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Exposure of commercially exploited shellfish to changing pH levels: how to scale-up experimental evidence to regional impacts

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Ocean acidification has become one of the most intensively studied climate change topics and it is expected to have both direct and indirect impacts on species, ecosystems, and economies. Experiments have been performed on different taxa, life stages, and at different pH levels. Despite this wealth of information, several key challenges remain, including (1) uncertainty about how to incorporate current pH ranges and variability experienced by organisms into experiments, and (2) how to bring this information together to support analysis and assessments at the broader ecosystem level. Sophisticated modelling tools are needed to 'scale-up' from experimental results to regional-scale insights. This paper highlights the challenges of combining information to determine how commercially exploited species may be affected under future pH levels, and how modelling and experimental results might be better aligned, using northwest Europe and the waters around the British Isles as an example. We argue that in most cases the current evidence does not offer sufficient information into impacts at projected pH levels, and that future experiments should be designed to consider the pH levels actually experienced by organisms, as well as variability in pH. These types of study are key in safeguarding commercially exploited shellfish stocks.

Keywords: adaptation, climate change, experiments, fisheries, ocean acidification.

Introduction

As a result of anthropogenic activities, and in particular the burning of fossil fuels, carbon dioxide (CO_2) levels in the atmosphere are rising. Much of this atmospheric CO_2 eventually ends up in the ocean and the global oceans are acting as a major carbon sink, helping to offset the worse effects of global warming (Brewer, 1997; Riebesell and Gattuso, 2015, Gattuso *et al*., 2018; Vargas *et al*., 2022). When carbon dioxide dissolves into seawater, it forms carbonic acid (H_2CO_3). Some of the carbonic acid molecules dissociate into a bicarbonate ion and a hydrogen ion, thus increasing ocean acidity (H^+ ion concentration). This in-turn causes a decrease in pH and associated reductions in the saturation state of aragonite and calcite with serious physiological consequences for many shell-forming marine species (Feely *et al*., 2009; Lemasson *et al*., 2017; Kroeker *et al*., 2013; Sanders *et al*., 2013; Wittman and Pörtner, 2013; Calosi *et al*., 2016).

For at least three decades there has been an observed decline in pH in all ocean basins, and under the highest emissions scenario, global ocean pH may decline to <7.7 by 2100 (IPCC, 2021). Certain ocean basins and systems will be affected more than others depending on their particular oceanographic characteristics. In the northwestern European shelf seas, the effects of ocean acidification may be exacerbated by high-riverine input and degradation of organic matter (Artioli *et al*., 2014), which result in the release of CO_2 and a localized reduction in pH (Provoost *et al*., 2010); such processes add to uncertainty about near-shore carbonate chemistry. The effects of ocean acidification at the food web and ecosystem scale are also relatively uncertain (Doney *et al*., 2020). A number of widely cited meta-analyses and systematic reviews have now been carried out in an effort to draw conclusions about the possible impacts of ocean acidification on different types of marine organism (Hendricks *et al*., 2010; Kroeker *et al*., 2013; Leung *et al*., 2022), but there is still uncertainty because of the complexities of direct and indirect effects and predator–prey interactions (Busch *et al*., 2013).

When it comes to ocean acidification effects, molluscs and crustaceans are of particular interest, as their likely responses are relevant to human nutrition, food security, and livelihoods (San Martin *et al*., 2019). The level of understanding has greatly improved across these commercially important shellfish groups (Browman, 2016), and evidence is strong that marine calcifiers, dependent upon calcium carbonate ($CaCO_3$) to create shells or skeletons, are under direct threat from ocean acidification across all life stages (e.g. larval, juvenile, and adult stages; see Pörtner *et al*., 2014; Lemasson *et al*., 2017). A net decrease in the number of carbonate ions available may make it more difficult for marine calcifying organisms to form biogenic calcium carbonate, and such structures become vulnerable to dissolution (Roleda *et al*., 2012; Fitzer *et al*., 2019). It is important to also highlight the fact that additional energy is required to support effective calcification and to protect calcified structures from dissolution under acidified conditions. Saturation states of aragonite and calcite (Ω) under the value of 1 (anticipated in the future) will make organisms extremely sensitive to shell dissolution.

Recent meta-analysis of 985 studies, demonstrated that echinoderms, cephalopods, and crustaceans are on the whole capable of tolerating conditions expected in the future (a pH

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of ~7.1 by the 2100s), whereas coccolithophores, calcifying algae, and corals are more sensitive to these pH changes (Leung *et al*., 2022). Importantly, >70% of the studies considered by Leung *et al*., (2022) indicated calcification and growth responses that were non-negative. Further, many of the studies examined suggested acclimation capacity of calcifier species or multi-generational adaptation, and hence that deleterious effects may have been overestimated (Leung *et al*., 2022).

There is a scarcity of studies placing overall experimental responses in a context of how commercially exploited shellfish will be affected by changing climate and other stressors. However, there may be effects from ocean acidification on food security if shellfish populations are negatively impacted (Jennings *et al*., 2016; Lacoue-Labarthe *et al*., 2016). Shellfish landings are worth £262 million in the United Kingdom (2020 value based on Uberoi *et al*., 2021) and so any effect on shellfish production from ocean acidification could also have serious economic implications (Mangi *et al*., 2018). As such, there is a need to improve our understanding of responses to ocean acidification among commercially exploited species in the region by undertaking targeted experiments that provide real-world insights and yield numerical outputs of direct use for modelling. Some progress in understanding species responses and their energetic requirements (Dynamic Energy Budgets—DEB) coupled with biogeochemical models are advancing the relevant ecosystem interactions, for example, on oysters in Canada (Filgueira *et al*., 2014). These combined scales and responses are valuable to indicate commercially exploited species responses over spatial scales, which are needed for management and conservation.

Aims of this paper

We use the UK commercial shellfish fishery as a case study to demonstrate how misalignment between different types of scientific research (e.g. experimental research and modelling) may hinder progress in assessing the consequences of ocean acidification for commercially relevant species and hence associated impacts on economic activities. We combine published experimental evidence with maps of pH projections to the end of century, to determine whether the information currently available is sufficient to draw conclusions about the impact of declining pH on commercially exploited shellfish in the UK waters. We map areas where current and future pH range will overlap, to understand how experienced pH variability could have a bearing on adaptive capacity of species in the future.

We also explore the challenges experienced when working in coastal waters, where many economic and ecologically important species and habitats are distributed (e.g. bivalves, crabs, seagrass beds, etc.), and where localized factors such as plankton dynamics (e.g. eutrophication and/or seasonal dynamics), water discharges (e.g. riverine run-off or ice melting conditions) and coastal upwelling can all interact with the underlying trend in ocean pH, such that any organisms present may already be subject to very variable pH conditions or levels of ocean acidity not anticipated until much later in the 21st Century (Vargas *et al*., 2022).

Experimental studies

Laboratory experiments provide useful insights that help us understand whether or not species are able to withstand changes of pH, their tolerances or sensitivities and associated physiological responses to changes in pH (Ries *et al*., 2009; Wittmann and Pörtner, 2013). This can be particularly useful to fisheries managers when species' responses to these changes are tested. In experiments to date, a range of physiological responses and sensitivities have been documented with responses differing across life stages (Small *et al*., 2016), sex (e.g. Ellis *et al*., 2014; 2015) and between species (e.g. Gazeau *et al*., 2007; 2013). These differences depend on the individual life histories, physiological needs, and capabilities of the species concerned, including regulatory mechanisms, shell composition, and growth patterns, and there can be both direct (e.g. shell erosion) and indirect (e.g. trophic/energetic) effects (Klok *et al*., 2014). Whilst a wide range of experiments and several end points have been measured (Leung *et al*., 2022), it has generally been difficult to draw conclusions because there has been a lack of common methodology used across the experimental evidence base with a range of the variables tested, and treatments used. This creates a difficulty when trying to compare common responses across studies, species. and regions. In particular, most early experiments involved only short-term toxicity tests on adults (often at unrealistically high CO_2 levels), whereas later studies have included longer term or multigenerational experiments involving acclimation or adaptation (Browman, 2016), particularly those conducted in Europe and the United Kingdom.

The European Project on Ocean Acidification (EPOCA) produced early guidance on carrying out experiments on ocean acidification and recommended a set of thresholds so that experiments were comparable across species (Riebesell *et al*., 2011). Even so, pH varies temporally and spatially even within small areas (Provoost *et al*., 2010) and with water depth, and so globally-applied pH thresholds do not necessarily take these important local differences into account. This is particularly relevant when considering how different life stages experience these variations. To progress on from the EPOCA guidelines, a study by Cornwall and Hurd (2016) drawing on 465 published studies emphasized the need for appropriate replication, manipulation of carbonate chemistry in the experimental set ups, and consideration of acclimation of organisms to natural environmental conditions. Browman (2016) also highlighted that studies (often on the same species) are offering many contradictory responses when ocean acidification effects are assessed under different experimental conditions. Research is continuing to develop highlighting levels of species adaptation (Leung *et al*., 2022).

There have been many ocean acidification experiments on marine crustacean and mollusc species of relevance to commercial shellfisheries in northwest Europe and the United Kingdom (summarized in Table 1). These have been carried out at varying pH levels, ranging from 6.5 to 8.3, with different physiological and behavioural effects measured. By comparing the pH levels that caused physiological responses in the experiments with projected pH levels from downscaled regional climate models, we can hypothesize if and where there may be localized impacts to commercial shellfisheries in the future.

While this approach has the advantage of being very simple, it has been shown that organisms that are naturally exposed to high levels of natural variability may be well adapted to changes in pH already and so less vulnerable to acidification as sometimes feared (Hendricks *et al*., 2010; Calosi *et al*., 2017; Vargas *et al*., 2017), thus mapping based on the results of one experiment is likely to give an oversimplified result. It

Table 1. A summary of key findings from ocean acidification experiments relevant to the UK commercially exploited shellfish species.

Study	Species	Mollusc or crustacean	pH levels tested	Life stage and physiological effects tested and findings
Berge *et al.*, 2006	Blue mussel *Mytilus edulis*	Mollusc	6.7; 7.1; 7.4; 7.6; 8.1	Adults. No growth at pH 6.7, reduced growth at 7.1.
Bechmann *et al.*, 2011	Blue mussel *M. edulis*	Mollusc	7.6; 8.1	Larvae. No effect on fertilization success, development time, d-shell abnormalities, and feeding. Larvae were smaller at the lower pH.
Lesser, 2016	Blue mussel *M. edulis*	Mollusc	7.9; 8.1	Adult. Low pH resulted in metabolic depression and reduced thermal tolerance.
Sanders *et al.*, 2013	King scallop *Pecten maximus*	Mollusc	7.58; 7.68; 7.95; 7.99	Juveniles. None of exposure levels had effects on oxygen consumption, clearance rates, cellular turnover, and shell growth.
Schalkhausser *et al.*, 2013	King scallop *P. maximus*	Mollusc	Total pH 7.65; 8.08	Adult. Low pH narrowed thermal tolerance, reduced shell clapping performance, and aerobic scope.
Ellis *et al.*, 2014	Blue mussel *M. edulis*	Mollusc	6.5; 7.35; 7.60; 7.80; 8.05	Adults. Assessed temperature and pH. Lowest pH affected response to pathogen. Differences between males and females.
Ellis *et al.*, 2015	Blue mussel *M. edulis*	Mollusc	6.5; 7.35; 7.60; 7.80; 8.05	Adults. Assessed temperature and pH. Lower bacterial growth inhibition at low pH. Temperature increased sensitivity of animals to pH.
Klok *et al.*, 2014	Common cockle *Cerastoderma edulis*	Mollusc	6.7; 6.95; 8.3	Adults. Reductions in shell length and weight, and flesh weight at low pH.
Lemasson and Knights, 2021	Pacific oyster *Magallana (crassostrea) gigas*	Mollusc	7.68–7.97	Adult. Shell weaker under low pH.
Lemasson and Knights, 2021	Native oyster *Ostrea edulis*	Mollusc	7.77–8.04	Adult. No impact on shell strength under reduced pH
Agnalt *et al.*, 2013	European lobster *Hommarus gammarus*	Crustacean	7.62; 7.79	Larvae and juvenile. Larval and juvenile deformities at lower pH.
Rato *et al.*, 2017	European lobster *H. gammarus*	Crustacean	7.85; 8.15	Larvae. Increased oxidative stress, increased inter-moult period, and reduced growth at lower pH.
Bechmann *et al.*, 2011	Shrimp *Pandalus borealis*	Crustacean	7.6; 8.1	Larvae. No effect on survival. Development time was delayed.
Styf *et al.*, 2013	Norway lobster *Nephrops norvegicus*	Crustacean	7.47–8.11	Embryos. Lower oxidative stress at lower pH levels. No significant effect on oxygen consumption, cardiac performance, or development rate.
Hernroth *et al.*, 2012	*N. norvegicus*	Crustacean	7.5; 7.6; 7.7; 8.1	Adult, 4 month exposure. Immune suppression at lower pH.

therefore becomes important to understand what is the level of variability that the organisms tested in experiments today are actually experiencing in the wild and what will be the variability they will experience in the future. This information that is not often considered in experiments, nor are the particular chemical characteristics of the location from where the source animals were derived. Individuals of the same species from a more variable environment may be pre-adapted to be more robust than individuals of the same species obtained from a more variable location. If those individuals came from areas with a pH range that spans the lower values tested (e.g. 7.6), that is, anticipated future conditions, then the response observed is from individuals that have already pre-adapted to low pH and might not be representative of the response of the population as a whole.

Several recent studies have explored the ability of marine organisms to adapt to new conditions, considering their adaptation potential (e.g. population size, standing genetic variations, and generation time etc.). This will also be governed by the rate and extent of acidification, which could be acting alongside additional stressors and environmental changes, such as temperature change and impacts on food availability (Sunday *et al.*, 2014; Calosi *et al.*, 2016). Dedicated experiments have indicated that marine organisms are capable of adaptation, including over multiple generations in some cases (e.g. Byrne *et al.*, 2020; Gibbs *et al.*, 2021). Conditioning bivalve parents to low pH over multiple generations does not always lead to improved pH tolerance, however, several bivalves have exhibited improved stress tolerance and phenotypic plastic traits that may be associated with genetic adaptation (Byrne *et al.*, 2020). Phenotypic adjustment and/or genetic selection may be possible for some species, particularly in very high-CO_2 upwelling zones, and around hydrothermal CO_2 vents (Byrne *et al.*, 2020). Similar applications have been applied across the North Sea for fish assemblages, considering their natural affinities and responses to climate change under the concept of ‘ecotypes’, helping to elucidate wider responses across important spatial scales (Engelhard *et al.*, 2011).

Vargas *et al.*, (2022) considered the localized responses of crustaceans and molluscs from coastal regions of the eastern South Pacific coast of Chile. The authors mapped the natural distribution of the partial pressure of carbon dioxide (pCO_2) values along the coast and compared these to known tolerances and sensitivities from experimental studies, both locally and globally (Vargas *et al.*, 2022). These types of approaches can yield important insights to help assess the most relevant traits of commercially exploited species and their

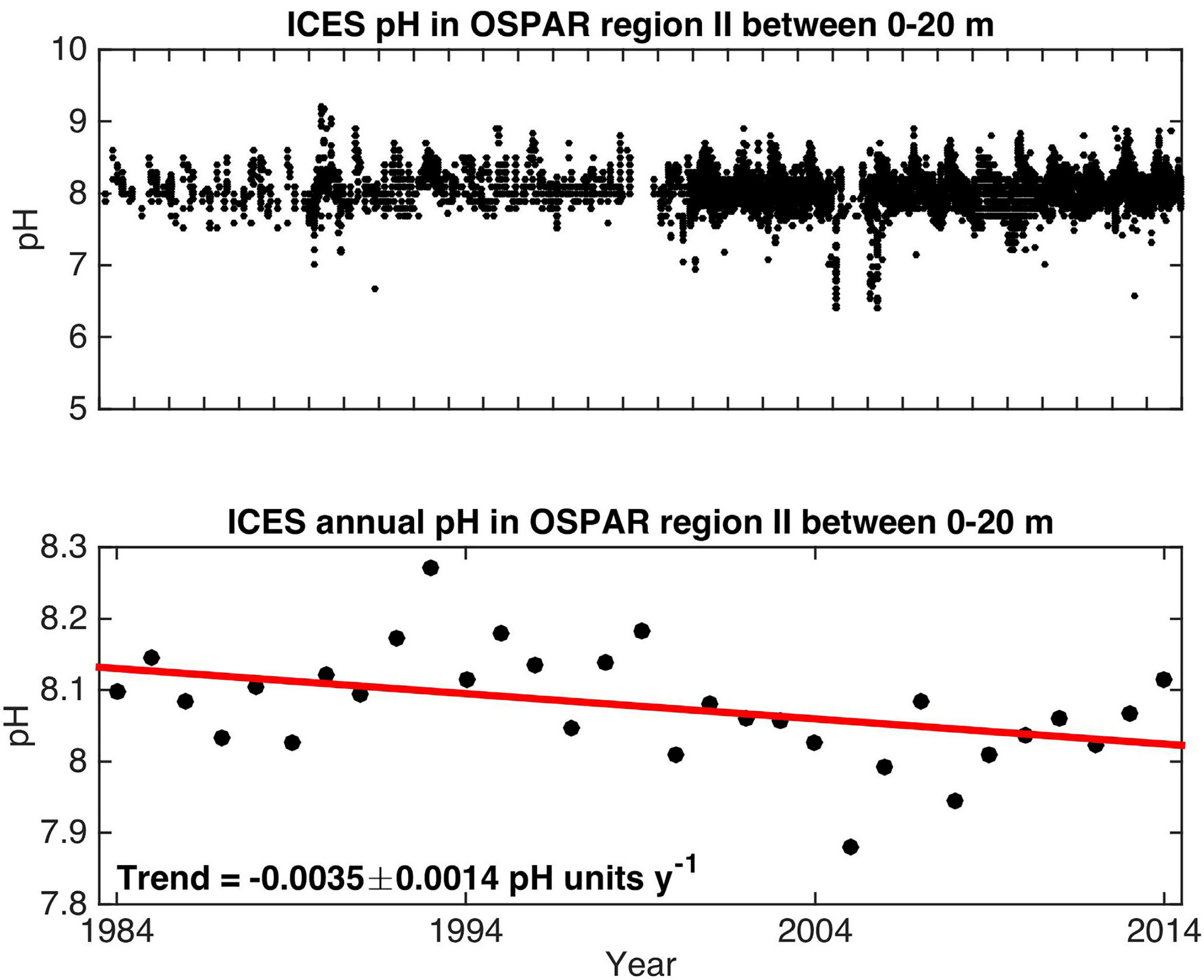

Figure 1. ICES pH data for depths between 0 and 20 m from the 1980s to 2010s in OSPAR region II—Greater North Sea (top). The annual mean pH data with trend (bottom). Reproduced from Ostle *et al.* (2016).

sensitivities, and understand how different types, species or strains of organisms respond to pCO_2 variability and ocean acidification across individual and global systems.

The physiological studies that have been carried out to date tend to suggest that the most vulnerable groups are those that are unable to compensate for the changes imposed by elevated pCO_2 and reduced pH levels. These species tend to be poor iono- and osmoregulators, living in low energy environments with low metabolic rates and low routine levels of activity. Some experimental work suggested that these species are characterized by low-buffering capacities and a general inability to mobilize HCO_3^- ions from the seawater or from the exoskeleton to buffer the acid–base disturbances caused by ocean acidification (Whiteley 2011).

Projecting ocean acidification trends and variability of pH

Variability of pH in the marine environment occurs at different temporal scales, from seasonal (or shorter) to inter- or multi-annual scales. Some open ocean sites experience very little variability of only 0.15 pH units between years (Bates *et al.*, 2014; Ostle *et al.*, 2016), but coastal sites are likely to experience much greater variability (Duarte *et al.*, 2013; Ostle *et al.*, 2016). In the North Sea, for instance, pH levels vary each year due to seasonal and interannual variability as well as spatially (Provoost *et al.*, 2010), and past measurements show that between 1984 and 2014 this variation was quite large, with extreme local values of ~6.5 and 9.3 in the top 20 m of the water column (Figure 1) (Provoost *et al.*, 2010; Ostle *et al.*, 2016). While these are extreme values that have been measured in specific locations and moments, the seasonal and interannual variability in the North Sea is commonly of the order of 0.3 pH units (Ostle *et al.*, 2016). Despite this variability, the underlying signal is of a long-term, steady decrease in pH, of $\sim 3.5 \times 10^{-3}$ pH units yr^{-1} over the past 30 years (Ostle et al., 2016).

Further ocean acidification research and modelling is needed to anticipate how much pH will continue to decline in the future, but also how much the variability of pH will change, and the degree of overlap between present day and future ranges. Projections from global climate models (e.g. Bindoff *et al.*, 2019) enable research on large-scale effects. However, in coastal and shallow waters, the acidification trend is likely to be obscured due to co-occurring secondary drivers like changes in riverine discharges (both quantity and

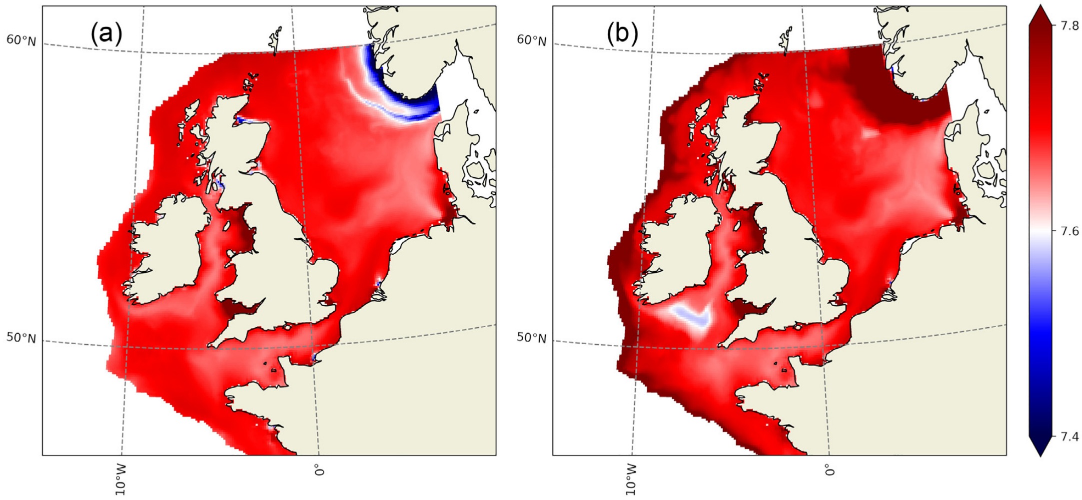

Figure 2. Minimum monthly mean pH of the climatological year in the period 2080–2099 under an RCP 8.5 scenario for the northwestern European shelf. Surface waters are shown on the left, and bottom waters on the right. The blue areas denote the area with pH minima <7.6.

quality), habitat and circulation (Provoost *et al.*, 2010), which will affect the intensity of acidification. Regional downscaled projections (e.g. Hauri *et al.*, 2013; Artioli *et al.*, 2014; Mongin *et al.*, 2016) enable us to address that question to some degree and provide a better characterization of pH ranges; the seasonal and interannual variations that species and different life stages are likely to experience in the future in coastal seas. In the North Sea, for example, the trend shown in Figure 1 continues, with a projected mean decrease of 0.0036 pH units year^{-1} to the end of century (2080–2099) under the IPCC AR5 high emissions scenario (RCP8.5), with variation both temporally and spatially (Ostle *et al.*, 2016). The lowest surface pH occurs in winter, when solubility of CO_2 is highest and leads to local undersaturation of aragonite. In bottom waters, the minimum pH occurs in late summer/autumn, sometimes accompanied by undersaturation of aragonite, caused by accumulation of dissolved inorganic carbon in stratified water (Artioli *et al.*, 2014).

The average minimum monthly mean of surface and bottom waters pH for a period at the end of century (2080–2099) is shown in Figure 2, as projected by the NEMO-ERSEM model forced by the Earth System model HadGEM2-ES under the IPCC AR5 scenario RCP 8.5. Details of the model implementation and performance can be found in Wakelin *et al.*, (2020). It can be seen from Figure 2 that in most cases the lowest pH values used in experiments (Table 1) are not projected to be experienced in the UK waters by the end of this century. Indeed, at the pH minima shown in Figure 2, the experiments listed in Table 1 mainly show no effect. From all these experiments, critical effects were only recorded at very low pH of ∼7.0 or below, a value that will not be experienced by the end of the century, even in the more extreme RCP8.5 emission scenario, which is now viewed as being increasingly unlikely (Hausfather and Peters, 2020). Under the RCP8.5 scenario, the regional model of the northwestern European shelf projects that the climatological pH range of bottom water pH rarely goes <7.6 (Figure 2), a value of pH that experimental evidence suggests most of the species seem able to resistant, as only sub-lethal impacts have been recorded (e.g. lowered immune response in Norway lobster, reduction in size in blue mussels and common cockle). Larval deformities in European lobster were also recorded at this pH, although a projection showing a single pH value does not reflect the varied conditions experienced by pelagic larvae in the oceans. The notable geographical exceptions are the Norwegian Trench, where surface waters are anticipated to experience a pH decline to <7.6, and also a small area of the Celtic Sea south of Ireland, where bottom waters are anticipated to decline to <7.6. This latter area is important for the Celtic Sea for Norway lobster (*N. norvegicus*) fishery.

On first analysis, it would seem therefore that the impact on commercially exploited shellfish in the UK waters will be rather limited. There are however two major caveats. First, the model horizontal resolution of ∼7 km, which is an improvement compared to global ocean models, is still too coarse to be able to fully capture the dynamics of pH in the near coast or inshore waters such as around estuaries where most aquaculture and shellfisheries are concentrated in this region. Second, the model also suggests that populations will experience an entirely different pH range compared to that they see today except for some coastal areas. This was assessed by comparing the overall range of pH in the recent past (based on the monthly mean in the period 1990–2009), with that projected by the model in the near future (2040–2059; Figure 3a and b), and end of the century (2080–2099; Figure 3c and d). Much of the northwestern European shelf will experience novel pH by the end of the century, especially in bottom waters. This suggests that even if individuals are not projected to experience pH levels beyond the critical thresholds highlighted by experimental work, they will most likely be exposed to a pH level never witnessed in the past. It becomes important therefore, to consider within experimental work the environmental variability previously experienced by the source animals tested, because different responses could be observed in individuals that have pre-adapted to different environments (Vargas *et al.*, 2017). Unfortunately, information about the environmental variability experienced by source populations is rarely available, and therefore, the degree of overlap between current and future variability of pH can only provide insights of indicative risks, that is, even though the pH level does not pass certain thresholds, individuals could still be affected by acidification if they experience an entirely new level of acidification.

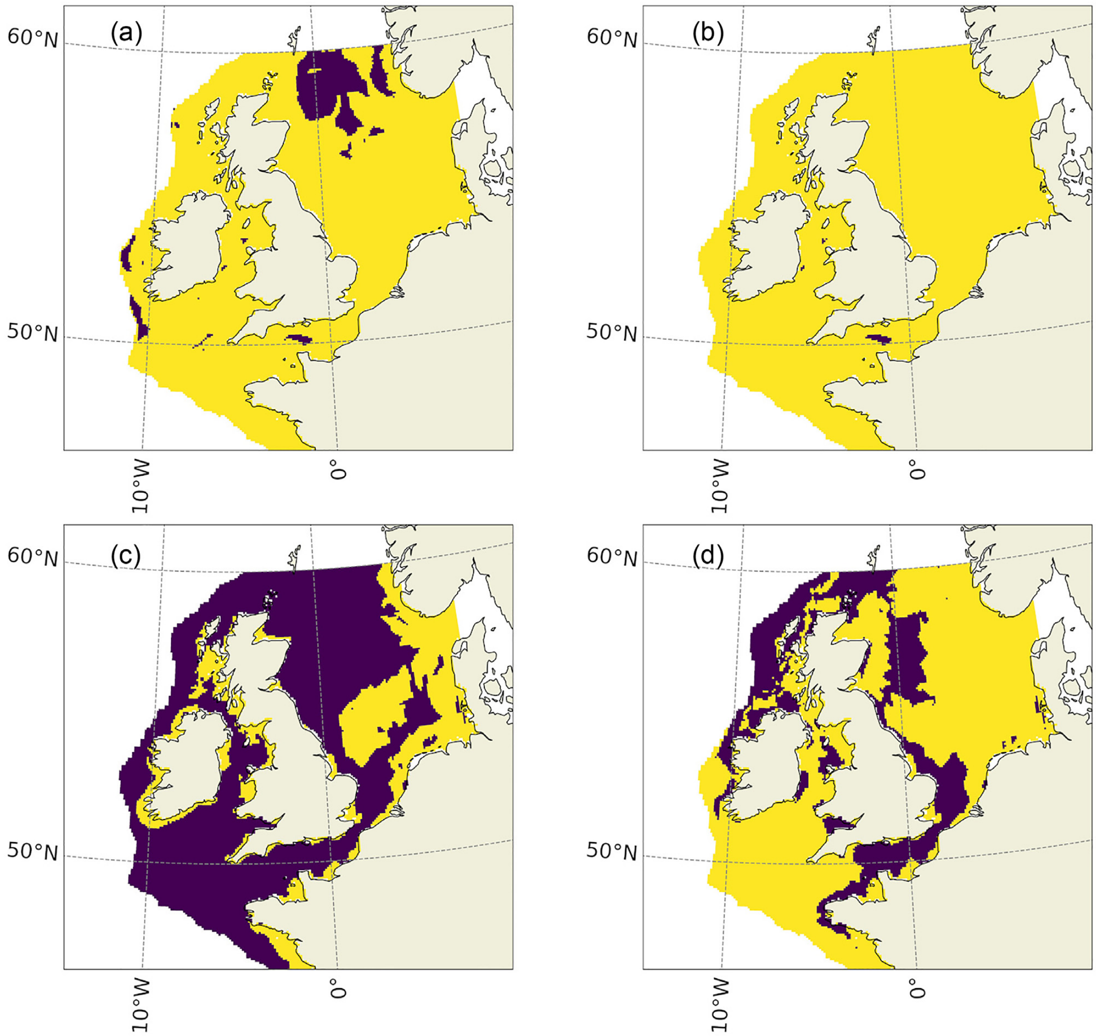

Figure 3. The overlap in the pH range around the United Kingdom between the recent past (1990–2009) and the mid (2040–2059, panels a and b) or end of century (2080–2099, panels c and d). Panels a and c show the overlap between pH ranges in water above the seafloor, while panels b and d show surface data. Yellow areas indicate that future pH range overlaps for at least 1 month in the 20-year period, purple areas indicate where the pH range are completely separate (at monthly resolution).

Moving forwards

The field of ocean acidification research continues to expand and become more sophisticated. It is now moving from experimental studies on single species with single stressors to integrated experiments across multiple generations as well as modelling that considers multiple stressors across a range of spatio-temporal scales. More integration is still needed to bring together the different results of ocean acidification research to determine the ecosystem and policy implications (Le Quesne and Pinnegar, 2012; Gattuso *et al.*, 2018; Doo *et al.*, 2020).

As we move forward, specific areas that need advancing are:

(1) development of a framework for experiments;
(2) incorporation of other co-varying parameters (e.g. temperature, food availability, and oxygen concentrations);
(3) incorporation of an understanding of the extent to which challenged organisms are pre-adapted to pH ranges or low pH;
(4) consideration of changes in pH ranges and variability; and
(5) jointly planning physico-chemical and biological assessments across spatio-temporal scales.

An experimental framework could include new protocols, which select the organisms and test and document the extent to which they are pre-adapted to their environment and may respond to future changes. Such methods could be used in specific areas, such as proposed aquaculture sites, to help ensure that the locations remain suitable for shellfish farming in the long term. Doo *et al.*, (2020) have proposed monitoring a suite of physiological and structural changes and different life stages during experiments to identify specific traits that can be linked to ocean acidification impacts, alongside a range of physical and chemical environmental parameters. Sex is also rarely considered in experimental studies (only 4% and 63.5% of studies on molluscs and crustaceans, respectively, published between 2008 and 2016), but pH can affect sex determination as well as have lethal and sub-lethal effects (Ellis *et al.*, 2017). Some of these aspects are already being addressed in other parts of the world, but there is less work in Europe bringing these different experimental components together.

Three dimensional coupled biogeochemical models, such as the one presented here are able to provide indications of the real-word conditions that experimental treatments should try to replicate in order to test realistic responses of marine organisms to future ocean acidification. These, indeed, will not depend purely on the atmospheric pCO_2 levels, but will also depend on local factors from riverine inflow to seasonal stratification intensity and duration to biological processes, such as respiration and break-down of spring phytoplankton blooms. Some experimental studies have attempted to replicate daily or seasonal cycles of pH, though this requires high levels of experimental precision and control (e.g. Cornwall *et al.*, 2013; Kapsenberg *et al.*, 2018). Elsewhere, modelling outputs concerning biogeochemical conditions within the California Current System have been used to inform experimental setups (e.g. Gruber *et al.*, 2012; Hauri *et al.*, 2013). When such data is available elsewhere in the world, similar studies would give detailed insights into the effects of acidification on commercially exploited shellfish.

Organisms that are exposed to natural pH variations during their life cycle might be expected to be more robust to acidification in the future (Browman, 2016) and a small number of multigenerational experiments have also demonstrated that offspring from parents exposed to acidified conditions may be better able to tolerate acidified conditions (Parker *et al.*, 2012; Byrne *et al.*, 2020; Gibbs *et al.*, 2021). For these reasons, it is important to understand the local variability of a species' environment and organisms' potential plasticity, either through acclimation or multi-generational adaptation (Vargas *et al.*, 2017; Lagos *et al.*, 2021; Vargas *et al.*, 2022). Experiments can also consider pH seasonality and how it coincides with developmental life stages of shellfish. Future modelling could use results from longer-term and multigenerational experiments if they could incorporate aspects of adaptation and/or tolerance levels of different species and life stages, and the responses of organisms to a range of different environmental conditions. These can then be extrapolated upon when considering specific locations.

Vargas *et al.*, (2017) assessed the pH tolerance of species in different environments (e.g. estuaries, rivers, and open water) of Chile, demonstrating the importance of understanding a species' native environment and their adaptative capacity, rather than only thinking about experimental conditions. Some commercially exploited species (e.g. mussels, abalone) are distributed across a wide range of environmental conditions, therefore an individual's tolerance to experimental pH changes is likely to vary considerably and to be dependent upon their native conditions (Vargas *et al.*, 2017).

Silburn *et al.*, (2017) highlighted the need to better understand the pH conditions experienced by benthic species when buried in different sediment types (from cohesive sediments to coarse sands). This study used microelectrodes to record pH profiles in the top few centimetres of sea-bed sediments, obtained from the Celtic Sea. Clear differences in profiles were observed between sediment type, location, and season. Notably, very steep pH gradients exist within the surface sediments (10–20 mm), where decreases >0.5 pH units were observed. This study helps to characterize the natural variability within sediments, and is highly relevant, as earlier assumptions (often not based on experimental evidence) indicated that even small changes in the water column pH might have adverse effects on benthic dwelling fauna (Widdicombe and Spicer, 2008). Realizing that benthic organisms could in fact be pre-adapted to both lower pH and higher variability changes our understanding of risk to these species and their long-term resilience.

There are other aspects that affect response to pH in an experimental setting, such as food supply. Calcification and the prevention of shell dissolution under acidified conditions require energy. In some cases, experiments have demonstrated that unrestricted food can compensate for the effects of low pH, as demonstrated by Sanders *et al.*, (2013) with scallops. Ramajo *et al.*, (2016) found that the role of food may be able to counteract the stress produced by low pH levels in a broad range of different organisms by alleviating growth suppression.

There are few studies that combine biological responses with modelled data and which help to map and assess potential future trends. In two examples relevant to the UK waters, the effects of acidification and warming on the dogwhelk (*Nucella lapillus*) (Queiros *et al.*, 2015), blue mussel, common cockle, and scallop (Fernandes *et al.*, 2017) were assessed using inferences from experimental data and a suite of coupled hydrodynamic–biogeochemistry models, like the one shown here, and dynamic bioclimatic envelope models. Similar attempts have been explored in Canada, to assess ocean acidification effects on the life-stages and spatio-temporal patterns of catch and revenues of American lobster (*Homarus americanus*) using bioclimate envelope models (Tai *et al.*, 2021). While studies like these will always be limited by the data and model projections available, they are nonetheless useful as they provide valuable information for managers about the direction and magnitude of change expected in commercially exploited shell fisheries.

More of this type of combined observation/modelling study could be possible if more experiments test the effects on organisms at realistic future pH levels, instead of at levels that are unlikely to be reached. In the future, with a series of improved biological studies, we will be in a much better position to indicate the exposure and impacts of individual development stages, across different times and study areas.

Cumulative impacts of multiple stressors

It is also pertinent to identify some of the current gaps in our understanding of observed patterns in pH and organism responses. For example, the identification and assessment of cumulative effects on the marine environment resulting from single and multiple stressors is one of the key challenges to understand interactions between human activity and ocean ecosystems (Willsteed *et al.*, 2017, Willsteed *et al.*, 2018a; Willsteed *et al.*, 2018b; Methratta, 2020).

There are high levels of analytical complexity when it comes to scales, processes, and marine ecosystem dynamics, particularly in the context of multiple pressures, which can make these assessments very challenging. However, there are already several attempts to develop strategies and case studies to illustrate the different types of pressures and the impacts they cause in the marine environment (Piet *et al.*, 2021). Current best practice (Willsteed *et al.*, 2018b) has also been proposed to enable assessors, scientists, and regulators to consider the most urgent pressures and potential impacts. Similarly, new approaches considering risk identification, risk analysis, and risk evaluation are providing information at the science–policy interface with considerations for ‘real management’ processes (Stelzenmüller *et al.*, 2018). These tools will be extremely valuable to support ongoing efforts to refine methodologies for cumulative effect and multi-stressor assessments.

Willsteed *et al.*, (2017) identified temporal and spatial accumulation, ecological connectivity, and purpose and context as some of the key components of cumulative impacts. There is a need to study the different types of short- and long-term perturbations resulting from single to multiple stressors in local habitats and their species across their natural and disturbed areas. Similarly, the risk of “shifting baselines” is becoming increasingly challenging to define because of the difficulties of determining an area’s original state and how species have already and will become adapted to these sites under a suite of multiple accumulating stressors. This area of research is still in its infancy.

Implications for commercial fisheries

Integrated studies, combining experimental observation of ocean acidification impacts on organisms with information about projected trends and variability are crucial for better characterizing the impacts of ocean acidification on the economy and livelihoods. So far, there have been relatively few economic analyses that consider the effects of ocean acidification globally, however Mangi *et al.*, (2018) estimated the economic impacts of projected changes in pH on the UK shellfish industry, and Fernandes *et al.*, (2017) used habitat suitability and mechanistic niche modelling to assess the combined effects of acidification and temperature change on the UK fin and shellfish fleets. Both studies suggested that there are likely to be direct and economy-wide economic effects caused by shellfish production losses by the end of the century, with Fernandes *et al.*, (2017) projecting a loss of £229.2 million by 2090 to the shellfish fleets of the United Kingdom under a high-carbon emissions scenario (RCP8.5), and Mangi *et al.*, (2018) suggesting direct potential losses due to reduced shellfish production, ranging from 14 to 28% of fishery net present value.

Economic analyses conducted across Europe by Narita and Rehdanz (2017), suggested that the United Kingdom annual economic losses by 2100 could amount to US$ 97.1 million under a high emissions scenario (RCP 8.5), mostly due to impacts on scallop fisheries. Updating these economic analyses with more appropriate and sophisticated experimental data could produce a more accurate assessment of the loss to the UK economy and help to prioritize policy decisions, aquaculture planning, and climate adaptation measures.

Conclusions

Science-based evidence is needed to support action on climate change. In particular, appropriate experimental studies are required whereby pH conditions better replicate the anticipated future projections locally (including daily, seasonal, and inter-annual variability), and more factors that affect organisms (e.g. food availability or temperature) are incorporated into modelling. We have described other factors that should be considered in experimental design, including local variability and organism adaptation. Continued pH monitoring is needed within the shelf seas to help characterize local changes or natural background levels in pH that organisms already experience, and therefore their possible extent of pre-adaptation. There are a number of ongoing efforts internationally to support and coordinate monitoring of carbonate chemistry, such as the ‘Global Ocean Acidification Observing Network’ (http://www.goa-on.org/). In addition, the United Kingdom has a stated ambition to expand its monitoring programmes and thereby to enhance understanding of ocean acidification effects in national waters (Defra, 2020).

While these efforts continue to increase the knowledge-base, many gaps remain. In some instances, experiments are clearly advancing, however our ability to scale-up to ecosystem level effects and economic consequences is still very much evolving. Much that we know about the impacts from ocean acidification concerns single level effects, which must be considered in combination with other multiple stressors (e.g. low oxygen, rising temperature) (Montgomery *et al.*, 2019).

As ocean acidification research continues to evolve, these findings will need to be cascaded to the groups that are most heavily reliant on these resources (e.g. fisheries and aquaculture). Recent studies have attempted to expand beyond the observed physiological effects on marine organisms, and have demonstrated additional effects of relevance to human consumers of shellfish (e.g. from impacts on appearance, to changes in the taste, or nutritional content), which could result in further challenges for the seafood sector (e.g. fisheries and aquaculture) (Martin *et al.*, 2019).

Overall, the field of ocean acidification research has evolved at a rapid pace in the last 15 years. However, our ability to integrate experimental and modelling studies is advancing relatively slowly. We have attempted to combine different datasets and have found clear challenges across differing scales. Nevertheless, these types of approaches are necessary and will help to advance our current position in order to manage commercial species and safeguard livelihoods. The forthcoming 5th symposium on the “Ocean under a High CO_2 World” (5th International Symposium on the Ocean in a High CO_2 World (highco2-lima.org) will no doubt continue to explore some of these key evidence gaps and challenges outlined here. Ocean acidification is acting across species and habitats, and it is vital that this community continues to develop our understanding and ensure that robust fisheries and aquaculture can persist in the future under high CO_2 applications.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution

BT: conceptualization, analysis, methodology, and writing—original draft; YA: analysis, methodology, visualization, and writing—review and editing; JP: conceptualization and writing—review and editing; and SB: conceptualization, methodology, project administration, and writing—original draft.

Data availability statement

No new data were generated in support of this research. The analysed data is available on request to the corresponding author.

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