia (British Columbia, Canada). The water masses connecting the semi-enclosed estuary of the Fraser river to the outer shelf of the Pacific Ocean are subject to the effects of large scale upwelling and downwelling on the outer coast leading to different trends in pH and aragonite saturation ~~differing~~ in the tributaries (Haro and Juan de Fuca) feeding the Strait of Georgia ~~and causing~~as well as overlapping gradients ~~to occur~~ (Ianson et al., 2016). The use of these dynamic coastal environments ~~can~~ may offer insight in~~-~~to the long-term~~s~~ effects and adaptation of organisms to changing oceanic conditions. Unlike the CO$_2$ seep systems these estuarine habitats cover a greater spatial range and ~~due to this the~~~~so~~, thus, carbonate chemistry gradients are likely to be less steep possibly limiting gene flow among populations to a rate lower than selection, facilitating adaptation (Kawecki and Ebert, 2004; Savolainen et al., 2013)~~.~~

To date there has been limited research using mosaics to look at the chronic and/or acute effects of carbonate chemistry drivers ~~-~~on organismal performance and fitness. One ~~of~~ such study examined the effect of salinity and pH gradients on the spatio-temporal variation in communities of phytoplankton in Sungai Brunei and Brunei bay estuarine system which identified the highest algal densities occurring at the highest pH (pH 7.8) and highest salinity (salinity 27) and the number of taxa present decreased with decreasing pH (Majewska et al., 2017). A similar salinity and pH gradient located in the same estuary (Sungai Brunei estuary) has also been used to determine correlations between shell dissolution in the gastropod *Thais gradate* and ~~water chemical properties~~carbonate chemistry drivers (pH, salinity, calcium concentration). At decreased pH (6.83 ± 0.39), lower calcium and low salinity (13.50 ± 5.49), individuals exhibited higher levels of shell erosion and smaller standardised shell length compared to individuals acclimatised to higher pH (8.02 ± 0.15) and salinity (27.17 ± 3.0). ~~Although not pronounced as smaller scale habitats (tide pools, mangroves), t~~These estuarine scale gradients can ~~still becan still~~ be subject to temporal changes based on daily cycles (e.g. salinity, temperature) although these are usually not as pronounced as smaller scale habitats such as tide pools and mangroves~~.~~

There are however larger scale mosaics, ~~such as continental upwelling,~~ which offer the opportunity to study the effects of changing carbonate chemistry at continental scales. For example, at the continental shelf upwelling on the western cost on North America from central Canada in northern Mexico, where although seasonal upwelling of low pH water is a natural phenomenon the extent of the affected area is increasing with OA (Feely et al., 2008). One such mosaic has been identified in the California current system where, due to ~~the water source and~~ constant upwelling, a spatial mosaic of carbonate chemistry is formed. ~~Previously this analogue has been used to analyse the potential interactions between~~ This large (1280 km of coastline) environmental mosaic -of overlapping temperature, ~~pH~~ carbonate chemistry and chlorophyll-*a* gradients has been used to investigate how multiple interacting stressors associated with global change ~~and the combined~~ impact ~~they may have on~~ the growth and predation vulnerability ~~in~~of the California blue mussel *Mytilus californianus* (Kroeker et al., 2016). This study demonstrated that dynamic environments with frequent exposure to low pH seawater and consistent food showed highest growth rate and lowest predation vulnerability. Whereas, growth was limited in areas with frequent low pH and less consistent food availability and with extremes in low tide body temperature (Kroeker et al., 2016). Other potential sites for large scale mosaics can be found in the eastern Pacific Ocean -the Arabian sea where overlapping gradients in temperature, oxygen, and carbonate chemistry have be used to assess the relative inference of these climate change associated drivers on macrofaunal diversity and evenness (Sperling et al., 2016). In this study oxygen levels expand most of the variation in species diversity, whale, carbonate chemistry was the best explanatory variable in the Arabian sea it explains less of the variation in the Pacific. ~~, and the north-western coast of America (Feely et al., 2008).~~

Chemical oceanography and possible natural analogues in Arctic and sub-Arctic ecosystems

The potential is large for investigating natural analogues of multiple carbonate chemistry drivers to better understand the possible effects of climate change on the physiological, ecological and ~~adaptive~~ evolutionary capacity of individuals and communities~~ is clear~~. However, to date such sites ~~are~~ have been exclusively ~~located~~ identified in temperate and tropical seas, despite the importance and possibly greater sensitivity of sub-Arctic and Arctic regions to OA. Potential sub-Arctic volcanic CO_2 seep~~vent~~ sites may be found in Iceland. Other possible study sites may be found at varying depths around Jan Mayen in vent fields between the Greenland and Norwegian Seas, and off the west coast of Spitsbergen. The consequence of OA on ecosystems and biogeochemical cycling in this area is unknown. The increased acidity due to CO_2, associated with corrosive volcanic input and increased Arctic water masses, and potential vulnerability of key species, calls for the investigation of pH and other carbonate chemistry variables, as well as vulnerable species and processes (Fauchald et al., 2014). Other gradients in carbonate chemistry may be associated with large stocks of methane hydrate that exist in the sub-Arctic and the Arctic. Warming of seawater can destabilize methane hydrate and release~~ing~~ methane (CH_4) to the water column. A recent study demonstrated that the majority of this CH_4 is oxidized in the water column to CO_2 without escaping to the atmosphere (Myhre et al., 2016). Release of CH_4 from the sediment and subsequent oxidation to CO_2 in the water column were modelled and attributed to prolonged OA (Boudreau, et al, 2015). Methane cold seep sites are found extensively in the polar oceans, for example, East Siberian Shelf (Shakhova et al., 2017), off Svalbard (Myhre et al., 2016), Baffin Island Shelf (Punshon et al., 2014), and the Barents Sea (Hong et al., 2017; Serov et al., 2017). Although, cold seeps may provide sites for studying natural gradients in carbonate chemistry in polar oceans investigations of the chemical oceanography, including confounding effects of CH_4~~methane~~, and the biology of such sites are in their infancy and their depth and remoteness makes them logistically difficul~~tdefaultt~~. Other mosaics in carbonate chemistry drivers that may drive plankton communities can be found marginal ice zone of the Arctic ocean (e.g. Lewis et al., 2013; Barber et.al., 2015; Jule et al., 2018).

Coastal regions in high--latitude oceans are influenced by freshwater such as rivers, glaciers and sea ice melt. Each freshwater source has different carbonate chemistry and affects local acidification states (Chierici and Fransson, 2009). In the Hudson Bay (Canada), the rivers flowing into the western bay have higher alkalinity than those in the eastern bay due to the difference in watershed geology. Watershed of the western rivers is composed of lime stones, while that of eastern rivers is basaltic. Consequently, carbonate saturation states and pH in the western bay is higher than those in the eastern bay (Azetsu-Scott et al., 2014). Similar gradients of pH, carbonate saturation state and alkalinity are observed in the Spitsbergen/Svalbard fjord system in different years due to drainage of meltwater containing calcareous minerals from the bedrock (Fransson et al., 2015; 2016). These heterogeneous chemical environments can be studied in detail together with individual species and ecosystem responses. In addition to freshwater runoff from glacial melt water in Arctic fjords, there can also be upwelling near the glacier fronts affecting the biogeochemical gradients and ecosystem (e.g. Straneo et al. 2012; Lydersen et al. 2014; Meire et al. 2015). Chemical gradients are also observed in polar fronts where warm, Atlantic water meets cold, polar water, such as in the Barents Sea and Fram Strait (Chierici et al. 2016). To use naturally occurring gradients as analogues to study effects of climate change and OA to marine ecosystems, we also need to clarify how the sites represent the future marine environments beyond the carbonate system. For example, some sites may provide pH gradients with an extreme dissolved oxygen range, or pH may fluctuate outside that predicted for OA. Also, pH variation can be attributed to other factors than the carbonate system, such as H_2S at volcanic seeps. Variable responses by organisms and ecosystems in chosen sites may be the results of multiple environmental drivers such as, nutrients, salinity, temperature, dissolved oxygen and the TA of terrestrial runoff from glaciers and rivers. To address these questions, it is necessary to understand temporal and spatial variability of carbonate chemistry, controlling mechanisms of OA and chemical compositions of seawater such as heavy metals, nutrients, hydrogen sulfide and methane. Although many confounding factors associated with chemical composition can be controlled by monitoring, modeling and careful site selection, ~~others~~ factors such as salinity, TA and temperature may be more variable particular in coastal environments.

Target habitats and species

In all ecosystems, there are some species or taxonomic groups that play a disproportionately important functional role, e.g. as prey, as habitat engineers or in the recycling of nutrients. If such species suddenly ~~become more or less~~increase or decrease in abundance~~t~~, ~~(~~due to changes in the abiotic environment~~)~~, the community structure might change or even regime shifts ~~to entire~~ ecosystems may occur in the ecosystem (Kortsch et al., 2012; Fossheim et al., 2015). Polar ocean ecosystems in general are characterized by having pathways of energy flow from lower to higher trophic levels dominated by a small number of species (Murphy et al., 2016), e.g. the copepod *Calanus glacialis* and the shell-bearing pteropod *Limacina helicina* constitute the main food source for a large variety of large zooplankton, juvenile fish, baleen whales and birds in northern ecosystems (Last, 1980; Lowry, 1993; Karnovsky et al., 2003; Hop and Gjøsæter, 2013).

Shell-~~-~~bearing ~~Pteropods~~ pteropods are generally thought to be extremely sensitive to reduced pH because they exert little control over the pH and carbonate chemistry of their calcifying fluid (Ries, 2012; Manno et al., 2017). Indeed, shell dissolution has been observed in some ocean areas where aragonite saturation state is around 1 (Bednaršek et al., 2012). However, recent studies from the California Current Ecosystem~~-~~, ~~(~~that naturally experiences undersaturated waters with respect to aragonite due to seasonal up-welling) have shown that ~~the pteropod~~ *Limacina helicina* individuals that originate from areas with naturally lower aragonite saturation state exhibit a higher survival rate as ~~comparted~~compared to individuals from areas with a higher aragonite saturation state when exposed to high pCO$_2$ waters in laboratory (Bednarsek et al., 2017). Similarly, different responses to ~~ocean acidification~~ OA were observed in three geographically separated populations of *C. glacialis* (Thor et al., 2017). ~~Copepodites~~ Copepodids collected from Kongsfjorden and Billefjorden (Svalbard) showed severe reductions in ingestion and an increased metabolic cost when exposed to high pCO$_2$ waters in laboratory whereas no effects were observed in ~~copepodites~~ copepodids collected from Disko Bay (west Greenland). ~~Studies on another copepod species, *Pseudocalanus acuspes*, show fast adaption to OA and that physiological differences among locally isolated populations may occur as a result of local adaptation (Thor and Dupont 2015; De Wit et al., 2015).~~In addition, ~~N~~northern populations of the gastropod *Littorina littorea* ~~in Northern Norway were the only ones along the entire geographical range of distribution of this species to~~ showed no ability to modulate their metabolic rates in response to the exposure to OA conditions. In addition, they showed the greatest shift in metabolomic profiles and shell dissolution (Calosi et al., 2017). This may suggest that northern populations of warm-adapted species ~~may~~are not be able to deal with low pH regimes typical of subpolar and polar environment~~, being adapted to warmer-higher pH seawater conditions~~.

Gradients in pH, carbonate saturation state and alkalinity occur~~s~~ in several Svalbard/Spitsbergen fjord systems where pteropods and copepods could be studied (e.g. Fransson et al., 2015; 2016). However as pelagic organisms can be exposed to abrupt changes in seawater carbonate chemistry as they move across smaller scale natural gradients (e.g. Kroeker et al., 2011), larger scale open~~-~~-ocean gradients in carbonate chemistry, such as in the Barents Sea and Fram Strait polar fronts (Chierici et al., 2016) may be more suitable as natural~~ly~~ laboratories to investigate the sensitivity of different zooplankton populations to OA, compared to smaller special gradients.

Polar coastal ecosystems support extensive biogenic habitats in the form of coralline algae beds and cold-water coral gardens and reefs. Coralline algae and cold-water corals are considered ecosystem engineers as they play a prominent role in the polar carbonate cycle and act as habitats for thousands of other benthic species (see e.g. Freiwald and Henrich, 1994; Teichert 2014; Henry and Roberts, 2017~~; Teichert 2014~~;~~ Freiwald and Henrich, 1994~~). It is expected that any changes in the secondary production of these benthic ~~habitat~~ habitat-building taxa would have scaling effects on ~~the~~ polar food webs. Studies assessing the effects of OA on them are therefore of utmost interest for both fisheries and environmental management. In some ~~of the~~ Arctic fjords (in both northern Norway and

Greenland), cold-water corals have been observed where chemical gradients can be investigated ~~(T. Kutti, pers. comm.)~~. Extensive cold-water corals reefs and coral gardens occur in northern Norway, Iceland, western Greenland and eastern Canada (Buhl-Mortensen et al., 2016). Coralline algae beds have been described from the euphotic zone in the fjords of northern Norway and Svalbard (Brodie et al., 2014; Teichert and Freiwald, 2014), eastern and western Greenland (Jørgensbye and Halfar, 2017) and eastern Canada (Halfar et al., 2013). Laboratory studies have yielded contrasting results regarding coralline algae and cold-water coral performance under elevated temperature ~~elevation~~ and ~~increased~~ *p*CO_2 (~~see~~ e.g. Ragazzola et al., 2013; Büscher et al., 2017 and references therein). Several factors, such as seasonality, food availability and species-specific traits, have been ~~used~~ proposed to explain the discrepancy between studies. What is clear is that many coralline algae and cold-water coral species have the ability to upregulate pH at the site of calcification and thus continue to grow even in corrosive water (McCulloch et al., 2012; Cornwall et al., 2017b);~~,~~ however, often at a reduced rate. Furthermore, the dissolution of the unprotected skeleton (forming the main part of the coralline algae beds and cold-water coral reefs) is always ~~enhanced~~ faster under corrosive conditions. Short-term laboratory studies, however, cannot test the ability of these species, ~~that~~ which have very slow growth and long generation times, to acclimate and/or adapt to ocean warming and acidification. ~~Coralline algae beds have been described from the euphotic zone in the fjords of northern Norway and Svalbard (Brodie et al., 2014; Teichert and Freiwald, 2014), eastern and western Greenland (Jørgensbye and Halfar, 2017) and eastern Canada (Halfar et al., 2013). Extensive cold-water corals reefs and coral gardens occur in northern Norway, Iceland, western Greenland and eastern Canada (Buhl-Mortensen et al., 2016).~~ Many of ~~these~~ sites with corals or coralline algae show mosaics in carbonate chemistry, temperature and food availability (driven by up-welling and glacial melt) and could hence be used to assess the long-term ability of these species to acclimate/adapt to higher CO_2 and temperature. It is plausible that, similarly to pteropods and copepods, geographically separated populations might respond differently to exposure to high CO_2 waters. However, such future studies would require long-term data on carbonate chemistry, temperature, and perhaps even ecological parameters such as food availability/seston concertation and quality. Although at specific locations there is a growing understanding of natural spatial and temporal gradients in carbonate chemistry for example Hudson Bay (Azetsu-Scott et al., 2014) and Kongsfjorden (Fransson et al., 2015) an increased monitoring and modelling efforts will be required. In general, the Arctic Ocean and adjacent seas (Barents Sea and Norwegian Sea) are little investigated with regard to carbonate chemistry. The longest, northernmost time series study site is located in the Iceland Sea (Olafsson et al., 2009). On other sites such as Svalbard fjords, Fram Strait and the Barents Sea repeat measurements along hydrography sections was initiated in 2011. Biological and physical parameters have been sampled systematically in the Barents Sea since 1950's through the Institute of Marine Research (Norway) ecosystem surveys, The Fram Strait has annual cruises with carbonate chemistry since 2011 and in recent years also pteropod collection. There are also several moorings with proposed plans to extend the sensor systems to include carbonate chemistry for data collection throughout the year. However, in the Arctic Ocean, data still relies on research projects and distributed biological observatories (DBO) such as in the Chukchi Sea. DBO's which may be extended to include more parts of the Arctic Ocean.

Conclusions

High latitude oceans are particularly sensitive to climate change, due to naturally low pH and $CaCO_3$ saturation caused by changing freshwater content, and high solubility of CO_2 due to relatively low temperatures (AMAP AOA 2013; Chierici and Fransson, 2009; Chierici et al. 2016). However, despite the northern oceans being in a state of rapid transition, little is known about the possible effects of predicted OA on ecologically important species and communities. What is known comes mainly comes from relatively short-term laboratory incubations to isolated carbonate chemistry drivers (i.e. pCO_2, salinity or temperature independently). These studies give little opportunity to investigate either the bidirectional interactions between responses at the individual, population and community levels, or the possible capacity for transgenerational adaptation of species to climate change drivers. However, in a number of tropical and temperate ecosystems these questions have been successful addressed by using natural gradients in carbonate chemistry as analogues for predicted OA, where species have potentially adapted/acclimatised over multiple generations within naturally assembled communities. Despite the clear potential for using such analogues also at high latitudes, this remains to be investigated.

To date such studies in tropical and temperate ecosystems have mostly focused on volcanic CO_2 vent sites that~~which~~ are often carefully selected to avoid confounding factors such as H_2S, heavy metals, salinity or temperature. Potential Arctic volcanic CO_2 vent sites are reported in the Jan Mayen vent fields and off the west coast of Spitsbergen. Furthermore, methane cold seeps are found extensively in northern oceans. However, the chemical oceanography, including possible confounding effects of methane, H_2S or heavy metals needs further investigation. The depth and remoteness of these sites also makes them logistically ~~default~~~~difficult~~demanding. The research value ~~strength~~ of CO_2 vent sites studied to date is their relatively simple experimental design with relatively short gradients and limited confounding drivers. However, this can also be a limitation due to increased gene flow across shorter gradients making it difficult to investigate adaptive capacity, and a lack of opportunity to study the interaction of multiple drivers. Consequently, a number of recent studies have investigated larger scale sites such as areas of coastal upwelling and estuaries where gradients in carbonate chemistry (e.g. salinity, total alkalinity, $p\mathrm{CO}_2$ and temperature) intersect to produce an environmental mosaic. This has the potential to allow work on natural analogues to move forward and encompass multiple climate change drivers. At high latitudes, such mosaics occur at different scales from coastal regions and fjords influenced by fluctuations in temperature, salinity and total alkalinity of freshwater (e.g. rivers, glaciers and sea ice melt) to polar fronts where warm, Atlantic water meets cold, Arctic water: ~~(~~e.g. Barents Sea and Fram Strait~~)~~. Although beyond the scope here, it should be noted that similar mosaics in carbonate chemistry drivers have been described in the Southern Ocean. With seasonal wintertime minimum in carbonate ion concentration south of the Antarctic Polar Front, which is predicted to lead to aragonite undersaturation when atmospheric CO_2 levels reach above 450 ppm (McNeil and Matear, 2008). In the Ross sea surface pH varies from (7.890–8.033) with the highest values in Terra Nova Bay and Ross Sea polynyas. Intrusion of the Circumpolar Deep Water can also lead to low pH values (7.969±0.025) in the Ross Sea shelf area (Rivaro et al., 2014). Such natural fluctuations in carbonate saturation have been shown to inference the shell dissolution in the Southern Ocean pteropod *Limacina helicina Antarctica* (Bednaršek et al., 2012).

It is important that appropriate analogue sites are selected to investigate particular~~ly~~ key species, habitats or processes. For example, smaller scale analogues within fjords may be used to investigate the effects of multiple interacting drivers on key benthic biogenic habitats (e.g. coralline algae and cold-water corals) scaling between individual physiological effects and community level responses. Larger scale gradients in big fjords and coastal upwelling areas are more suitable for species with a higher mobility. Larger analogues allow for target populations to be more genetically isolated and are therefore more suitable for investigating the capacity for local and regional adaptation. When investigating ecologically important pelagic organisms (e.g. zooplankton) that can be exposed to abrupt changes in seawater carbonate chemistry as they move across smaller scale natural gradients, lager scale open-ocean analogues may have some advantage: ~~(~~e.g. gradients in carbonate chemistry across polar fonts in the Barents Sea and Fram Strait~~)~~. However, as the scale of gradients increases it becomes more difficult to understand the role of individual confounding drivers, which are often connected and correlated. Although many confounding factors can be controlled for by using appropriate monitoring and modeling to inform site selection, some carbonate chemistry drivers in more complex systems are likely to co-vary. Consequently, as we move toward a more realistic understanding of multiple carbonate drivers in the field, it is not suggested that such studies replace laboratory incubations but rather that both methods complement each other with natural analogues used to validate responses observed in the laboratory and laboratory incubations used to disentangle cofounding drivers observed in natural systems. It is clear, that if used and selected appropriately to fit the question, and combined with monitoring and modeling of the chemical oceanography, natural analogues will be a powerful tool to achieve a better understanding of the possible effects of climate change on high latitude species, communities and ecosystems.

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