

Impacts of climate change on fish, relevant to the coastal and marine environment around the UK

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EXECUTIVE SUMMARY

- The appearance of warm-water (Lusitanian) fish species in UK waters along with local declines of some cold-affinity species provides the most compelling evidence of a climate-change effect.
- Distinguishing between climate-induced effects on fish distribution and other drivers is a key challenge. Some past studies have not accounted for geographic attachment and population structure in studies of distributional shifts in species including Atlantic cod and mackerel.
- The synchrony between winter–spring hatching fish larvae (e.g. cod, sole, sandeel) and their plankton prey appears to be changing, with consequences for recruitment. These changes reflect both changes in the timing of fish reproduction as well as that of their plankton prey.
- Temperature changes are affecting fish growth and age at maturation. Rising temperatures also decrease oxygen solubility and increase metabolic costs and there is now considerable debate as to whether this is limiting the maximum size that fish species can attain.
- Fin-fish larvae may be sensitive to expected changes in ocean acidification, but species have shown a variety of responses in experiments. For example, the use of end-of-century CO₂ concentration under the IPCC RCP 8.5 scenario resulted in a doubling of daily mortality rates in Atlantic cod larvae, but only had a minor effect on European seabass and herring larvae.

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Advances in both statistical and mechanistic models have increased our ability to provide future projections for climate change impacts on fish. Scientists have started to provide ‘forecasts’ for some species at the seasonal

to decadal time horizon, but there have been insufficient runs to yet be confident in these projections.

1. WHAT IS ALREADY HAPPENING?

Research since 2013 has largely focussed on the three key responses of fin-fish to climate change: distributional shifts, changes in the timing of life history events (phenology) and effects on body size. Added to this, there is an increasing body of research into the effect of ocean acidification on fish physiology and early survival. Except for pelagic species, the majority of research into distribution, phenology and body size changes has focussed on North Sea fish, as discussed in previous MCCIP report cards. The following sections review recent evidence on the three key responses. Projections about the future effects of warming and ocean acidification are then discussed.

Sea temperatures around the British Isles have typically been high during the review period, but exceptionally so in the central and southern North Sea in 2014 and 2018 and to a lesser extent in 2016 and 2018 (<https://ocean.ices.dk/iroc/#>). Details of recent changes in sea temperature and ocean circulation can be found in accompanying 2020 MCCIP reports.

Effects on distribution

Rising sea temperature has often been linked to changes in fish distribution in waters around the UK. Warming periods tend to be associated with observed increases in the abundance of Lusitanian fauna (organisms traditionally found in warmer waters) and reductions in the abundance of Boreal species (Sunday *et al.*, 2012). Temperature is considered to be a primary constraint on marine ectothermic organisms, such as many fish species, because of the effects on critical biochemical and physiological rates, including oxygen demand, development and behaviour (Sims *et al.*, 2006; Pörtner and Peck, 2010; Freitas *et al.*, 2015). Distributional shifts have led to substantial changes in fish communities in UK waters during the last few decades. While in some cases recent research supports evidence presented in previous MCCIP reports, there have been some new insights into the magnitude and scale of change. For example, a more-comprehensive analysis of fish diversity from west of Scotland research surveys found that latitudinal differences in species richness have declined since 1985, as southern species expanded north, despite smaller increases in temperature than observed in some other sea areas (Magurran *et al.*, 2015).

The ability of marine species to move in response to temperature varies depending on a range of factors, including their physiological capacity to

acclimatise and respond to acute stress as well as their degree of geographical attachment or the responses of their prey. Distribution shifts may thus reflect movement in species with little or no geographical attachment (termed ‘thermal-’ or ‘niche-tracking’), but can also arise as a consequence of localised declines in species with a strong geographical attachment. Geographical attachment in this context means that the distribution of the species is linked to some spatially restricted habitat, for at least one of its life stages. Such attachment is commonly seen in terms of specific habitat requirements for spawning or nursery grounds, and this dependence may affect the species’ or population’s ability to avoid unfavourable environmental conditions (Petitgas *et al.*, 2013). While many past studies have found that temperature can account for a significant component of the variation in fish distribution, recent studies have highlighted that the potential interaction with geographical attachment, population level responses and exploitation have not been properly considered (Heath *et al.* 2014; Bonanomi *et al.*, 2016).

The clearest distributional indicator of a changing climate has been the increased occurrence of species with warmer water affinity in UK waters. Warming enabled the population expansion of seabass, *Dicentrarchus labrax*, in the 1990s and early 2000s, although over-fishing and a few cooler winters (in 2009/10 and 2010/11) seem to have halted the expansion of this species (ICES, 2018). Nevertheless, the importance of warming to the range expansion of this warm affinity species and conversely the decline of eelpout *Zoarces viviparus*, a cold affinity species, has been clearly demonstrated by contrasting trends in abundance in the Wadden Sea (van Walraven *et al.*, 2017). The increase of some Lusitanian species may also reflect a proliferation of an existing local population, as in the case of the European anchovy, *Engraulis encrasicolus*, in the North Sea (Petitgas *et al.*, 2012; Beare *et al.*, 2004). This anchovy population has expanded its range probably because warmer temperatures have allowed more individuals to reach an overwintering size (Raab *et al.*, 2013). There was another increase in anchovy abundance across the southern and central North Sea in 2014 and 2015 associated with these warmer years (Figure 1).

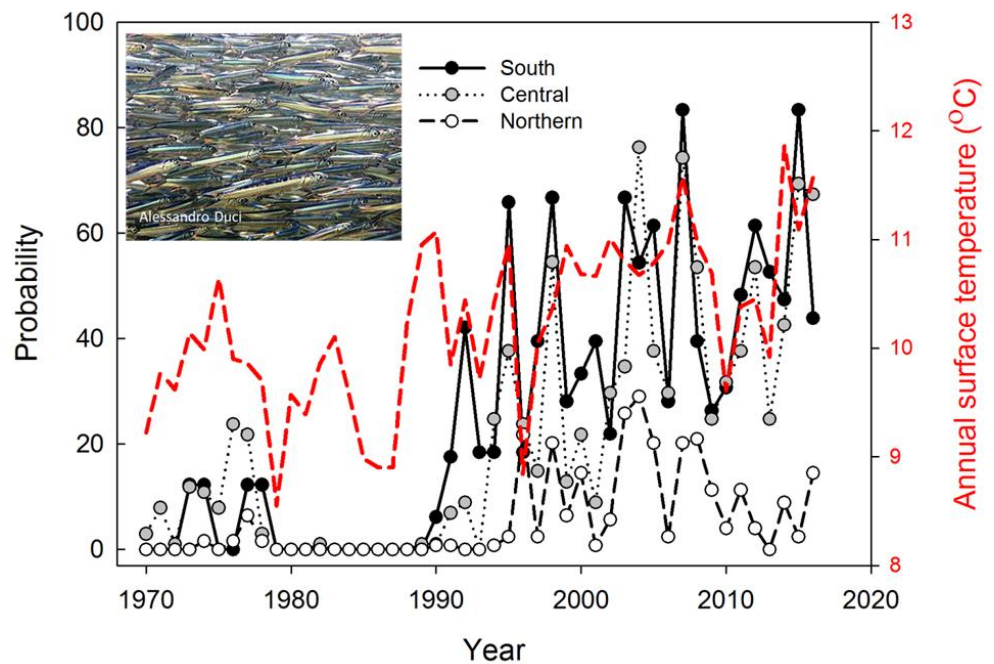


Figure 1: Occurrence probability of anchovy, *Engraulis encrasicolus* (see inset) in the south, central and northern North Sea from 1970–2016. Redrawn from ICES FishDish 2016 fig.3.1.1. Average annual sea surface temperature from Helgoland Roads (Alfred-Wegener-Institut (AWI), Helmholtz-Zentrum für Polar- und Meeresforschung) is given for comparison (dashed red line).

The frequency of occasional visitors to UK waters has attracted the most media attention, although the relative contribution of warming to recent sightings is uncertain. Bluefin tuna, *Thunnus thynnus*, have appeared many times in the North Sea during the last century but their abundance has never been particularly high, especially in the later part of the 20th century (Bennema, 2018). However, in recent years, there have been many more sightings of bluefin tuna from around the UK (Bennema, 2018; Faillettaz *et al.* 2019). Distribution modelling suggests that bluefin tuna track changes in water temperature, currents and prey and so their re-appearance is probably linked to the combination of warmer water temperatures, the expanding range of mackerel as well as increasing overall stock size (Dufour *et al.*, 2010; Druon *et al.*, 2016; ICCAT https://iccat.int/Documents/SCRS/ExecSum/BFT_ENG.pdf). A recent study also suggests that ocean circulation linked to the Atlantic Multidecadal Oscillation (AMO) is a key driver of Atlantic bluefin tuna across its oceanic range (Faillettaz *et al.*, 2019).

In comparison to species with strong geographical attachment, it has been proposed that the distribution of migratory pelagic species should respond rapidly to temperature change because of the effect on their prey, such as zooplankton, and their thermal niche, although the latter may depend on their

physiological tolerance. Montero-Serra *et al.* (2015) examined the occurrence and mean latitude of common planktivorous pelagic species in the North Sea in relation to temperature and the distribution of two important prey species with different climate affinities: *Calanus finmarchicus* that has a cooler water affinity, and *C. helgolandicus* a warmer-water affinity. They found that the occurrence of species with southerly and shelf-edge distributions (European pilchard, *Sardina pilchardus* and European anchovy, *Engraulis encrasicolus*, Atlantic mackerel, *Scomber scombrus* and Atlantic horse mackerel, *Trachurus trachurus*) was positively correlated with sea-surface temperature (SST), but the opposite was found for more-northerly distributed species (Atlantic herring, *Clupea harengus* and European sprat, *Sprattus sprattus*). They also found a positive correlation between sprat occurrence and *C. finmarchicus* abundance, suggesting this cold-water species was important, although this link may be questionable as Lynam *et al.* (2017) found a positive relation between the abundance of sprat and *C. helgolandicus*.

Mackerel distribution has changed extensively in terms of range and extent in the last two decades. Data from egg surveys to the west of the British Isles which have been conducted every three years have been used in several statistical models examining the importance of physical influences on spawning distribution. While a northward expansion in mackerel spawning distribution in response to warming has generally been proposed, recent studies that have also considered depth and geographical attachment suggest that climate is just one of several contributory factors (Hughes *et al.*, 2014; Bruge *et al.*, 2016). For example, the model of Brunel *et al.* (2018) found that geographical position was more influential than any environmental factor. Their study suggests that the expansion may also have been related to density-dependence as mackerel used areas of lesser habitat suitability in years when the stock size was large (particularly in 1992 and 2010), although there was no consistent density effect.

While able to respond rapidly to temperature over much of their lifecycle, pelagic species may still be constrained by the need to spawn at specific localities that promote the transport of offspring to suitable nursery areas. Atlantic mackerel, horse mackerel and blue whiting all have nursery areas to the west of the UK and Ireland, and seem to adopt a relatively demersal habit during this phase (Heath *et al.*, 2012). Similarities in the first year otolith growth pattern between juvenile mackerel along the coast and adults caught during the spawning period, suggest that fish return to spawn at the latitude where they spent their first months of life (Jansen *et al.*, 2013), which would explain why Brunel *et al.* (2018) found that geographical position was so influential in their model of spawning distribution. Herring are also constrained by the need to spawn at specific localities as they are demersal spawners, depositing their sticky eggs on coarse sand, gravel, small stones and rock. Röckmann *et al.* (2011) examined the realised habitats of North

Sea herring for two larval and two juvenile stages over the past 30 years. The realised temperature habitats of the newly hatched larvae did not change over time, but the habitat of juveniles in summer was sometimes associated with higher temperatures. Juveniles aged one year in winter were typically found in cooler waters, a result also reflected in their geographical shift east into shallower water. The results suggest that juveniles could be limited by temperature in the future, but may also track changes in food or predator distribution.

Most demersal species have some type of geographical attachment because of their reliance on habitats for protection and prey resources (food) during at least part of their life-cycle. Close associations with a specific habitat type or high fidelity to specific spawning grounds means that some fish populations are heavily impacted by changes in local environmental conditions. Sandeels (*Ammodytes* spp.) for example, spend much of their life buried in the sediment following a planktonic larval phase, and as a consequence they move very little once settled (Haynes and Robinson, 2011; Gibb *et al.*, 2017; Wright *et al.*, 2019). Management advice for the sandeel has thus been based on a sub-North Sea level since 2011, in order to reflect such population structure. Recent declines in some sandeel sub-populations largely appear related to climate, especially in the north-west North Sea, where much of the area is closed to fishing (Regnier *et al.*, 2017; Lindegren *et al.*, 2018).

In the North Sea, two populations of cod have been identified from genetic differences (Heath *et al.*, 2014) and electronic tagging and otolith chemistry studies indicate that their life-stages rarely overlap spatially (Neat *et al.*, 2014; Wright *et al.*, 2018). Tagging has shown that adult cod experiencing the warmest summer waters in the southern and central North Sea reduce their activity and do not migrate to nearby cooler waters (Neat and Righton, 2007). These fish can experience an average temperature range of 5.5–16.5°C, compared to only 7.0–10.0°C in the north-east North Sea (Righton *et al.*, 2010; Neat *et al.*, 2014; Figure 2). Hence the widely reported northward shift in the distribution of North Sea cod (Perry *et al.* 2005; Engelhard *et al.*, 2014) actually appears to be caused by differences in population growth rates (Holmes *et al.* 2014), rather than a northward movement of individual fish avoiding warming waters. It is also notable that the initial recovery of the North Sea cod stock that began this decade has only occurred in the north (ICES, 2016). The faster rate of decline in the southern cod population during the 1980s–1990s (Holmes *et al.*, 2014) corresponds with a higher and more-intensive fishing effort compared with the north-east (Engelhard *et al.*, 2014). This work highlights that current stocks, like North Sea cod, are often not the appropriate unit to understand changes in distribution. Furthermore, as with other recent studies (Engelhard *et al.*, 2014; Adams *et al.*, 2018), it highlights the importance of considering the spatial distribution of fishing pressure,

alongside the impact of climate change on populations, in interpreting distributional shifts.

As mentioned above, electronic tagging is starting to provide an understanding of how warming affects habitat use at the level of individual fish (Metcalf *et al.*, 2012). Cod have been shown to avoid important foraging habitat when temperatures exceed 15°C, if cooler, deeper, areas are within a daily movement range (Freitas *et al.*, 2015, 2016). However, when moving to cooler waters would require more-substantial migration, cod have been found to remain in waters up to 19°C (Neat and Righton, 2007), but become less active (Turner *et al.*, 2002). In addition, movement to deeper waters also occurs at lower average temperatures in large cod (Freitas *et al.*, 2015), which may reflect theoretically predicted sized-based limitation on oxygen requirements (Pörtner, 2008). These behavioural responses to temperature would indicate that warmer summer and autumn temperatures will lead to reduced growth, and there is observational evidence of this phenomenon from studies of fisheries survey data (Gjosæter and Danielssen, 2011; Rogers *et al.*, 2011).

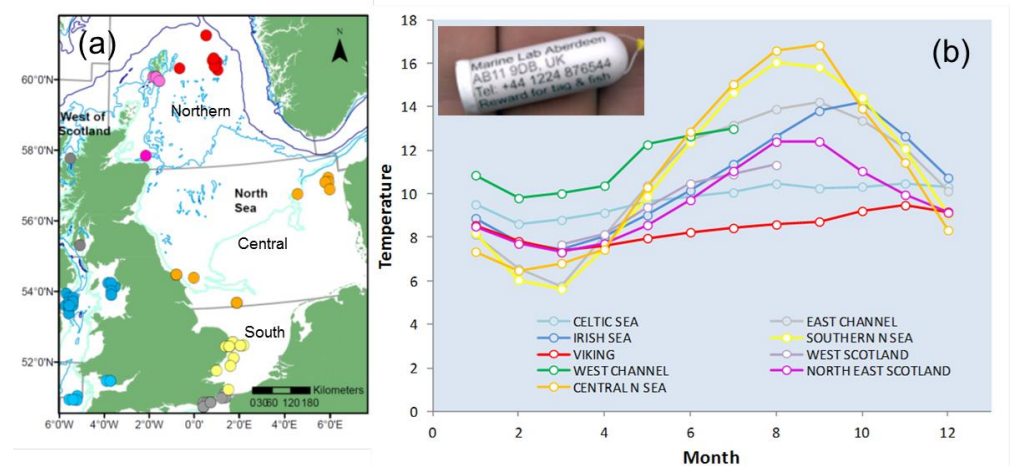


Figure 2 (a) Chart showing sites around the UK where groups of Atlantic cod were tagged with electronic archival tags and released and (b) average monthly temperatures the released cod experienced, as revealed by retrieved tags. (From Neat *et al.*, 2014.)

There has been a major shift from a dominance of larger, commercially valuable elasmobranch (sharks and ray) species to a prevalence of smaller, more-productive elasmobranch species often of low commercial value in the North Sea (Sguoutti *et al.*, 2016). While these authors found that most declines could be linked to fishing, the starry ray, *Raja radiata*, has a preference for cooler waters and so the recent warming of the southern North Sea may have been a contributing factor to the recent decline at the southern limit of its biogeographical range. Although the decline in spurdog, *Squalus acanthias*, is largely due to the overexploitation of the stock in the 1960s (De

Oliveira *et al.*, 2013), there are also potential impacts of climate change as this species was revealed to have a preference for cooler water (Sguoutti *et al.*, 2016).

While most research has focussed on the effect of temperature, oxygen concentration is also a key constraint on fish distribution and is affected by nutrient inputs as well as temperature and, in some areas, storminess (Greenwood *et al.*, 2010). Townhill *et al.* (2017) used a hydrodynamic-biogeochemical model together with fish physiological data, such as laboratory-derived critical thresholds, to hind-cast habitat suitability and project future oxygen limitation in the North Sea. The recent extent of areas with the lowest oxygen levels was smaller than during the 1970s, but oxygen levels were predicted to decrease again in the coming century, although not to the minima of previous decades. In the future, it is anticipated that the eastern side of the North Sea will witness lower oxygen levels and hence could have a temporary impact on fish physiology in late summer, affecting the swimming performance, growth, ingestion and metabolic scope of adult fish.

Studies of single species distribution clearly show that it can be difficult to distinguish between the role of direct impacts of temperature change on an organism's physiology versus other factors that affect movements, for example tracking of prey or dependence on specific habitat. One way in which researchers have tried to capture the overall changes in marine communities in response to warming is through the Community Thermal Index (CTI; Bowler and Böhning-Gaese, 2017). For North Sea demersal fishes captured in the International Bottom Trawl Surveys (IBTS), the CTI has been increasing in recent years suggesting that the community as a whole is shifting towards one more-dominated by warmer-water species. However, interpretation of CTI is complicated where the changes in abundance could be attributable to other non-climate related factors. For the demersal fish an obvious complicating factor is fishing. If species associated with cooler water are more desirable for capture, then fishing pressure could be partly responsible for changes in the CTI. Such bias could arise because cooler-preference species like cod have higher market value. Bowler and Böhning-Gaese (2017) considered this and produced a model that corrected the CTI for fishing desirability traits. When this model was applied to the North Sea IBTS data, the increase in CTI persisted but it was less obvious than using the uncorrected index. This suggests that fishing pressure has to some extent contributed to the observed changes in the fish community of the North Sea.

While there is little published work on temperature effects on deep-sea fish communities, a recent size-based indicator study using Marine Scotland Science survey data from the Rockall Trough was able to exclude temperature as a possible contributor to changes in the fish community as there was no

significant change in this factor over the 1998–2013 study period (Mindel *et al.*, 2018).

Phenology and the impact on recruitment

It is widely recognised that the timing of cyclic and seasonal natural phenomena is changing in response to climate change (Beaugrand *et al.*, 2003). Studies of this process (phenology) in fish have found evidence of shifts in the timing of spawning, hatching and migration. Fincham *et al.* (2013) examined the date of peak spawning for seven sole stocks around the UK based on the maturity state of market samples from England and the Netherlands. Four of the seven stocks exhibited a significant long-term trend towards earlier spawning at a rate of 1.5 weeks per decade since 1970. Lacroix *et al.* (2018) then simulated the possible consequence of a future 2°C warming on spawning and the early conditions that sole would experience. As with the Fincham *et al.* (2013) study, they predicted that future warming would lead to earlier spawning and, together with projected wind change, a much greater dispersal distance (+70%) and pelagic larval duration (+22%). Consequently, larval recruitment to nursery grounds was predicted to be affected but with a likely positive impact on recruitment.

Like sole, the rate of gonad development in cod is positively correlated to temperature under experimental conditions, and this relationship can explain the general trend for earlier spawning in warmer-water masses seen across the North Atlantic (Kjesbu *et al.*, 2010; Wright, 2013). Temperatures experienced during gonad development were not found to explain inter-annual variation in cod spawning time when examined at the whole North Sea scale (Morgan *et al.*, 2013) but a significant negative relationship was found for the northern and central North Sea when only autumn sea-surface temperature was considered (McQueen and Marshall, 2017). Unfortunately, neither study accounted for the depth-related variation in temperature that different North Sea spawning groups experience (Neat *et al.*, 2014; Figure 2) or explained the related spatial differences in spawning onset found in the North Sea (Brander, 1994; Gonzalez-Irusta and Wright, 2016). Winter temperature may also have a direct effect on where cod spawn, as survey analysis and data from electronically tagged cod indicate an avoidance of waters ≥ 8 °C (Righton *et al.*, 2010; Gonzalez-Irusta and Wright, 2016).

In contrast to sole and cod, warming delays reproductive development in Raitt's sandeel, *Ammodytes marinus*, probably because this species is dependent on their stored energy both to survive the winter buried in sand and to reproduce (Wright *et al.*, 2017a, b). However, while a 3°C difference was observed to have a significant effect on ovarian development under laboratory conditions, a 1.3°C annual variation in the field during the same over-winter period was not found to be sufficient to lead to differences in spawning time,

although other factors such as a size effect were found to be important (Boulcott *et al.*, 2017).

Our understanding of the role phenology in fish recruitment is still poor despite a century of research. Consequently, many studies have focussed on correlating recruitment time-series derived from fisheries stock assessments with zooplankton abundance and temperature. Further, due to a scarcity of information on the early life-stages of copepods (Pitois and Fox, 2006), most studies have used adult copepod abundance to infer the prey availability to fish larvae, even though these are not the prey items selected by most fish larvae (e.g. Heath and Lough, 2007). Although direct links to recruitment are hard to demonstrate, Capuzzo *et al.* (2018) found that recent declines in recruitment in several commercial fish species corresponded to a decline in small copepod species that in turn could be linked with reduced primary production. Declines in copepod prey have also been associated with low herring larval abundance (Alvarez-Fernandez *et al.*, 2015) and low larval survival of sandeels in the Dogger Bank area (Lindegren *et al.*, 2018). Reduced recruitment has also been related to warmer winters in many Boreal species (Ottersen *et al.*, 2013; Péchuchet *et al.*, 2014; Lindegren *et al.*, 2018), although temperature can sometimes be a poor proxy for the prey resource available to winter hatching fish larvae (Eerkes-Medrano *et al.*, 2017).

While there have been many studies that have correlated temperature and North Sea cod recruitment (O'Brien *et al.*, 2001; Nicolas *et al.*, 2014; Akimova *et al.*, 2016), the precise mechanisms operating are still not clear. Most attention has focussed on what effects changes in prey fields could have for growth and survival of the larvae. Unfortunately, Individual-Based Model (IBM) simulations have not demonstrated consistent results. For example, Pitois and Fox (2008) could not find a strong impact on the growth of cod larvae from temperature related changes in their planktonic prey, but, using a combination of size-spectra modelling to simulate the prey field and IBMs for larval growth, Huebert *et al.* (2018) found that the growth rate of larval cod could be food-limited in February, around the peak hatch time, and that in-turn was correlated with subsequent recruitment strength. A major problem with validating such studies is the lack of direct observations of the actual prey field which fish larvae experience, and direct evidence of starving cod larvae in the field. There is thus little direct information on the consequences of changes in spawning and hatching time, and how that interplays with changes in zooplankton prey. However, Regnier *et al.* (2017) did demonstrate that year-to-year variation in the match between hatching sandeel larvae and the availability of their prey could explain a large proportion of the variation in year-class strength in the north-west North Sea stock (ICES Sandeel Area 4). Poor synchrony, and hence small year-classes were primarily a function of the late timing of copepod egg production, but were also influenced by inter-annual variations in sandeel hatch date. This finding was consistent with

Cushing's (1975, 1990) match-mismatch hypothesis, which has been widely cited as explaining recruitment variation in winter spawning species (Durant, 2007).

Demographic characteristics of fish populations may be important to climate resilience (Vasilakopoulos and Marshall, 2015; Lowerre-Barbierri *et al.*, 2017). In some populations of long-lived species, older fish spawn at different times and for longer in comparison with younger adults and this can reduce the potential for mismatch with suitable larval feeding conditions (Wright and Trippel, 2009; Tillotson and Quinn, 2018). High fishing-mortality usually leads to a truncation in the age and size composition of the spawning stock and this has been linked to higher sensitivity to climate fluctuations in some heavily exploited stocks (Ottersen, 2008; Rogers and Dougherty, 2019).

The role of water temperatures on predation rates of organisms feeding on the early life stages of fish is also potentially of great significance, but has received little attention. Species such as sprat and herring undoubtedly consume large amounts of fish eggs and/or larvae (Fox *et al.*, 2012), and their feeding rates are likely to change with temperature. Reductions in the abundance of predators on the shallow inter-tidal nursery grounds are one explanation for the exceptional year-classes that have followed several cold winters in North Sea plaice (Nash and Geffen, 2012). However, overall the top-down controls on fish early life stages are not well understood but may well be important in controlling year-class strength.

Warming-induced declines in mean body-size review

The third widely debated response to climate change is the effect of temperature on body size. Due to oxygen maintenance needs (Pörtner and Knust 2007) and temperature dependent costs of locomotion and digestion (Holt and Jørgensen, 2015), body growth and activity are expected to display a dome-shaped relationship with temperature, with juveniles often having a higher temperature optimum than adults (Ohlberger, 2013). Ectotherms (cold-blooded animals) generally develop faster and mature at smaller body sizes at higher temperatures, leading to smaller maximum body sizes overall. Hence, most fin-fish species reach a larger body size in the northern part of their range. This phenomenon is known as the Temperature–Size Rule (TSR; Atkinson, 1994) and there are several potential explanations for it, although the major focus has been on an observed decrease in oxygen solubility and increased metabolic costs at warmer temperatures limiting oxygen supply to larger fish (Pörtner and Farrell, 2008; Forster and Hirst, 2012; Audzijonyte, 2019).

Cheung *et al.* (2013) modelled the integrated biological responses of over 600 species of marine fishes due to changes in distribution, abundance and body size. Their dynamic bioclimate envelope model had an explicit representation of ecophysiology, dispersal, distribution and population dynamics and simulated changes in relation to projected annual average temperature, currents, salinity, oxygen concentration and sea-ice concentration. The authors predicted that assemblage-averaged maximum body weight would shrink by 14–24% globally from 2000 to 2050 under a high-emission scenario, with about half of this shrinkage due to a change in physiology linked to oxygen limitation. Consistent with expectations from this model by Cheung *et al.* (2013), Baudron *et al.* (2014) found a reduction in asymptotic body size in six out of eight commercial fish species examined from the North Sea over a 40-year period during which water temperature increased by 1–2°C. The range in estimates of shrinkage was from 1 to 29%, with an average decline of 16%.

Mechanisms underlying the TSR phenomenon are still intensely debated as it is very difficult to disentangle the possible causes with available data (Angilletta *et al.*, 2004; Atkinson *et al.*, 2006; Audzijonyte *et al.*, 2019). Even the concept of oxygen limitation as a determinant of body size has been questioned, as many physiologists think that oxygen uptake reflects oxygen demand in fish rather than the other way around (Lefevre *et al.*, 2017, 2018; Jutfeld *et al.*, 2018). Adult body size is also influenced by the age when fish begin allocating energy into reproduction (Audzijonyte *et al.*, 2016). A shift to earlier reproductive investment may have affected asymptotic body size in the study by Baudron *et al.* (2014), as four of the six North Sea species had similar time trends towards earlier and smaller size at maturity which could not be explained by temperature alone (Grift *et al.* 2003; Marty *et al.*, 2014; Wright *et al.*, 2011; Wright *et al.*, 2014; van Walraven *et al.*, 2010; Mollet *et al.*, 2007). These frequently observed declines in maturity-at-size and maturity-at-age also often correlate with high levels of historical fishing pressure, which may have driven an evolutionary response by fisheries-induced selection (Devine *et al.*, 2012; Audzijonyte *et al.*, 2013). Brander *et al.* (2016) also noted that half of the decline in asymptotic size in the Baudron *et al.* (2014) study took place prior to 1988, during a period when temperature declined, suggesting that other factors were also at work.

Changes in temperature may advance maturation independent of body growth, resulting in small adult body size due to earlier energy allocation to reproduction (Audzijonyte *et al.*, 2016). Experiments have shown that temperature can directly promote earlier reproductive investment through an effect on gonad development rate (Dhillon and Fox 2004; Tobin and Wright, 2011). However, accounting for such a temperature-dependent maturation threshold in haddock, *Melanogrammus aeglefinus*, did not explain the observed increase in proportion maturing over time, although did explain

some of the inter-annual fluctuations (Wright *et al.*, 2014). While no one type of response appears to explain the observed declining trends in body size, earlier energy allocation into reproduction due to a combination of direct temperature effects, and evolutionary responses to elevated adult mortality from temperatures or fishing, together with the susceptibility of large fish to decreased oxygen supply in warming waters can all be expected to be involved (Audzijonyte *et al.*, 2016).

In addition to changes in size at the individual level, the average size of the fish community appears to be declining due to the increasing number of Lusitanian species, which tend to be smaller and have shorter life spans (Montero-Serra *et al.*, 2015 van Walraven *et al.*, 2017). Queirós *et al.* (2018) reported that the species that have the largest effect on the Marine Strategy Framework Directive (MSFD) Large Fish Indicator (LFI) are all Boreal and likely to be adversely affected by warming waters, while the abundance of smaller Lusitanian species is likely to continue to increase. Marshall *et al.* (2016) also found regional differences in the LFI within the North Sea, with the central North Sea witnessing the greatest decrease whereas the Norwegian trench showed the greatest increase. While the decrease in LFI in the central North Sea appeared to be related to fishing, consistent with the purpose of this indicator, the increase in LFI in the Norwegian trench was linked to warming. Consequently, climate change may affect targets used to infer ‘good environmental status’ that are assumed to be indicative of more immediate anthropogenic pressure, and the current reporting areas (e.g. Greater North Sea) may be too large to disentangle the contributions of fishing and climate.

Effects of ocean acidification

Oceans absorb CO₂, removing 25–30% of the emissions added to the atmosphere, but this is increasing the concentration of hydrogen ions in seawater, as dissolved CO₂ produces carbonic acid (Williamson *et al.*, 2017). This effect is termed ‘Ocean Acidification’ (OA). Alongside the acidification is a reduction in carbonate ions that is linked to the saturation state. The saturation state for a mineral in seawater is a measure of the potential for the mineral to form or to dissolve. If the saturation state is reduced, as under OA, then carbonate ions are more likely to dissolve. Data on seawater chemistry from ICES for the North Sea for the period 1984–2014 suggests that pH values have declined relatively rapidly compared to the surface Atlantic as a whole (Williamson *et al.*, 2017). Future pH and aragonite saturation state for the North Western European Shelf has been modelled within the Regional Ocean Acidification Modelling project forced with data from the IPCC AR5 RCP 8.5 (see Ostle *et al.*, 2016). The model suggests a clear decrease in both pH and aragonite saturation state, with areas around the south coast of Norway showing the strongest decrease. Surface waters will start to become

under saturated gradually from around 2030, and more rapidly from 2080. By the end of the century, the model estimates that an area of surface water of approximately 300,000 km² could become undersaturated with respect to aragonite.

Unlike organisms with external hard structures, such as shellfish, the internal chemistry of fin-fish is to some extent buffered and under homeostatic control. Thus, although the concentration of CO₂ in the surrounding seawater positively influences CO₂ diffusion into the bloodstream of marine fin-fish, this is generally compensated within a few hours to days. However, such compensation may increase the energy required for acid–base regulation. There could also be chronic impacts on cellular metabolism (Strobel *et al.*, 2013), metabolic rate (Michaelidis *et al.*, 2007, Enzor *et al.*, 2013), and respiratory performance (Couturier *et al.*, 2013) although the mechanisms are not yet fully understood (Browman, 2016). In addition, behaviour and sensory systems of fish can be impacted by elevated CO₂ levels, including impaired olfactory, visual and hearing abilities (Jutfelt and Hedgärde, 2013), although this is not seen in all species at projected future pH (Jutfelt and Hedgärde, 2015). In sharks, warming combined with acidification can impair growth and hunting behaviour (Pistevos *et al.*, 2015). Consequently, ocean acidification is expected to act synergistically with warming, leading to a narrowing of thermal survival windows of marine fish across different life stages (Pörtner and Peck, 2010).

Experiments suggest variable responses between fish species to ocean acidification, but the early life stages will probably be more vulnerable because they lack the fully developed capacities for acid-base regulation of juvenile and adult fish. For example, subjecting cod larvae to an end-of-century CO₂ concentration, predicted under the IPCC RCP 8.5 scenario (~1100 µatm), resulted in a doubling of daily mortality rates in the first 25 days post hatching compared to present-day CO₂ concentrations (Stiansny *et al.*, 2016). However, CO₂ effects on European seabass (Pope *et al.*, 2014) and herring (Sswat *et al.*, 2018) were less marked and appeared negligible compared to the direct effects of temperature increase.

2. WHAT COULD HAPPEN IN THE FUTURE?

There has been a marked increase in research using both empirical (statistical) and mechanistic models to examine the impacts of climate change on marine fin-fish since 2013, employing four broad categories of modelling approach; statistical species distribution models, physiology-based biophysical models, food web models, and end-to-end models (Peck *et al.*, 2018). Predictions from any one approach are subject to uncertainty, including the many detailed aspects of species' ecological and physiological constraints that are still

largely unknown (Rijnsdorp *et al.*, 2009). However, confidence in projections of changes in fish distribution and productivity can be increased by using an ensemble of these models, that yield more-robust conclusions overall.

Although statistical (correlative) approaches based on historical baselines may break down as the environment moves into a previously unseen condition (Payne *et al.*, 2015), they can be readily applied across a large number of species at a range of spatial scales and are probably reasonably reliable in the short- to medium-term. An important recent North Sea example comes from Rutterford *et al.* (2015). The study used Generalised Additive Models (GAMs) to model fish distribution in relation to physical factors (depth, temperature, salinity, fishing pressure), in order to explain past trends in commercial fish distribution and then, with recent climate model outputs, to predict the future distribution over the next three decades. The thermal experience was predicted to change for a number of a shallow-water species in the southern North Sea such as Common dab (*Limanda limanda*), leading to increasingly sub-optimal habitat. While the predicted annual mean surface temperature rise of $2.9^{\circ}\text{C} \pm 0.8^{\circ}\text{C}$ over the next 80 years across the north-west European shelf (see Tinker *et al.*, 2015, 2016) will still be within observed thermal limits for most commercial species examined in the study, competition among species is likely to increase as temperatures rise towards the thermal preference of warmer-water species using the same habitats, and hence such models predict a reshuffling of the fish assemblage. Rutterford *et al.* (2015) suggested that the availability of suitable habitat could become a major constraint on the distribution of some of major commercial species around the British Isles. Similar statistical distribution models (e.g. Jones *et al.*, 2013; Lenoir *et al.*, 2011) also indicate a future contraction in suitable habitat but the degree of confidence in such projections was considered quite low by the ICES Working Group on Fish Distribution Shifts (WKFISHDISH) in November 2016. The main reason for this was an apparent lack of strong evidence for particular drivers of distributional change, such as warming and the limited understanding of the interplay between different drivers. Nevertheless, the number of long-term projections for fish distribution and productivity around the British Isles has steadily increased and, in addition, the first generation of short-term marine fish distribution forecasts has started to emerge that are built upon accurate physical forecasts for seasonal (3 months) to decadal (5–10 years) time spans (Payne *et al.*, 2017).

Incorporating physiology into spatial models of habitat characteristics is starting to provide a mechanistic, cause-and-effect understanding of observed changes in productivity and distribution of organisms such as fishes (Pörtner and Peck, 2010). Sophisticated mechanistic models that incorporate bioenergetics and evolutionary constraints have been developed for a few well-studied species such as north-east Arctic cod (Holt and Jørgensen, 2015) but usually for only part of the life-history. Developing full life-cycle models

is important as climate processes may affect each life stage differently. Rochette *et al.* (2013) developed such a model for sole (*Solea solea*) in the eastern English Channel which took account of spatially separated habitats, a population model for adults, a drift model for eggs and larvae and a juvenile habitat suitability model. This enabled the authors to consider the various interacting pressures including fisheries-induced changes in adult age composition and the consequences for coastal habitat degradation, but so far this has not been used to project climate-induced changes in population dynamics. Beraud *et al.* (2017) developed an IBM to investigate the factors affecting seabass settlement on nursery grounds around the southern British Isles and French coast. Seabass populations are known to be heavily influenced by seawater temperature and the geographic extent of spawning is thought to be bounded by the 9°C isotherm, but can expand both as the season progresses and in warmer years. The IBM developed by Beraud *et al.* (2017) attempted to track egg and larval development. The aim was to simulate pelagic migration from spawning ground to nursery area, by defining growth and behaviour that was dependent on the physical environment. The IBM was coupled with a three-dimensional hydrodynamic model to derive current vectors and water temperatures for the particle tracking model. The IBM successfully predicted inter-annual differences in settlement, regardless of larval behaviour. Dispersal was driven mainly by the influence of wind on residual currents and water temperature, with warmer temperatures reducing the duration of the pelagic phase and stronger current increasing the potential to drift further. Progeny spawned in the central western English Channel settled in both England and France, with movement from the central to the eastern English Channel occurring only in warm years. As both temperature and sea circulation will be affected by climate change, the supply of larvae to nursery areas may change, as predicted for North Sea sole (Lacroix *et al.*, 2018).

Most models have focussed on single species but the trophic interactions among species are likely to be a major factor in determining which species expand or decline. It is possible to include thermal preferences into food web models, although this is based on simple relationships between temperature and performance. Serpetti *et al.* (2017) used an integrated ecosystem model (Ecopath with Ecosim) that included fishing and the impact of rising temperatures, to assess the cumulative effect of future climate change and sustainable levels of fishing pressure on the commercial fish community off the Scottish west coast (ICES Division VIa). Rising temperature was predicted to cause declines in species with a narrow temperature tolerance, such as cod, herring and haddock, while thermally tolerant species were not affected. The positive effect of a higher optimum temperature for whiting, *Merlangius merlangus*, in parallel with declines of its predators such as cod and grey seals, resulted in a strong increase by 2030 under rising temperature scenarios, with the rate of whiting increase from 2030 until the end of the

century matching the trend in temperature. Consequently, this study predicted that there might be an increase in the contribution of whiting to the demersal fish community on the west of Scotland. However, such approaches have not, to date, factored in possible complications, such as changes in the plankton food web or interactions between increasing temperature and ocean acidification. The results of such models are thus best thought of as projections of ‘possible futures’ rather than ‘predictions’ of what will happen.

The most-complex models available attempt to represent all trophic levels, from phytoplankton to top predators, with their physical environment (hydrography, biogeochemistry) and include the dynamics of human pressures affecting marine systems. These ‘end-to-end’ models attempt to tackle the interacting processes and feedback of critical importance to marine systems (Fulton *et al.*, 2011) but their complexity does make them unwieldy. ‘End-to-end’ models are thus often used for strategic explorations (‘what if’) rather than tactical (‘how now’) decision making (Peck *et al.*, 2018). Such models are being developed for the seas around the UK and could be critical in assessing the ecological and economic trade-offs of different management strategies. Lately, the implementation of the ATLANTIS ecosystem model has been conducted in the English Channel (Girardin *et al.*, 2018), Nordic and Barents seas (Nielsen *et al.*, 2018), as well as the North Sea (EU-FP7-VECTORS, <http://www.marine-vectors.eu/>). Using this model, Griffith *et al.* (2012) explored the interaction effects of fishing, ocean warming, and ocean acidification on 60 functional groups of species in the south-eastern Australian marine ecosystem. While they found that ocean acidification had a negative effect on total biomass, fishing and ocean warming together with ocean acidification had an additive effect on biomass.

Experimental observations have begun to be integrated into models in order to project the combined effects of ocean warming and acidification. For example, Koenigstein *et al.* (2017) used experimental results concerning temperature and CO₂ effects on egg fertilization, egg and larval survival and development times, together with different prey availability scenarios to predict possible changes in the Barents Sea cod stock. The model showed severe reductions in average age of recruitment of young under one year of Barents Sea cod under projected warming and acidification toward the middle to end of this century, unless fish were able to adapt. This is despite the fact that recent warming seems to have favoured this stock, illustrating that it cannot be assumed that short- to medium-term benefits of warming will persist. Similarly, Fernandes *et al.* (2017) made use of available observational, experimental, and modelling approaches to quantify potential impacts of OA and warming on future fisheries catches, as well as revenues and employment in the UK fishing industry. Across all scenarios, bivalve species were suggested to be more affected than fin-fish species. Moreover, effects of OA may be partially mitigated through trans-generation effects as,

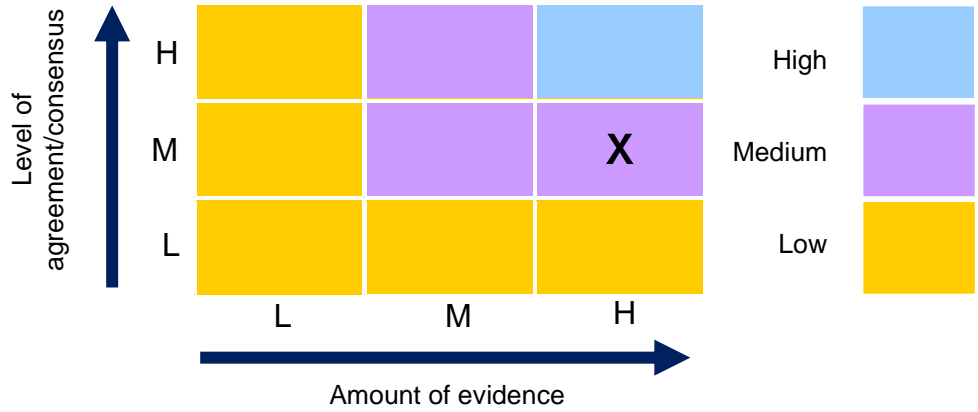
in cod, the offspring of parents maintained at high CO₂ typically do better in high CO₂ conditions, at least when food is abundant (Stiansy *et al.*, 2018).

The largest impacts of OA on fish may not be direct, but rather may arise due to changes in other trophic levels. Calcifying phytoplankton are an important prey for copepods, which in turn are a key prey of both young and plantivorous fish species. Unfortunately, however, there is considerable uncertainty about the magnitude of these effects, but complex secondary impacts of OA through marine food-webs are possible (Hildebrandt *et al.*, 2016).

3. CONFIDENCE ASSESSMENT

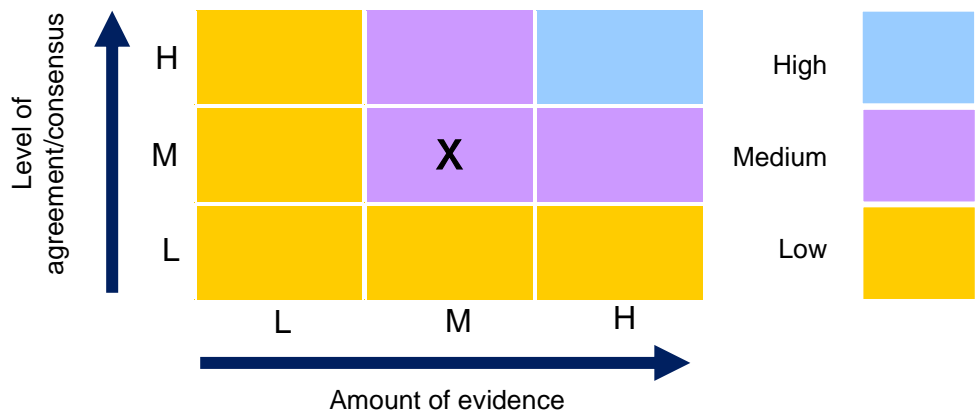
The amount of information on climate impacts on fish has grown substantially since the previous 2013 MCCIP fish review (Simpson *et al.*, 2013). There is generally a high level of agreement between studies about changes in composition and size of fish communities, with a range expansion and population growth of Lusitanian species within UK waters. Concurrently, there has been a decrease in the habitat extent and quality for many Boreal species. However, the contribution of climate to some well-reported distributional shifts, including that of Atlantic mackerel and cod in the North Sea, has been questioned based on an increased understanding of their biology. There is high agreement that plankton communities have undergone substantial changes, and this appears to be reflected in the high frequency of poor year-classes in many Boreal fish stocks. There is only a medium level of evidence, with more work needed on links between fish larvae and their prey, on links between mean size and temperature and direct and indirect effects of ocean acidification on fin-fish populations. Most of the evidence linking fish recruitment with timing and abundance of prey remains correlative. There are important gaps in available observational time-series for the smaller plankton that are the main prey for fish larvae that make addressing this question difficult. Consequently, the overall assessment has changed from the 2013 report card in that the amount of evidence that climate change is affecting fish is now high, whilst the level of agreement is now medium because we are now more aware of a number of additional complicating factors.

What is already happening?



With regard to what might happen in the future, there is substantial effort being made to combine and develop various modelling approaches to predict future distributions and abundances of fish species, including predicting species that may invade suitable habitat in future conditions. However, there is between low to medium level evidence available for what could happen, with the majority of insights about the possible processes by which fish respond to climate change coming from modelling rather than empirical studies. As a result, the level of evidence and agreement has not changed from that stated in the 2013 Annual Report Card, i.e. a medium level of evidence and consensus.

What could happen in the future?



4. KEY CHALLENGES AND EMERGING ISSUES

The three top priority challenges which need to be addressed to provide better advice on the responses of fin-fish to climate change can be summarised as: (1) contribution, (2) multi-level data integration, and (3) model testing.

As demonstrated above, it is difficult to isolate the climate contribution to many of the reported changes in fish distribution, productivity and size. Robust projections of climate-related changes in productivity and distribution at a species level requires a better integration of data on survival, distribution, movements, aerobic scope, growth and reproductive schedules into statistical, process-based and ecosystem models. More validation of model assumptions is needed by combining modelling approaches and conducting empirical studies to better parameterise models and test assumptions. This process has begun but needs to increase in order to consider habitat dependency, integration of physiological processes and the combination of individual (e.g. archival tags) and population level data to understand the nature of climate responses. Identifying bottlenecks in the life-cycle where species are most sensitive to climate change, such as shallow coastal nursery areas, is also important in finding ways to minimise human pressures on struggling stocks. Given these requirements, it will probably never be possible to obtain detailed information on more than a limited number of species. Although studies have tended to focus on commercial species (e.g. cod, haddock, plaice, herring), climate change could also affect species of conservation importance to the UK (e.g. flapper skate, basking shark). Such impacts would have implications for the effectiveness of marine conservation measures so that these species should not be ignored in setting marine climate research priorities.

Emerging issues

Little is known about natural variation and the adaptive capacity of fish to climate change. Studies using genomics and transcriptomics are improving our understanding of the capacity of fish populations to acclimate and cope with acute temperature stress. Populations of the same species can exhibit different responses to temperature due to differences in gene expression (Veillux *et al.*, 2018), and so it is unclear if some species will be able to persist through shifts in warm-adapted populations. Increased adult mortality whether from fishing or climate change is expected to lead to the evolution of 'faster' life histories: Earlier maturation at smaller sizes and shorter life spans (Waples and Audzijonyte, 2016). Other traits such as spawning time have been found to evolve rapidly when a species is exposed to a different environment (Quinn *et al.*, 2000). Epigenetic effects may also be important as experiments on cod suggest that the offspring of parents subjected to high CO₂ do better in high CO₂ conditions, at least when prey density is high (Stiansy *et al.*, 2018).

There is increasing concern among many scientists about sudden, dramatic and long-lasting shifts in ecosystem structure and function (regime shifts) that may be caused by climate change and other anthropogenic pressures (Mollmann *et al.*, 2015). Theory and empirical evidence suggest that ecosystems may have system boundaries or tipping points. Identifying the tipping points for climate-driven shifts is very challenging and many possible mechanisms have been proposed including changes in the interactions between predatory fish and their fish prey (Gårdmark *et al.*, 2015) or between temperature change and differences in species thermal niche (Beaugrand, 2015). Whatever the cause, being able to define a safe operating space over which a regime shift is unlikely to occur is a very important field of research that could inform climate adaptation strategies (Ratajczak *et al.*, 2018).

Finally, research to date has tended to focus on annual or seasonal average temperatures. However, there is increasing interest in the impacts of short-term events, such as heat-waves (Frölicher *et al.*, 2018). Climate change projections suggest that extreme weather events may become more frequent and it should be remembered that, despite the thermal buffering effect of seawater, such short-term events can still have substantial impacts on marine species, particularly in inshore waters.

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