Impacts of climate change on shallow and shelf subtidal habitats, relevant to the coastal and marine environment around the UK

P.J. Moore [1] and D.A. Smale [2]

[1] *Institute Biological, Environmental and Rural Science, Aberystwyth University, Aberystwyth SY23 3DA, UK*
[2] *Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, UK*

EXECUTIVE SUMMARY

- A comprehensive review of the literature identified thirteen new relevant studies published since the MCCIP 2013 report on 'what is already happening', of which all but one were conducted in UK waters. A further four studies have been published since 2013 on 'what is likely to happen in the future'.

- North Sea infaunal (burrowing) species have shifted their distributions in response to changing sea temperature, however, most species have not been able to keep pace with shifting temperature, meaning that species are subjected to warmer conditions. Leading (expanding) edges are responding more quickly than trailing (retreating) edges, which has been observed elsewhere in the world.

- Analysis of a 40-year data–series found that small, generally shorter-lived, infauna experienced some changes in community structure related to changes in Sea-Surface Temperature (SST), but this affect was dampened because increased food availability meant that temperature-induced rises in energy use were counteracted. This was not the case for large-bodied species that experienced increased competition leading to altered community structures. This highlights that changes in non-climate drivers may interact with climate change to mediate species – community level responses and that responses may depend on species life-history traits.

- A number of UK kelp species have experienced changes in abundance linked to altered SST. In particular the warm-water species, *Laminaria ochroleuca*, has increased in abundance and expanded its distribution into more wave-exposed conditions. While superficially similar, there are differences between warm-water and cold-water species in terms of life history characteristics (e.g. cold-water species such as *L. hyperborea* and *L. digitata* are perennial, whereas the warm-water species *Saccorhiza polyschides* is a pseudo-annual), and habitat provision (e.g. *L. hyperborea* supports diverse epiphyte assemblages whereas *L. ochroleuca* does not).

Therefore, changes in the relative abundance of warm- and cold-water kelp species are likely to alter the structure, functioning, and ecosystem services provided by kelp forests, as these species continue to alter their biogeographic distributions in response to climate change.

- A number of studies have used modelling approaches to predict changes in the distribution and/or abundance of kelp and cold-water corals at the UK scale, and benthic infauna and epifauna within the North Sea. All suggest significant shifts in species ranges into the future leading to altered community structures. This is likely to have implications for food-web dynamics, fisheries, carbon cycling and ultimately human society.

- Collectively this review has highlighted new evidence for changes in species abundance and distribution in response to climate change, which in some instances has altered community structure and potentially ecosystem functioning. Of concern is that studies are limited to a small number of species and/or regions.

1. INTRODUCTION

The current review provides a comprehensive overview of the evidence for climate-change impacts on biological systems that have occurred since the last shallow and shelf seas MCCIP Annual Report Card released in 2013, by focusing on invertebrates and macroalgae from both hard and soft substrates. A brief overview of past evidence is provided in places for context. The review excludes fish, plankton and invasive species which are included in separate report cards. Seagrass is also not included as it is covered by the accompanying intertidal habitats MCCIP report (Mieszkowska *et al*., 2020).

Climate change is leading to increases in ocean temperature, changes to ocean chemistry, sea-level rise, changing salinities and oceanographic patterns and increased extreme events including storminess and marine heatwaves (Stocker, 2013). The main focus of this report is the observed responses of biota to changes in ocean temperature, as this is the primary climate driver for which time–series observations exist. There is a large body of experimental evidence for the impacts of ocean acidification, which has mostly focused on single species experiments over short timescales. These studies have demonstrated positive, negative and neutral effects of ocean acidification on species physiology, demography and ecology (see reviews Harvey *et al.* 2013; Kroeker *et al.* 2013 for details). While negative impacts on individual species and communities cannot be ruled out, to date there has been no observed impact of altered ocean chemistry in UK waters. Stochastic events are increasingly being seen as key drivers of species-range shifts and community re-organisation. Evidence is provided below on the biological impacts of extreme storm events. While these storms cannot be attributed (nor ruled out) to anthropogenic climate change they provide insight into the likely impacts of such increased storminess. Marine heatwaves (MHWs) have also recently been shown to be a key driver of species range shifts (Wernberg *et*

al., 2016; Oliver *et al.,* 2018), with recent analyses demonstrating that MHWs have increased in frequency and duration over the last 100 years linked with increases in Sea-Surface Temperature (SST) (Oliver *et al.,* 2018). Further, MHWs are predicted to increase in frequency, spatial extent and duration into the future (Frölicher *et al.,* 2018). While there is currently no published evidence of the impacts of MHWs in shallow and shelf seas in UK waters, this is likely to change into the future.

The annual report focuses on climate mediated biological responses to climate change, however, it is important to note that a range of anthropogenic and non-anthropogenic drivers interact with climate change affecting biological systems. While increasingly sophisticated analyses are enabling these different stressors to be disentangled it is not always possible to do so, particularly with observational field data such as that presented in this review.

There are subheadings for specific regions and where regional subheadings are missing this means that evidence does not exist for that region.

2. WHAT IS ALREADY HAPPENING

2.1 Soft-sediment

North Sea
There is a long history of marine research in the North Sea with large-scale investigations showing the structure and distribution of North Sea macrofauna is influenced by temperature, differing water masses, sediment type and food supply (Reiss *et al.* 2010; Kroencke *et al.* 2011). There are numerous North Sea time–series studies, some going back many decades, which have provided and continue to provide evidence for the impacts of climate change on soft-sediment communities. For example, the 'Dove Time Series' located off the north-east coast of England provides the UK's longest-existing soft benthic time–series record with biannual (spring and autumn) surveys conducted for the last 40 years. This time–series has played an important role in identifying phase shifts and changes in community structure related to extrinsic drivers. For example, changes in population and community structure have been linked to year-to-year variation in SST and/or changes in pelagic primary production (Buchanan *et al.,* 1978; Buchanan and Moore, 1986; Buchanan, 1993; Frid *et al.,* 1996). The time–series records show that the North Sea has become warmer and more productive over time, which has coincided with a dampening of observed fluctuations in assemblage structure (Frid *et al.,* 2009). Studies conducted in north-east England, but not as part of the Dove Time Series, have also demonstrated the importance of temperature in structuring benthic communities with warmer temperatures, associated with a positive North Atlantic Oscillation Index (calculated as the difference in surface sea-level pressure between the Subtropical (Azores) High and Subpolar Low) in the preceding year, resulting

in reduced densities and diversity of species (Rees *et al.,* 2006). Since the last MCCIP report card a number of studies have analysed/reanalysed time–series data to understand changes in distribution, abundance and community structure in relation to increased temperature.

Hiddink *et al.* (2015) examined geographical and bathymetric shifts of 65 benthic infaunal invertebrates in the North Sea comparing distributions in 1986 with those of 2000. They went on to determine whether these species were tracking their thermal niche by examining whether these species were tracking the direction and speed of shifts in temperature isotherms (Velocity of Climate Change, VoCC) using minimum, maximum and mean SST and Sea Bottom Temperature (SBT). They found temperatures had increased throughout the North Sea coinciding with a north-westerly shift (range-centre, leading and trailing edge) and deepening of many species ranges, mirroring results observed for fish in the North Sea (Perry *et al.,* 2005; Dulvy *et al.,* 2008). In particular, leading edges expanded faster than trailing edges (Hiddink *et al.,* 2015), which has also been noted in global-scale analyses (Poloczanska *et al.,* 2013). Distributional shifts (centroid 3.8-7.3 km per year interquartile range) lagged behind shifts in SBT and SST (8.1 km per year) suggesting species were not able to track climate warming and were therefore experiencing warmer temperatures (Hiddink *et al.,* 2015), which in the long term could affect performance (e.g. growth, reproduction, survival). Mean SST VoCC accurately predicted the direction and magnitude of distributional centroid shifts, while maximum SST VoCC was a good predictor of the same for trailing edges, suggesting that these metrics could be used to predict future distributional shifts. SBT was not a good predictor for range shifts, and no good predictor was found for leading edge expansion (Hiddink *et al.,* 2015). While the authors do not speculate why SBT is not a good predictor of species range shifts, other studies have suggested that changes in productivity (potentially mediated by warmer SST) and hence food supply can be an important driver of community structure, dampening the effects of warming (Clare *et al.,* 2017; see below). This may explain why SBT is a poor predicator and why species are not keeping pace with VoCC.

While Hiddink *et al.* (2015) were looking at range shifts within the North Sea, Neumann *et al.* (2013) highlighted the range expansion of the angular crab, *Goneplax rhomboids*, from North-east Atlantic coasts into the Moray Firth (2000) and southern North Sea (Oyster Ground, 2003) driven by increased SBT and favourable prevailing hydrodynamic conditions. This perhaps counter intuitive eastwards and southern shift in species ranges into the North Sea has also been observed in intertidal species (Mieszkowska *et al.,* 2006) with the explanation that these shifts are likely a response to the cooler North Sea becoming warmer and more habitable for species that have historically been limited to the warmer North-East Atlantic (Mieszkowska *et al.,* 2006).

Species range shifts in response to climate change and there idiosyncratic nature is likely to lead to altered patterns of community structure. Clare *et al.*

(2017) analysed data from station M1 of the Dove Time Series (1972–2012) to investigate the influence of changes in SST and primary productivity (a proxy for food availability) on benthic community structure. In general, large, long-lived fauna experienced changes in relative abundance concordant with changes in food availability. The authors suggest that increased detrital production allowed species that were food limited to increase in abundance and out compete species that had lower energy requirements leading to the observed changes (Clare *et al.,* 2017). They also found that small, generally shorter-lived fauna, experienced some changes in community structure related to changes in SST, but this effect was dampened as food availability increased (Clare *et al.,* 2017). The authors suggest that increased food availability nullified the effect of increased temperatures because there was sufficient food to meet the increased metabolic demands associated with increased temperatures. Pelagic primary production is under climatic influence (Behrenfeld *et al.,* 2006; Boyce *et al.,* 2010; Blanchard *et al.,* 2012), with some studies, at a global scale, suggesting increased SST will lead to reduced primary productivity (Behrenfeld *et al.,* 2006). At a regional scale the patterns are more complex, but for much of the British Isles, with the exception of the west coasts of Ireland and Scotland, a negative relationship between increasing SST and primary productivity has been observed (Dunstan *et al.,* 2018). Such a reduction in primary productivity with increased SST is therefore likely to lead to food shortages for smaller bodied infauna and increased community fluctuations. This study highlights that understanding the mechanisms leading to change can provide important predictive insights as well as demonstrating that other drivers of distribution and abundance can mask the impacts of increased ocean temperature.

Western English Channel
The western English Channel forms part of the boundary between cool boreal and warmer Lusitanian waters and has served as an important area to monitor the impacts of environmental change on marine organisms (see Southward *et al,.* 2005 for a review). There have, however, been few studies on the effects of climate change on subtidal benthic soft-sediment communities. One such study compared benthic communities sampled in 1958/59 with those sampled in 2006 and found no broadscale temporal differences related to warming, although four warm-water affinity species were detected in the later survey, but not in the earlier one (Hinz *et al.,* 2011). The authors suggest this could have been in response to climate warming (Hinz *et al.,* 2011).

More recently, Navarro-Barranco *et al.* (2017) investigated changes in amphipod assemblages between 2008–2014 at station L4, which forms part of the Western Channel Observatory (https://www.westernchannelobservatory.org.uk) and is one of the most well-studied marine areas in Europe. Amphipod abundance, richness and community structure were influenced by seasonal and year-to-year variability, however, increased SBT resulted in a significant increase in amphipod abundance and richness with this environmental driver accounting

for 57% and 23% of the variability in abundance and richness, respectfully (Navarro-Barranco *et al.,* 2017). The other environmental drivers examined (phytoplankton biomass and chlorophyll *a* concentration) had no significant influence on amphipod numbers, even though these drivers have been shown to be important in other coastal areas (Zhang *et al.,* 2015), suggesting food limitation is not driving amphipod dynamics in this system (Navarro-Barranco *et al.,* 2017). The authors highlight the potential for amphipods to be included as climate indicator species.

2.2 Hard-substrate

Canopy-forming algae

Although there are no regional or UK monitoring programmes of subtidal hard-substrate habitats there has been a considerable increase in the number of studies exploring the impacts of climate change on subtidal kelps and kelp forests since the last MCCIP review in 2013. These studies have included collation and analysis of existing data as well as the collection of new contemporary data. Much of this work has been regionally focused, particularly in south-west England, but some UK wide studies have also been conducted. Previous MCCIP Report Cards have noted a decrease in the abundance of *Alaria esculenta* around south-west England, near its southern range limit (Vance, 2004). Anecdotal observations of an increase in *Saccorhiza polyschides* intertidally (but see quantitative analysis below) have also been noted (Birchenough *et al.,* 2013).

UK overview

Yesson *et al.* (2015) collated and analysed data on changes in large UK brown algal abundance based on national and regional surveys, museum databases and literature searches that spanned the period 1974–2010. While the number of sites sampled and observations varied between species, some general trends were observed. At the UK scale, *Chorda filum*, *Laminaria ochroleuca*, *Saccharina latissima* all reduced in abundance, however, for the warm-water species, *L. ochroleuca,* this was not related to changes in temperature. Four kelp species showed significant relationships between abundance patterns and SST with *C. filum* abundance positively correlated with winter SST whereas *L. digitata*, *L. hyperborea* and *S. latissima* abundance was negatively correlated with winter SST. Interestingly for the cold-water species, *L. digitata* and *L. hyperborea,* abundance was positively correlated with summer SST. Abundance also varied across regions with a general pattern of relative stability or increased abundance through time in northern regions (Scotland, northern England) and a reduction in abundance in southern regions (south-west England; see regional sections, below). While this data provides a comprehensive review of regional changes in macroalgal abundance not all changes were related to SST and it should be noted that 74% of site level studies were based on just two time points with only 3% of sites having four

temporal observations for any species and therefore the data are better interpreted at a UK rather than regional scale. Moreover, many of the recent observations were based on intertidal data. Kelp species are considered subtidal, with a limited number of species exposed to air on low spring tides. Subtle changes in atmospheric pressure influence tidal ranges and therefore apparent changes in abundance could be a function of different tidal heights between sampling periods. Results for kelp species from this study should therefore be interpreted with some caution.

English Channel, Western English Channel and Celtic Sea

The warm-water species, *L. ochrolueca*, reaches its northern range limit in the Western English Channel Channel and Celtic Seas, while the cold-water species, *A. esculenta*, reaches its southern range limit in the same region with both species proposed as good indicators for climate-driven changes in abundance and distribution (Mieszkowska *et al.,* 2006; Smale *et al.,* 2014).

There has been an observed increase in the abundance of *L. ochroleuca* linked to increases in SST at sites around Plymouth, the Scilly's and Lundy, with this species becoming a significant member of the kelp assemblage and in some cases the species dominant (Plymouth and Isles of Scilly) (Smale *et al.,* 2014; Teagle and Smale 2018). In contrast, others have suggested an overall decline in this species at sites off Plymouth and the Scilly Isles, however, this decline was not linked to changes in summer or winter SST (Yesson *et al.,* 2015). The contradiction in results between these studies may be a product of the different methodologies used. Yesson *et al.* (2015) collated their data from a variety of sources including surveys undertaken intertidally. In contrast, Smale *et al.* (2014) and Teagle and Smale (2018) surveys were undertaken subtidally. While *L. ochroleuca* can be found in the low intertidal, generally below the *L. digitata* zone (King *et al.,* 2017b), this species is predominantly found subtidally and therefore intertidal surveys may not accurately capture changes in abundance (see above).

Declines in abundance were also noted for *S. polyschides* in the Western English Channel and Celtic Seas and *C. filum* and *L. hyperborea* in the English Channel (Yesson *et al.* 2015). While the decline in *S. polychides* was not related to changes in SST, at the UK scale, the declines in *L. hyperborea* and *C. filum* were correlated with SST (see above). In a comparison of *L. hyperborea* abundance between 1999 and 2013 there was no change noted at a single subtidal site off Plymouth (Smale *et al.,* 2014). Declines in the abundance of *A. esculenta* have been previously observed in this region (Vance, 2004), however, the more detailed study of (Yesson *et al.,* 2015) suggests a non-significant increasing trend in abundance unrelated to temperature for this species. While declines in the dominant intertidal/shallow subtidal kelp *L. digitata* have not been observed in the UK, declines have been observed along the Brittany, Normandy and French English-Channel coasts which have been linked to harvesting pressures as well as climate change (Raybaud *et al.,* 2013). Given that *L. digitata* found in south-

west England occupies the same temperature isotherm as French populations (King *et al.,* 2017b) it is highly likely that *L. digitata* abundance will decline in the western English Channel in the not too distant future (see Section 3.2).

Changes in subtidal macroalgal distribution have also been noted, with recent analysis comparing historical (1951–1999) and contemporary (2000–2013) data showing *L. ochroleuca* to have expanded its range from 32 to 60 recorded sites off Plymouth with this species expanding onto moderately-exposed coastlines where it had previously been absent (Smale *et al.,* 2014). These authors noted that this change in distribution has coincided with a period of rapid warming in the area (Smale *et al.* 2014).

In addition to increases in ocean temperatures, climate change is predicted to result in increased storm events. The North-East Atlantic storm season of 2013–14 was particularly severe with two 1-in-30 year events occurring. Smale and Vance (2015) investigated the impacts of these storms on monospecific kelp stands of *L. hyperborea* and mixed stands of *L. hyperborea*, *S. latissimi* and *L. ochroleuca*. They found no difference in *L. hyprborea* abundance before or after the storms. In contrast, there was a reduction in the abundance of *S. latissimi* and *L. ochroleuca* after the storm season, leading to an overall reduction in kelp abundance within mixed stands. *L. ochroleuca* is already expanding its range into more wave exposed sites (Smale *et al.* 2014) and there is evidence that this species is increasing in abundance in other locations. It is therefore likely that kelp forest resistance to storm disturbance will erode with increased storminess (Smale and Vance 2015).

Irish Sea
Significant increases in the in the abundance of *C. filum*, *L. hyperborea* and *S. polychides* have been observed, correlated to increases in summer and winter SST at the UK scale (Yesson *et al.,* 2015). At the regional scale, however, the drivers of change are difficult to determine with the quality of the data (see above).

Western Scotland
A. esculenta has increased in abundance over the last few decades in western Scotland, but this was not correlated with summer or winter SST (Yesson *et al.,* 2015).

North Sea
L. digitata has increased in abundance in the northern North Sea (Yesson *et al.,* 2015), which at the UK scale was linked to changes in summer and winter SST.

Subtidal invertebrates

Celtic Sea: Severn Estuary/ Bristol Channel
Long-term monitoring of crustacean populations based on standardised monthly sampling at Hinkley Point power station since the 1980s have demonstrated changes in the abundance of shrimps (*Crangon crangon*, *Pandalus montagui*, Pasiphaea sivado), prawns (*Palaemon serratus*), crabs (*Necora puber*, *Polybius henslowii*, *Carcinus maenas*) and mysids (*Schistomysis spiritus*, *Gastrosaccus spinifer*, *Mesodopsis slabberi*, *Neomysis integer*) (Henderson and Bird 2010; Henderson *et al.* 2011) as well as changes in breeding activity/ success of two mysid species (*M. slabberi*, *S. spiritus*) (Plenty, 2012). It has been suggested that these changes may be linked to climate warming (Birchenough *et al.,* 2013), however, quantitative evidence for climate mediated changes only exist for *P. montagui*, *P.serratus* and *C. crangon* (Henderson and Bird, 2010; Plenty, 2012). Other identified drivers include changes in North Atlantic Oscillation Index (NAOI) (e.g. *C. crangon*; Henderson *et al.,* 2011), density dependent control (e.g. *C. crangon*; Henderson *et al.,* 2006) and changes in salinity (e.g. *P. montagui*, *P. serratus*, *C. maenas*; Henderson *et al.,* 2011), while no climate drivers have been found to explain changes in the abundance of other species (e.g. *Pasiphaea sivado*; Henderson *et al.,* 2011).

More-recent analysis of the same data set spanning 1988–2013 has found that both mysid and caridean decapod richness and abundance has increased, however, this is unrelated to water temperature, salinity, NAOI or winter (Dec–Feb) NAOI, which, with the exception of NAOI, did not change over the time–series study period (Plenty *et al.,* 2018). This study also demonstrated a weak, but significant, change in community structure through time, which seemed to be strongly related to changes in abundance (Plenty *et al.,* 2018). Analysis suggests that this pattern of community change was not driven by water temperature, salinity, NAOI or winter NAOI. The authors state that the likely drivers of change are improved water quality over climate change (Plenty *et al*., 2018). This study highlights the importance of considering both climate and non-climate drivers of change and the difficulties in separating complex interacting stressors.

Northern Ireland
Goodwin *et al.* (2013) compared community structure and the presence/absence of species with warmer and cooler water affinities from before 1986 (surveys undertaken between 1982 and 1986) and post-2006 (surveys undertaken between 2006 and 2009) in three subtidal (>15m depth) mixed-sediment locations in Northern Ireland (Rathline Island, Skerries, Strangford Lough). They showed that benthic communities had changed at all three locations between the two time periods, however, most of these changes were driven by species at the centre of their biogeographical ranges, and therefore were unlikely to be in response to warming (Goodwin *et al.,* 2013). When the authors focused on changes in the frequency of occurrence

of species at their range margins they found little evidence for decreases in cold-water species, however, warm-water species increased at two of the three locations investigated (Skerries and Strangford Lough) with the authors linking these changes to rising SST (Goodwin *et al.,* 2013). Similar positive responses to warming have been experimentally demonstrated for epifaunal species from the United States at their northern range margin (Lord and Whitlatch, 2015). The authors also found changes in the spatial distribution of a number of species between the two time periods. Of 13 cold-water affinity species, seven reduced their distributional range (Table 1) while six showed no change or an unclear change. 19 warm-water affinity species increased their distribution, seven decreased (Table 1) and 18 showed no or an unclear change (Goodwin *et al.,* 2013). Other studies have also shown that leading edges are responding faster than trailing edges (Poloczanska *et al.,* 2013).

Table 1: Cold-water and warm-water affinity species that either increased or decreased their distribution between pre-1986 and post-2006 in three locations in Northern Island. (Based on data from Goodwin et al.*, 2013.)*

Cold-water decreasing	Warm-water increasing	Warm-water decreasing
Antedon petasus	*Archidistoma aggregatum*	*Diazona violacea*
Cuthona concinna	*Axinella damicornis*	*Galathea nexa**
Diphasia fallax	*Axinella dissimilis*	*Janolus hyalinus*
Ophiopholis aculeata	*Bugula turbinata*	*Onchidoris oblonga*
Leptasterias muelleri	*Caloria elegans*	*Palinurus elephas**
Solaster endeca	*Crimora papillata*	*Polycarpa gracillis*
Synoicum pulmonaria	*Doto maculata*	*Pyura microcosmus**
	Facelina annulicornis,	
	Hormathia coronata	
	Hexadella racovitzai	
	Liocarcinus corrugatus	
	Lomanotus genei	
	Maja brachydactyla	
	Megalomma vesiculosum	
	Okenia elegans	
	Parazoanthus axinellae	
	Pentapora fascialis var. *foliacea*	
	Phellia gausapata	
	Simnia patula	

* Goodwin *et al.* (2013) suggest that the decline in some warm-water species distributions was a function of fishing pressure and habitat destruction rather than changes in SST.

Cold-water corals, maerl beds, horse mussels

There continues to be a lack of direct evidence for the impacts of climate change for cold-water corals, maerl beds and horse mussel beds. However, this is likely to be due to a lack of dedicated monitoring programmes than the habitats not responding, as experimental work suggests that these species are

vulnerable to both warming and ocean acidification (Martin and Hall-Spencer, 2017; Gibson *et al.,* 2011), with recent modelling providing predictions on the effects of ocean acidification for cold-water corals (see below).

MCCIP report cards have recently been developed for all these habitats and can be found at http://www.mccip.org.uk/adaptation-action/climate-change-and-marine-conservation/

Synthesis

Our comprehensive review of the literature identified thirteen new studies published since the 2013 annual report on observations of species responses to climate change in UK shallow and shelf seas. On the whole, these showed that many species across ecosystems were responding to climate change, but this was not universal and in many cases was dependent on where the study was performed in relation to the species biogeographic range. A couple of studies found that leading edges were responding more quickly than trailing edges, which has also been observed at the global scale. In addition, a number of studies identified the interactive effects of other climate and non-climate stressors as well as the influence of life history traits on observed outcomes.

3. WHAT COULD HAPPEN IN THE FUTURE?

The 2013 MCCIP Annual Report Card primarily based predictions of future change on qualitative assessments of the drivers of change, including natural and anthropogenic causes, and how this was likely to alter species distributions. Since then, four studies using environmental niche models have been published providing predictions of species range shifts under different climate models and scenarios. This provides managers and policymakers with specific information to allow planning as well as providing a null model, which researchers can use to disentangle non-climate drivers and biotic interactions to help explain why species may not be tracking these models precisely.

3.1 Soft-sediment benthos

Infaunal and epifaunal species, collected from three North Sea data sets spanning 1999–2004, were chosen based on (1) being characteristic of at least one North Sea community; (2) high abundance; or (3) having an important role as an ecosystem engineer (Weinert *et al.,* 2016). An Ecological Niche Model (ENM) based on IPCC SRES scenario A1B climate model (Nakicenovic and Swart, 2000; mean 2.8°C; range 1.7–4.4°C) was then used to predict the 2099 distribution of the 75 chosen species. The model predicted bottom temperature increases of 0.15–5.4°C across the North Sea with an increase in salinity of 1.7 in the northern North Sea and off the Dutch and

Belgian coasts. For 18 (50%) of 36 epifaunal species the ENM predicted a northward range shift with the brittle star, *Ophiothrix fragilis*, predicted to shift up to 109 km, and 65% of all epifaunal species investigated were predicted to shift their range between 10 and 50 km. A further 18 (50%) epifaunal species were predicted to shift southwards with 16 of the18 species shifting in a south-easterly direction. The hermit crab, *Pagurus prideaux* and its associated cloak anemone, *Adamsia carciniopados* were predicted to shift southwards by 105 km, with 50% of all species predicted to shift 10–50 km. A greater number of infaunal species are expected to shift their distribution in a more-expected northward direction (77%). Shifts of 60 km or more were predicted for the bivalves *Nucula nitidosa* (60 km) and *Ennucula tenuis* (76 km), the brittle star *Acrocnida brachiata* (60 km), the amphipod *Harpinia antennaria* (75 km) and the mollusc *Chaetoderma nitidulum* (88 km). Overall, 60% of species were predicted to shift ranges by 10–50 km towards the north. Only 9% of infaunal species were predicted to shift range towards the south (Weinert *et al.,* 2016). The potentially unexpected southward shifts, particularly for epifauna, may be a consequence of regional conditions and other interacting affects (Junker *et al.,* 2012; VanDerWal *et al.,* 2012) as well as a key habitat barrier in the North Sea being the 50 m contour separating the shallow southern North Sea with the deeper northern North Sea. That may act as a barrier to northward extension of some species (Weinert *et al.,* 2016)

In terms of changes in habitat space, 58% of epifauna and 72% of infauna were predicted to see a reduction in the availability of suitable habitat, while 38% of epifauna and 2% of infauna were expected to experience range expansion. Greater habitat loss was predicted for northward-shifting species due to an environmental barrier along the 50 m contour separating the shallower southern with the deeper northern North Sea, with a number of characteristic species and some ecosystem engineers being at particular risk (Weinert *et al.,* 2016). Changes in community structure could alter ecosystem functioning and trophodynamics of North Sea benthic habitats. In turn this may impact important ecosystem services, e.g. biogeochemical processes, nutrient cycling, water quality, fisheries. For example, predicted loss of ecosystem engineers such as the burrowing shrimp *Callianassa subterranea* and the sea urchin *Brissopsis lyrifera* could alter community structure and ecosystem functioning (Weinert *et al.,* 2016). At the same time, changes in the distribution and abundance of benthic communities may alter trophodynamics and competition (Kirby *et al.,* 2007). However, such ecosystem-level responses will depend on the species involved, with some studies suggesting ecosystem functioning and service provision remaining stable over long periods of time (Clare *et al.,* 2015; Frid and Caswell, 2015).

3.2 Canopy-forming algae

A number of recent studies have used Ecological Niche Models (ENMs) to provide predictions of changes in the abundance and distribution of European kelp species to future warming. Raybaud *et al.* (2013) used two climate

models (CNRM-CM5 and MPI-ESM-LR) and three Representative Concentration Pathways (RCP: 2.6, 4.5, 8.5 – see Table 2 for an explanation of these RCPs and predicted temperature changes) to calculate the average probability of occurrence of *L. digitata*. Depending on the magnitude of warming their models suggest that by 2020 there will be a reduction in the abundance of *L. digitata* across much of southern and central England and Wales (English Channel, Western English Channel, Celtic Seas and Irish Sea) with 50 to100% of their model runs predicting loss of this species in parts of these regions by 2050. By 2050 it is likely that Scottish populations will also have experienced a reduction in abundance, however, this species is likely to persist in Scotland beyond the end of the century (Raybaud *et al.,* 2013). Another study using ENMs based on two climate models (AOGCM and MIROC5) and two climate change scenarios (RCP2.6 and 8.5) predicted by 2090–2100 that the warm-water kelp *L. ochroleuca*, currently limited to south-west England, would remain stable in its current range, but expand through south-west England and Wales under RCP 2.6 and throughout the entire UK where suitable habitat exists (i.e. southern and south-west England, Wales, Northern Ireland and western and northern Scotland, including the Orkney and Shetland Islands) under RCP8.5 (Assis *et al.,* 2018). In contrast, *L. hyperborea* and *A. esculenta* would be lost from southern England and Wales under RCP8.5, but persist in these regions under RCP2.6 (Assis *et al.,* 2018). Under RCP 8.5, loses of *S. latissima* and *L. digitata* are predicted in south-west England by 2090–2100, but these species remain stable throughout the rest of the UK (Assis *et al.,* 2018). The predicted range contraction for *L. digitata* is slightly more conservative than that reported by Raybaud *et al.* (2013) and is likely a result of different methodologies, climatic predictors and climate models used. Assis *et al.* (2018) also suggested that *S. polychides* populations would remain stable in the UK.

Table 2: IPCC Assessment Report AR5 projections of global warming (°C) (Stocker et al, 2013.)

Scenario	2046–2065 Mean and likely range	2081–2100 Mean and likely range
RCP2.6 (emissions peak 2010-2020 and then drop)	1.0 (0.4–1.6)	1.0 (0.3–1.7)
RCP4.5 (emissions peak 2040 and then drop)	1.4 (0.9–2.0)	1.8 (1.1–2.6)
RCP8.5 (emissions rise throughout 21st century)	2.0 (1.4–2.6)	3.7 (2.6–4.8)

It is important to note that while ENMs have provided accurate predictions of species current distributional range (Raybaud *et al.,* 2013; Assis *et al.,* 2018), they do not take into account biotic interactions (e.g. competition, predation, facilitation) which have been shown to mediate species responses to climate change and may change in the future. In addition, ENMs generally assume that species have similar thermal tolerances throughout the species range.

Recent analysis suggests that this is unlikely to be the case, especially for macroalgae that have limited dispersal ability, meaning that local thermal adaptation is common (King *et al.,* 2017a). This might mean that species at the centre of their range may be equally susceptible to relative increases in temperature as those at their trailing (equatorward) range edge (King *et al.* 2017a). More work has to be done to investigate the prevalence of local thermal adaptation to ensure predicted range shifts using ENMs are as accurate as possible.

Kelps are considered ecosystem engineers providing habitat and food which supports highly diverse communities, including species of commercial importance (Smale *et al.* 2013; Wernberg *et al.* 2018). Changes in the relative abundance or distribution of different kelp species may, therefore, have knock-on effects for the wider community. While superficially similar, recent research has demonstrated that stipes of the cold-water species dominant, *L. hyperborea* support 12 times as many sessile taxa (flora and fauna) and over 3600 times as much epibiota biomass as the warm water species, *L. ochroleuca* (Teagle and Smale, 2018). This was primarily due to 55% of *L. ochroleuca* stipes being completely devoid of any epiphytic material whereas there were no *L. hyperborea* stipes devoid of epiphytes (Teagle and Smale, 2018). Epiphytes provide food and shelter for a diverse assemblage of epifaunal species with in excess of 60 species and 55,000 individuals found on *L. hyperborea* stipes in Norway (Christie *et al.,* 2003). Teagle and Smale (2018) also showed that holdfast communities differed between these species, though to a lesser extent than the stipes, supporting previous research which compared *L. ochorleuca* holdfast communities with the colder-water species *L. digitata* (Blight and Thompson 2008). Few organisms directly consume live kelp in the UK, however kelp detrital material is consumed by a range of organisms both within and outside kelp forests. Of those species that do directly graze kelp it has been found that higher densities are associated with the warm water species compared to *L. hyperborea* and in feeding trials *L. ochroleuca* is preferentially consumed (Pessarrodona *et al.,* 2018). These authors have also shown that *L. ochroleuca* accumulated and released 80% more biomass than *L. hyperborea*, with this occurring throughout the year rather than being primarily limited to specific seasons in the cold-water species. Moreover, *L. ochroleuca* detrital material broke down over six times faster than the cold water species (Pessarrodona *et al.,* 2018). Collectively these results suggest that climate mediated changes in kelp identity may result in wide scale ecological change that has implications for higher order consumers such as crustaceans and finfish and therefore fisheries and society.

3.3 Cold water corals

The scleractinian cold-water coral, *Lophelia pertusa*, forms deep-water reefs which act as a habitat supporting a rich diversity of associated species including species of commercial importance (Biber *et al.,* 2014). The majority of *L. pertusa* reefs are concentrated in the North Atlantic, and in a UK context

off the coasts of Northern Ireland, western and northern Scotland (Jackson *et al.,* 2014). While damage to reefs by commercial fishing practices remains and is predicted to continue to be the key threat to cold water corals, they may also be particularly susceptible to climate change. As a result of ocean acidification the Aragonite Saturation Horizon (ASH) is expected to become shallower resulting in cold-water corals, particularly reefs formed by dead coral skeletons, experiencing ocean chemistry conditions leading to dissolution of coral skeletons. Jackson *et al.* (2014) modelled ASH under four climate change scenarios (IS92a 'business as usual', IPCC SRES emission scenarios A2 and B1 and a SRES A2 No-Warming simulation [NW]) for the years 2020, 2040, 2060, 2080 and 2099. They found under A2 and B1 scenarios ASH is unlikely to reach the UK Exclusive Economic Zone (EEZ) prior to 2040, while IS92a predicted that ASH shoaling would incorporate a small proportion of reefs (<0.01%) by 2020, 0.6% by 2040 and 88% by 2060 (Jackson *et al.,* 2014). By 2060, under the A2 scenario, 15% of reefs would be in undersaturated areas with this increasing to 39% by 2080. While ASH had not reached reefs by 2020 under NW, 13%, 23% and 76% of reefs would be in areas of aragonite under-saturation by 2040, 2060 and 2080, respectfully. Interestingly, the interaction between fishing pressure and aragonite under-saturation is predicted to lead to reef loss of 1% by 2040 under NW, increasing to 3% by 2060, while under A2 2% of reefs are predicted to be lost by 2060. Models do, however, suggest that while extensive areas will be undersaturated, 47 and 15% of live reef may persist by 2080 under A2 and NW, respectfully. Moreover, shallower reefs are likely to remain above ASH and if under some form of conservation protection may be relatively unaffected by ocean acidification (Jackson *et al.,* 2014). The authors highlight the need to protect areas of reef from fishing pressures that may be above the ASH in the future, but also highlight that there is still little understanding of the true extent of cold-water corals in the UK EEZ, that fishing impacts are poorly monitored and there is little understanding of the impacts of multiple stressors on this system (Jackson *et al.,* 2014).

3.4 Maerl beds

Maerl beds are made up of living and dead calcareous red algae and support high levels of diversity (see recent Maerl Beds MCCIP Report Card http://www.mccip.org.uk/media/1812/mccip-maerl-report-card_second_run-v3.pdf). Maerl beds are considered to be particularly susceptible to changes in ocean carbonate chemistry, with experiments demonstrating reduced growth rates and structural integrity after ecologically realistic long-term (20 months) exposure to predicted carbonate chemistry conditions (Sordo *et al.,* 2018). Increases in SST/SBT are also likely to impact maerl beds as the development of reproductive conceptacles and growth optimally occur at lower temperatures (Martin and Hall-Spencer, 2017) than those predicted for UK waters into the future.

4. CONFIDENCE ASSESSMENT

What is already happening?
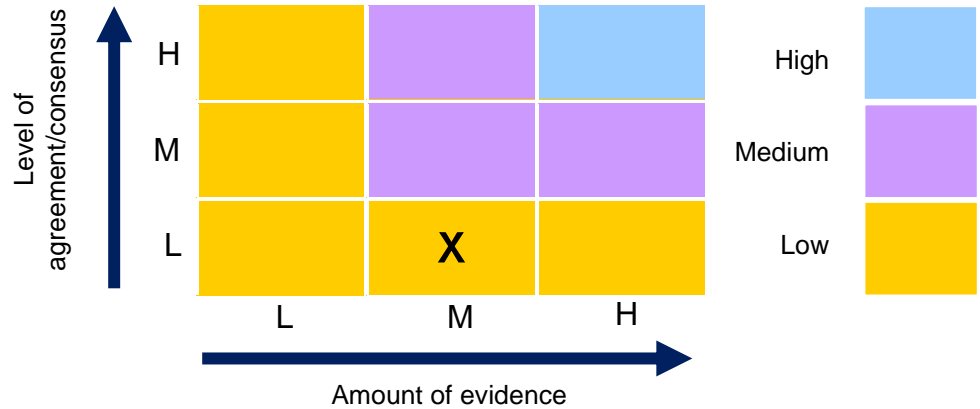
What could happen in the future?
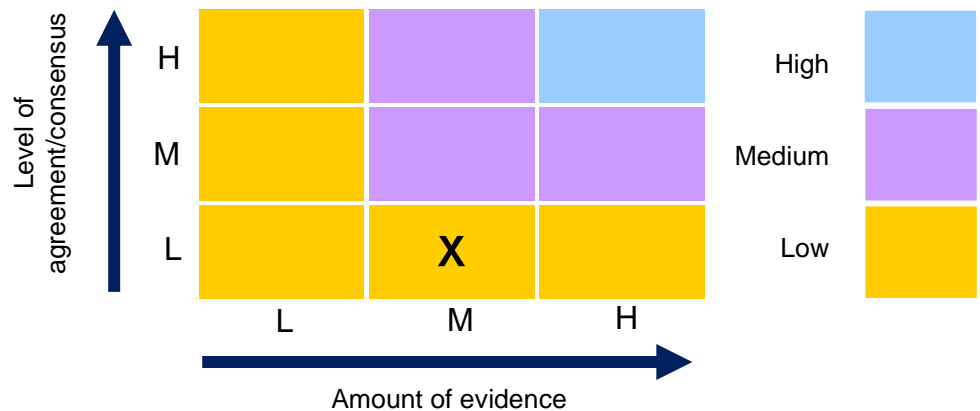
While there has been a substantial increase in the number of studies investigating the impacts of climate change in the UK's shallow and shelf seas since the last relevant MCCIP Report Card in 2013, we would suggest that this is for a limited number of species and over a limited spatial scale. For example, there is strong evidence that some species of kelp are responding to changes in temperature, but we know little about how this is affecting the large number of species reliant on kelp forests for habitat and food. We are also increasingly confident of the drivers of change in infaunal communities associated with a single long-term monitoring site in the North Sea, but have much less knowledge regarding the rest of the North Sea and other regions of the UK. For this reason, we assess that the observational evidence has increased from Low to Medium since the last review, but the level of consensus remains low.

ENMs are becoming increasingly sophisticated and estimate current species distributions with some confidence, but again these are limited to a small number of taxa. In addition, such models do not take into account interacting stressors or changes in biotic interactions that may occur in response to climate change. We therefore suggest that the evidence from models has moved from Low to Medium since the last review, but the level of consensus is still low due to the limited number of taxa investigated and the range of interacting factors that are not included in ENMs.

5. KEY CHALLENGES AND EMERGING ISSUES

Key challenges

1. Few of the studies presented here are based on long-term time–series data with most studies comparing two time periods which reduces the strength of the inferences that can be made as it is impossible to separate year-to-year variability in population dynamics from the climate signature. It is therefore vital that monitoring programmes are put in place to characterise year-to-year variability in population dynamics, identify change to ensure healthy and diverse seas now, and into the future.
2. A number of taxa highlighted in this review provide habitat and food for a diverse community of associated taxa and as such are considered ecosystem engineers (e.g. kelp forests, cold-water corals, maerl beds). While we are seeing changes in the structure of some of these habitats we have much less of an understanding of the implications of this for the functioning of these systems and for the goods and services these habitats provide human society. While it is important to describe changes in the abundance and distribution of these habitat formers it is also important to move beyond this to begin to understand the consequences of these changes to the wider community. Where such studies are occurring, substantial differences in structure and functioning are being observed (e.g. Pessarrodona *et al.,* 2018; Teagle and Smale, 2018).
3. Most of the systems examined here are subject to multiple climate and non-climate stressors. As seen above, long-term data series and more-sophisticated analyses can facilitate separation of different stressors, but for most species and ecosystems this is still a challenge especially as for many species and ecosystems existing baselines are still not fully elucidated, e.g. cold-water corals. It is therefore important to understand the various drivers of change which likely requires complementary approaches, including long-term monitoring, experimental studies allowing the elucidation of cause-and-effect as well as modelling of studies that incorporate a broad range of potential drivers so the relative importance of particular drivers can be determined.

Emerging Challenges

1. There is strong observational and empirical evidence that multiple stressors reduce the resistance and resilience of natural systems. As a global stressor, climate change is impossible to manage at a regional scale. From a policy perspective, difficult and cross-sectoral decisions will need to be made on how to manage our seas to increase their resilience in the face of these multiple stressors. For examples, policies on water quality, and managing invasive species, may make communities more resilient to climate change.

2. To date, most focus has been on decadal scale climate change for which climate-change predictions are relatively robust. Since that last review it has become increasingly apparent that extreme events such as increased storminess and marine heatwaves may play a disproportionate role in altering species abundances and ranges as well as driving local extinctions (Wernberg *et al.,* 2016; Smale *et al.,* 2019). The scale and impact of these stochastic events are hard to predict, which will make policy decisions difficult.

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