

Climate Change Impacts on Fish of Relevance to the UK and Ireland

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KEY FACTS

What is already happening?

- Increases in warm-water fish species in UK waters continue to be observed, along with local declines of some cold-affinity species.
- Research continues to support the hypothesis that temperature changes are affecting fish growth and age at maturation in UK waters.
- New experimental studies have shown that fin-fish larvae may be sensitive to changes in ocean acidification, but different species have shown a variety of responses.
- Several species of cephalopods have shown noticeable increases in abundance and geographical spread in UK waters, a change consistent with warming waters.
- Recent evidence supports the hypothesis that reproductive success in Atlantic cod is negatively impacted at temperatures above 9.6°C.

What could happen in the future?

- Ocean temperatures are expected to continue to rise and will affect species composition and abundances, particularly in shallower areas such as the southern North Sea.
- Shifts in food-webs may occur due to changes in species composition and abundances affecting predator-prey relationships.
- For important commercial species, such as cod, areas such as the northern North Sea will remain suitable habitat throughout the coming century but more southern areas will become less suitable.
- Such sub-regional effects will need to be taken into account in fisheries management plans and advice, and this may require changes in the spatial scales at which data are collected, reported and analysed in the coming decades.

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- By end of century, conditions could become favourable for warm-water species such as Mediterranean horse mackerel and bogue as far north as the middle of the Irish and North Seas.
- Experiments have suggested that effects from ocean acidification and oxygen depletion could lead to stress in some species under conditions expected by end of century but impacts on wild fish populations are hard to predict as only a limited range of species have been studied so far.

SUPPORTING EVIDENCE

What is already happening?

This MCCIP update reviews new research evidence and material on climate impacts on marine fish not covered by Wright *et al.* (2020). The main sources of evidence are studies conducted on species found in UK and Irish waters, although we occasionally draw on results from further afield where they concern species found in UK waters.

Globally, ocean surface waters have warmed by approximately 1.3°C over the past 100 years which affects other important physical characteristics such as oxygen solubility and pH. Oxygen solubility at sea level decreases by about 0.16 mg litre⁻¹ per 1°C increase and surface marine waters are now more acidic, by around 0.1 pH units lower than 250 years ago (Bindoff *et al.*, 2019). Future trajectories in these characteristics will be heavily dependent on global efforts to restrict greenhouse gas emissions. Although changes in average values in these physical characteristics are often quoted, it must be appreciated that there are large spatial and temporal variations comparing different regions, between coastal and oceanic waters and comparing different seasons. Seawater chemistry is also strongly influenced by biological activity leading to modifications in local oxygen levels and pH (Cartensen and Duarte, 2019). Whether a particular species will be negatively or positively affected by environmental changes will depend on a large array of factors including individual species responses, possible adaptation through behavioural or physiological modification, and interactions with diseases, parasites, food webs and other habitat alterations related to climate change.

Except for some fish such as tuna and some species of shark, most fish are strict ectotherms, with their internal body temperature reflecting ambient conditions. External water temperature together with effects on oxygen solubility thus affects metabolic, body growth and maturation rates. These dependencies can, in turn, have knock-on consequences for reproductive success including spawning times and the chances of early life stages to encounter favourable prey. Fish may respond to changes in environmental conditions by physically moving and this can lead to geographical range shifts. However, similar apparent effects can arise through differential reproductive success leading to an increase and decline in the population at different locations. Such effects may operate most strongly at the northern

and southern edges of the range. Furthermore, temperature is not fully determinative given the additional effects of habitat preferences, food availability and species interactions. In this respect, temperature impacts on certain physiological responses can be considered as well-established and to a degree predictable at the individual level. Population-level ecological and distributional responses to temperature are detectable but other factors will also be influential.

The impacts of climate change on fish in UK waters were last reviewed for MCCIP in 2020 (Wright *et al.*, 2020). That review focussed on effects of warming on distribution, phenology and recruitment and provided an authoritative summary of knowledge using a wide range of available literature. It drew the following conclusions:

- The synchrony between winter–spring hatching fish larvae (e.g. cod, sole, sandeel) and their plankton prey appeared to be changing, with consequences for recruitment. These changes reflected both changes in the timing of fish reproduction as well as that of their plankton prey.
- Spawning locations for some pelagic species such as mackerel have changed, and this is possibly linked to climate but transport to suitable nursery habitats is also a factor. Some species such as herring have specific spawning substrate requirements whilst spawning locations for demersal species such as cod appear more consistent over time and may be linked to seascape features (but see the following point).
- Apparent range shifts in adults may not necessarily be linked to active movements of post-juvenile or adult fish but can also result from changing recruitment success linked to changing environmental conditions at geographical range edges.
- Fin-fish larvae may be sensitive to expected changes in ocean acidification, but species have shown a variety of responses in experiments.

Ocean acidification is one area of climate change where there has been more recent research so this update includes a separate section on this topic. Generally, we have not repeated references cited in Wright *et al.* (2020) although there will inevitably be some overlap with the recently published MCCIP Review of Climate Change Impacts on Fisheries (Pinnegar *et al.*, 2023). The collected MCCIP studies on both fish and fisheries were considered in combination when undertaking the confidence assessment.

Reproduction

Since the 2020 review of fish biology (Wright *et al.*, 2020), knowledge of the impacts of warming on fish reproduction has become more firmly established. A comprehensive literature review by Alix *et al.* (2020) has summarised how every stage of fish reproduction, from maturation through

to spawning, is negatively impacted by warmer-than-optimal temperatures for a particular species. In female fish, delay or complete inhibition of final oocyte maturation and ovulation appears to be caused by thermal inhibition of physiological processes in the brain, pituitary and/or the ovary. Higher-than-optimal temperatures also negatively impact a range of parameters related to egg quality (Table 2 in Alix *et al.*, 2020). Applying these generic insights to the community of warm and cold temperate fish in UK waters suggests that species and stocks that are near or at their thermal maximum will be more at risk of reproductive failure as temperatures exceed that level.

Fish have specific tolerances for temperature that change throughout their life with the narrowest windows of thermal tolerance being for spawning fish (for successful reproduction) and their embryos (for successful development). Spawners and embryos can therefore be considered as ‘thermal bottleneck’ stages (Dahlke *et al.*, 2020; 2022). Much research relevant to UK waters has focussed on Atlantic cod (*Gadus morhua*) which spawn at temperatures between 0°C in the Labrador Sea to c. 6–9°C in the Irish and Celtic Seas. Experimental tracking of spawning behaviour and reproductive success in individual Atlantic cod females showed that the ovulation cycle, specifically the spawning frequency or interval between batches, becomes more erratic when temperatures exceed 9.6° C (Kjesbu *et al.*, 2022). This temperature may therefore present an upper threshold beyond which normal spawning of cod will be impaired. Based on temperature projections through to 2060, Kjesbu *et al.* (2022) postulated that the spawning of cod in the Celtic Sea and English Channel would not be viable in future and that cod spawning in the Irish Sea would be at risk.

Shifts in the timing of cyclic and seasonal events (phenology) are a well-studied response to climate change observable in both terrestrial and aquatic species. Detecting changes in the timing of seasonal events over decadal scales requires datasets having a high degree of intra- and inter-annual temporal resolution. Several studies are cited in Wright *et al.* (2020) where population-level data, collected through routine monitoring of commercial catches, were used to describe temporal trends in peak spawning time but we are not aware of more recent published research for species found in UK waters.

Recruitment and climate

In fisheries science, recruitment refers to the number of fish surviving to a certain age. Stock assessments often estimate this number at the end of year 1 or 2 so the recruitment processes occur during the one or two years of life and include the egg, larval and juvenile life stages. Research into the population dynamics of many fish species has often indicated a critical role for early life stage survival. This is a result of the high mortality experienced by many fish species during their early life stages where small changes in mortality rates can produce large changes in the resulting numbers of juveniles. Some species, such as haddock (*Melanogrammus aeglefinus*), seem to have particularly high interannual variability with the

appearance of occasional very large year-classes (Dickey-Collas *et al.*, 2003). Numerous studies have attempted to relate these interannual fluctuations to environmental conditions during the egg, larval and early juvenile stages, and in some cases there do appear to be reasonably consistent correlations.

When taken across years, the interannual fluctuations yield an averaged recruitment which is used to predict how the stock may develop in response to different levels of fishing pressure in the short- to medium-term. However, interannual recruitment fluctuations may not be completely random and often have some temporal structure. This structure can be self-generated because of internal population dynamics or related to external factors. Thus, stocks can go through periods of higher and lower than average productivity, i.e. the stock may exhibit runs of better than average or poorer than average year-class strength (Kjesbu *et al.*, 2022). These shifts can be dealt with by adjusting fishing mortality to try to ensure that the stock does not decline to a level where averaged recruitment is substantially impacted.

However, in relation to climate change, it is the medium- to longer-term trends in year-class strength which are most important. If a species early life mortality is negatively affected by climate related factors, such as higher temperatures, lower pH or changes in ocean circulation, the population will inevitably decline over time assuming levels of mortality on later stages remain constant. If the species is commercially important management can respond by reducing fishing mortality which may prolong the time that the population can persist under changing conditions (Clark *et al.*, 2003). Achieving this is particularly challenging in the context of mixed fisheries where efforts to conserve one species, such as cod, inevitably constrains fishing on other more abundant species. If a species is particularly sensitive to changes in the environment, then it may fail to recover or even continue to decline, even if effective limitations on fishing mortality are applied (Bentley *et al.*, 2020). Conversely, for other species early life stage survival may improve and, providing there is sufficient prey for later stages, their populations will increase. Finally, for many commercial species, fishing mortality has been reduced over the last decade or so and positive signs of stock rebuilding are being seen. Increases in both stock size and range expansion may thus be a result of effective fisheries management, and not necessarily linked to environmental changes (Baudron and Fernandes, 2014).

Because of their commercial and ecosystem importance, and preference for cooler waters, cod (*Gadus morhua*) have been the subject of many studies on climate change impacts around the UK where a general pattern of reduced recruitment in warmer years has been observed (Wright *et al.*, 2020) but more recent studies have investigated whether different sub-stocks within areas like the North Sea have shown differential responses. Núñez-Riboni *et al.* (2019) re-analysed cod records from the International Bottom Trawl survey and showed that the southern North Sea habitat has become progressively less suitable for juvenile and older cod, while

conditions in the northern North Sea have improved – a change the authors largely attributed to warming and one they projected to strengthen further under future climate change. The authors went on to discuss that the most likely underlying mechanism would be spatially differential recruitment success.

Romagnoni *et al.* (2020) presented a coupled physical-biological model for cod eggs and larvae in the North Sea. Egg and larval growth rates were assumed to be temperature related. Using the model to explore the possible effects of differences in drift from spawning in different parts of the North Sea showed that there could be lower levels of retention (defined as late-stage larvae successfully reaching known nursery areas) for the Viking (northern North Sea) compared to southern and northwestern sub-stocks. Adding a retention index to sub-stock stock-recruitment models which also included SST did explain a small additional component of the resulting recruitment, but comparing between the sub-stocks suggested transport was of less importance for the southern sub-stock. They concluded that future cod recruitment success in the North Sea may not only be affected by temperature dependent larval growth and mortality, but also by changes in water circulation and that the relative importance of direct and indirect effects on survival from larval to juvenile stages varies between the sub-stocks.

Bentley *et al.* (2020) used an Ecopath model (2020) to explore how the Irish Sea food web may have been affected by environmental factors as well as fishing pressure. The better fitting models included environmental drivers (such as primary productivity anomaly, the Atlantic Multidecadal Oscillation (AMO), sea temperature, zooplankton abundances) suggesting that it may be important to include environmental drivers when formulating stock management and rebuilding strategies. Although climate projections were not undertaken, the best fitting model included negative relationships between the AMO and cod and whiting recruitment success. Thus, both these species in the Irish Sea may be expected to struggle to produce larger than average year-classes in a warming climate, a conclusion in line with other studies cited in Wright *et al.* (2020) and this update.

At a larger spatial scale, Kjesbu *et al.* (2022) suggested that different temperature related mechanisms might be operating in different parts of the species range. In addition to the disruption of spawning above 9.6 °C described above, the abundance of *Calanus finmarchicus*, a key prey for larval cod, in the northern North Sea and *Para/Pseudocalanus*, which is more prevalent in the southern North Sea, has continued to decline. This continues a trend noted by Beaugrand *et al.* (2003) who suggested declining abundance of these prey could be negatively affecting the growth and survival of cod larvae.

Squid were not included in the review of Wright *et al.* (2020) as they are not fish but belong to the group of cephalopod molluscs. However, they have shown marked increased abundances between 1980 and 2014 in the southern North Sea (van der Kooij *et al.*, 2016). Statistically highly

significant relationships were found between catch rates and sea surface temperatures for all of the three taxa considered. The authors attributed the strength of these correlations to the short life cycle of these species and suggested that squid will be one of the groups likely to benefit from climate change. Oesterwind *et al.* (2020) also reported large increases in squid catch rates in trawl samples since 2010, with increases also in more northern parts of the North Sea in recent years. Furthermore, mature and spent *Illex coindetii* were recorded in some samples suggesting that this species is now breeding in this area.

Growth

The temperature–size rule (TSR) postulates that ectotherms living in warmer conditions grow faster as juveniles but attain a smaller adult body size relative to individuals occupying cooler conditions. Empirical support for the TSR comes from the long-term monitoring of size-at-age for commercial fish species and the implications of the TSR for fisheries productivity and community structure have been noted. The physiological mechanisms underpinning the TSR continue to be debated (Pauly, 2021; Wootton *et al.*, 2022) but none of the proposed explanations cover the full range of empirically observed body size responses to temperature (Verberk *et al.*, 2021). The TSR predicts faster juvenile growth rates at higher temperatures, i.e. the reverse of adult body sizes. Using research vessel survey data for four commercial species from the west coast of Scotland and North Sea Ikpewe *et al.* (2020) found that the mean length of juveniles (age 1 year; a proxy for juvenile growth rate represented by k in the von Bertalanffy growth model) was positively and significantly correlated with temperature. This suggests that these species have a faster juvenile growth rate, consistent with the TSR. However, the magnitude of growth responses to future warming is difficult to predict as realised growth will be impacted by other ecological and evolutionary factors.

Ocean Acidification

Links between ocean acidification and effects on marine fish is still a relatively new area of research with nearly all publications appearing in the last 15 years. Experiments have been conducted under laboratory settings but at present there are no major observational efforts to monitor effects of ocean acidification on fish stocks around the UK. The term ‘ocean acidification’ can be misleading when used in the context of fish, since the reduction in pH is not the main stressor, but rather the increased partial pressure of CO₂ ($p\text{CO}_2$ – called ‘hypercapnia’) (Esbaugh, 2017). Although changes in spatially averaged ocean acidification are often quoted (Bindoff *et al.*, 2019) there is substantial geographic variation. High latitude/cold waters acidify faster because of increased solubility of CO₂ with decreasing temperatures. Seawater carbonate chemistry is strongly affected by biological processes including primary production and the decay of organic matter. Thus, for all but very shallow well-mixed waters pH varies with depth as deep waters are dominated by organic matter decomposition rather than primary production. Seasonal changes are often due to phytoplankton

blooms, which reduce the carbon dioxide in the water, but can be followed by increased decomposition raising dissolved CO₂ again. Coastal areas can also experience periods of higher-than-average acidification due to upwelling of low pH deep water (Cartensen and Duarte, 2019).

Adult fish have the capacity to regulate osmotic pressure and internal CO₂ concentrations through active excretion of dissolved CO₂ across the gill membranes. They can therefore tolerate high levels of hypercapnia in the environment even over prolonged periods of time, though this comes at an energetic cost (Melzner *et al.*, 2009). Additionally, juvenile and adult fish are mobile and can generally often escape particularly unfavorable conditions, such as coastal or even estuarine areas by moving further offshore. On the other hand, early life stages of fish are often found in particularly high CO₂ environments, such as coastal or estuarine regions. Furthermore, they have underdeveloped mechanisms to regulate internal conditions as the body surface is semi-permeable and the gills are still developing. These features are thought to make larval stages of fish more vulnerable to the external environment compared with post-larvae.

It is becoming clear that vulnerabilities to hypercapnia differ greatly between life stages, but it may also differ between species and potentially even stocks. Several laboratory studies have shown negative effects of hypercapnia on early life stages of Atlantic cod, including reduced survival (Stiasny *et al.*, 2016), and negative effects on organ development and growth (Frommel *et al.*, 2012; Stiasny *et al.*, 2018; Stiasny *et al.*, 2019). When such effects were incorporated into population dynamics models the results suggested that future recruitment might be reduced by between 8 and 24% (Stiasny *et al.*, 2016). In contrast, other studies on temperate fish have reported either no effect of hypercapnia on reproductive traits, that there is an interaction with temperature (Lopes *et al.*, 2020; Concannon *et al.*, 2021) or even a positive effect (Faria *et al.*, 2018). However, these studies have not been repeated on species found around the British Isles. Additionally, Sswat *et al.* (2018) showed in a mesocosm study that hypercapnia can stimulate primary production which led to an increase in herring larval survival. Other laboratory studies have suggested that herring larvae are not strongly affected by increased dissolved CO₂ but they were negatively impacted by elevated temperatures (Sswat *et al.*, 2018). A similar fertilization effect was found for temperate rocky reef CO₂ vents (Nagelkerken *et al.*, 2021). The increased primary production appeared to benefit some species of fish living in the vicinity with the relative benefits being linked to species life-history and behavioral characteristics. It is currently unknown why sensitivities to hypercapnia differ between early life stages of different species.

There is also a reciprocal balance between the quantities of oxygen and CO₂ dissolved in seawater. Under low oxygen conditions (hypoxia), the concentration of dissolved CO₂ increases. Montgomery *et al.* (2019) studied the effect of this on juvenile sea bass (*Dicentrarchus labrax*) subjected to short-term hypoxia. Under increased dissolved CO₂ there was evidence that the fish developed an enhanced tolerance to hypoxia through changes in the

oxygen binding capacity of their haemoglobin. However, the authors pointed to several studies on other species in the literature which showed contrasting results.

In conclusion, rapid changes in seawater carbonate were initially thought to have minimal impacts on fish physiology due to their ability to regulate the balance of acid-to-base but recent research has identified potential impacts on early development (Stiasny *et al.*, 2019, Villalobos *et al.*, 2020, Baumann *et al.*, 2022), sensory performance (Williams *et al.*, 2019) and reproduction (Servili *et al.*, 2020). The impacts of ocean acidification on fish behaviour are more controversial (Clements *et al.*, 2022) but there is some evidence that ocean acidification can compromise the ability of fish to withstand acute stress (Servili *et al.*, 2023). Across studies, the effects of the interaction between dissolved oxygen and CO₂ have been inconsistent which could reflect differences between species. In summary, it is still impossible to generalize what the effects of ocean acidification and hypercapnia will be on fish found in UK waters as most species lack experimental data.

What could happen in the future?

Responses of fish populations to future warming: Emphasis on projections of fish distribution; reproduction and recruitment

Over the last decades, species distribution modelling has been used to produce scenarios of future geographical distribution for use in management and conservation advice. There are rather few studies forecasting changes in spawning habitat suitability of small pelagic fish, but the suitability of European sardine (*Sardina pichardus*) seasonal spawning habitats has been projected under the RCP8.5 climate change scenario by Lima *et al.* (2022). They found there could be a negative relationship between phytoplankton productivity and coastal habitat suitability induced by warming but future range expansions and contractions in spawning areas were highly variable. Contraction patterns in total spawning area were predicted for the English Channel and North Sea during summer, whereas expansions were projected during spring and autumn. The southern North Sea was projected to remain an important year-round spawning area for sardines under projected future conditions.

A worst-case climate change scenario was used to estimate future changes (2020–2100) to the thermal habitat suitability of North Sea cod (Núñez-Riboni *et al.*, 2019). The study used a regional climate model, which should be better able to resolve local temperature increases due to its higher spatial resolution and simulation of changes in ocean waves. The results showed that the southern Skagerrak, central and northern North Sea, and the edge of the Norwegian trench have become more thermally suitable, and will likely remain suitable for North Sea cod throughout the coming century, but habitat south of 56°N has become less suitable. Thermal suitability models are normally based on historical relationships between fish abundance and temperature but other factors including changes in fishing mortality, and

food web interactions must be considered. An alternate approach is to model the effects of temperature on the metabolism of individual fish with Dynamic Energy Budget models being one such approach. van de Wolfshaar *et al.* (2022) used a Dynamic Energy Budget (DEB) model of common sole (*Solea solea*) in different nursery areas of the North Sea and found that early arrival of fish larvae in their nurseries leads to higher mortality due to initially slow growth in spring. However, despite reduced survival during the first-year future climate scenarios, inspired by the 2040 IPCC projections, resulted in higher biomass due to faster growth of post-juvenile stages.

Although the examples above focussed on single species models, best practices recommend ensemble approaches, that is, the use of sets of models which then capture more of the uncertainty in the individual model predictions (Spence *et al.*, 2021). Using an ensemble approach, Schickele *et al.* (2021) investigated potential changes in the spatial distribution of seven commercially important small pelagic species. The study used eight Species Distribution Models (SDMs), five General Circulation Models (GCMs) and three emission scenarios (the IPCC Representative Concentration Pathways; RCPs). For all of the climate scenario GCM combinations and all of the species except Round sardinella, climate-induced northward distributional shifts were projected. Conditions in the North Sea were predicted to become less favourable for the temperate-cold species presently common in UK waters (Atlantic horse mackerel, *Trachurus trachurus* and European sprat *Sprattus sprattus*), and more suitable for species such as European pilchard (*Sardina pilchardus*) and European anchovy (*Engraulis encrasicolus*). By the end of the century, thermal conditions as far north as the middle of the Irish and North Seas could become favourable for species such as Mediterranean horse mackerel (*Trachurus mediterraneus*) and bogue (*Boops boops*) which are not common in UK waters at present.

Using emissions scenarios (RCP 2.6 and 8.5), a process-based fisheries model (SS-DBEM) forced with biogeochemical outputs, was applied to project future potential catches of the four main commercial pelagic species in the North-East Atlantic: Atlantic mackerel (*Scomber scombrus*), European sprat, Atlantic herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*). Potential catches were projected to increase in the northern area of the North-East Atlantic but to decrease in the southern area (Fernandes *et al.*, 2020). Specifically, in UK waters, herring was projected to decrease under the RCP8.5 scenario, whilst projections for blue whiting, Atlantic mackerel and sprat showed mixed responses.

Using a similar range of climate projections, the abundance of eight commercially important bottom dwelling fish species across the Celtic Sea, English Channel and southern North Sea has been modelled using Generalized Additive Models (Maltby *et al.*, 2020). Increases in abundance were projected for warm water associated species like red mullet (*Mullus surmuletus*), Dover sole (*Solea solea*), John dory (*Zeus faber*) and lemon sole (*Microstomus kitt*), whilst decreases in abundance were projected for those associated with cooler waters: Atlantic cod (*Gadus morhua*),

anglerfish (*Lophius piscatorius*) and megrim (*Lepidorhombus whiffiagonis*), and only European plaice (*Pleuronectes platessa*) appeared less affected by the projected temperature changes. Most projected abundance responses were comparable among climate projections, but uncertainty in the rate and magnitude of changes often increased substantially beyond 2040.

These recent studies add to the wider literature that has demonstrated range or depth shifts in response to warming (Wright *et al.*, 2020). For species favouring cooler temperatures and with narrow thermal ranges, agreement amongst projections has been especially strong. However, for other species, greater variability can be seen among projections. A further challenge is the prediction of abrupt community shifts as opposed to gradual, essentially linear responses to climate change (Beaugrand *et al.*, 2019). It is also worth noting that RCP8.5¹ which has been widely used in ecological modelling was developed as a greenhouse gas high-emission baseline scenario and was not intended to represent the most likely ‘business as usual’ outcome (<https://www.carbonbrief.org/explainer-the-high-emissions-rcp8-5-global-warming-scenario/>). Because of the problems with linking RCPs to greenhouse gas emission mitigations, future studies are likely to be based on the Shared Socioeconomic Pathways (SSPs) published in 2017. The basic SSPs consist of a narrative outlining broad characteristics of the global future and country-level population, changes in gross domestic product (GDP), and urbanisation projections. The SSPs are not scenarios in themselves but provide building blocks from which likely emissions pathways are developed. Possible resulting global temperatures are derived by combining the likely radiative forcings arising from GHG emissions with each SSP (Masson-Delmotte *et al.*, 2021).

Incorporation of ecosystem and foodweb interactions into models of fish abundance and distribution

Significant progress has been made in developing ecosystem models (Lynam *et al.*, 2017). Several new ‘end-to-end’ dynamic ecosystem models have been released that aim to predict the impacts of environmental change on the structure and function of marine food webs and the services they provide (Heath *et al.*, 2021). Bayesian joint models with integrated nested Laplace approximation (INLA) have been used to predict future spatial density distributions in the form of common spatial trends of predator–prey overlap (Sadykova *et al.*, 2020). This particular study illustrated the complex relationship between changes in physical habitat, and predator–prey interactions. The approach can be useful in informing the design of spatial management policies under climate change by using the potential differences in ecological costs to weigh up the trade-offs in decisions involving issues of large-scale spatial use of our oceans, such as marine protected areas and commercial fishing.

¹ The numerals after the RCP scenario names refer to the global radiative forcing in W/m² <https://www.metoffice.gov.uk/binaries/content/assets/metofficegovuk/pdf/research/ukcp/ukcp18-guidance---representative-concentration-pathways.pdf>.

It is widely acknowledged that the northern and southern North Sea have different hydrographical regimes and differences in their food webs. A separate northern North Sea Ecopath model has recently been constructed (Hill *et al.*, 2021) complementing the southern North Sea model of Stäbler *et al.* (2018). An EwE model for the Irish Sea revealed the indirect impacts of environmental change on fish biomass and catch through trophic interactions (Bentley *et al.*, 2020). The ecosystem model suggested that historical environmental change suppressed the overall production of commercial finfish, whilst also dampening the rate of stock recovery despite marked reductions in fishing effort. This suggests that failure to account for ecosystem-level information may lead to misconceived expectations and flawed fisheries management. Therefore, there is a need to operationalize ecosystem information through management procedures to support fisheries advice and improve understanding on ecosystem-level response to both climate and anthropogenic changes.

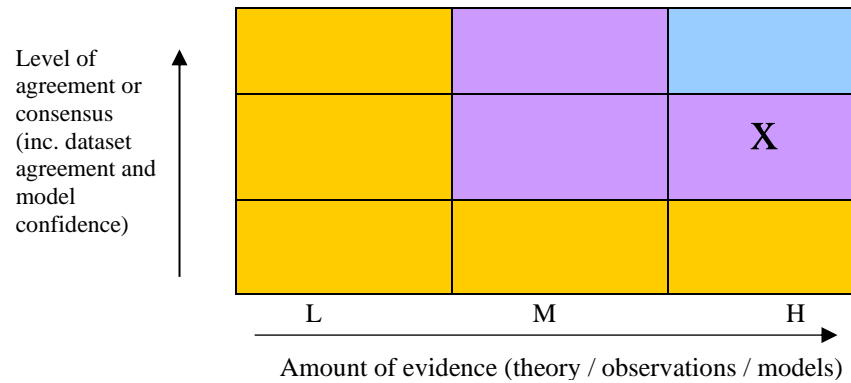
Dynamic Bayesian network ecosystem models which account for the multiplicity of interactions between physical (e.g. bottom temperature), biological (e.g. net primary production) indicators and anthropogenic marine use (i.e. fishing) and their changes across space and over time have been developed for contrasting habitats across the North Sea and West of Scotland within the last 30 years (Trifonova *et al.*, 2021). An important finding was the dramatic changes in the strength of many biophysical interactions over time. This suggests that physical and biological indicators should only be used with additional temporal information, as changes in strength led to the identification of two potentially significant periods of ecosystem change linked to physical pressures and primary production changes. The dynamic Bayesian network ecosystem models can be used to explore a range of ‘what-if?’ scenarios, based on potential physical changes in temperature, levels of stratification and anthropogenic marine use (increase vs decrease in fishing), and the specific trends (increases or declines) of different ecosystem components in response to these changes can be explored. By providing an understanding of the reactive responses across all trophic levels, tractable predictions of the true dynamic nature of bottom-up (e.g. driven by temperature and primary production) vs top-down (e.g. driven by fishing) effects across trophic levels and habitats can be made (Trifonova *et al.* 2017). Similarly, another ecosystem-level modelling study (Thorpe *et al.*, 2022) using StrathE2E (Heath *et al.*, 2021) has shown that warming is likely to have raised metabolic demands of omnivorous zooplankton and reduced their abundance, thus favouring benthivorous and piscivorous demersal fish but otherwise had modest effects on energy pathways and top predators.

These studies highlight the need of using ecosystem-level outputs to improve understanding of different ecosystem components in response to climate and/or anthropogenic change. Being able to predict implications of climate and other anthropogenic changes on ecosystem components and their relative adaptability and resilience will be useful to guide what species and/or habitats are more resilient/at-risk to what type of disturbances and therefore what management decisions are required for the future sustainable management of marine ecosystems under the influence of future climate and other anthropogenic changes.

CONFIDENCE ASSESSMENT

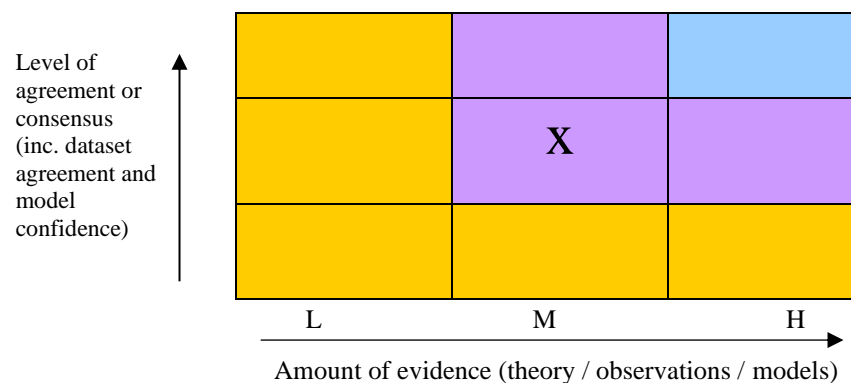
The confidence assessment was generated through a consensus agreement between the update authors.

What is already happening?



Since the last MCCIP assessment in 2020 (Wright *et al.*, 2020), further studies have been published on the changing distribution of species in UK waters, although there remains limited information on the impact of heat waves, although see Wakelin *et al.* (2021) for a study linking extreme thermal events with fisheries landings. We have also been unable to find any studies on the effects of observed pH changes on fish in UK waters. Nevertheless, fish and fisheries biology research have remained one of the most active fields in marine science so the amount of available evidence remains 'High' but, because of uncertainty in areas such as food- web and acidification responses, the level of agreement and consensus is still judged as being 'Medium'. Consequently, the overall assessment has not changed from the 2020 MCCIP Report Card.

What could happen in the future?



There are a range of marine ecosystem models which attempt to capture much of the uncertainty about marine ecosystem structure and function, however, the amount of evidence remains at 'Medium'. Although the likely broad responses to temperature increase are known, the level of consensus remains as 'Medium' because of uncertainties over the magnitude of responses throughout the food web. In addition, the number of ecosystem

models which can incorporate both climate change projections and can conduct ensemble exercises is still limited for UK seas.

KEY CHALLENGES AND EMERGING ISSUES

The three top priority challenges for providing improved advice on fish responses to climate change identified in Wright *et al.* (2020) were (1) contribution, (2) multi-level data integration, and (3) model testing. This update has identified some further limited progress as reported in the scientific literature. Research funding has become a serious problem with post-Brexit restrictions on EU funding and with resources in fisheries laboratories being diverted to issues such as offshore renewables and marine protected areas. Our perception is that this has led to a decrease in basic fish and shellfish biology and ecological studies. This is undesirable as robust projections of climate-related changes in productivity and distribution of fish still require better integration of data on survival, distribution, movements, aerobic scope, growth and reproductive schedules into statistical, process-based and ecosystem models.

Even though the range of marine ecosystem models available is increasing, we still need to make the best use of these models either through ensemble approaches (Spence *et al.*, 2021) or through the complementary inclusion of food web models with non-mechanistic models (Coll *et al.*, 2019). Rather than trying to choose the ‘best’ model, or taking some weighted average, it is important to exploit the strengths of each of the types of models, whilst learning from the differences between them and finding ways to generalize their outcomes to strengthen projections under a range of climate scenarios.

The need for validation of model assumptions remains, as does the need to consider habitat dependency, integration of physiological processes and the combination of individual and population level data to understand the nature of climate responses. Identifying bottlenecks where species may be most sensitive to climate change, such as shallow coastal nursery areas, remains important. Although studies have tended to focus on commercial species, climate change may also affect non-commercial species of conservation importance to the UK (e.g. flapper skate, *Dipturus intermedius* and basking shark, *Cetorhinus maximus*). Such impacts would have implications for the effectiveness of existing and proposed marine conservation measures so that non-commercial species should not be ignored in setting marine climate research priorities.

REFERENCES

- Alix, M., Kjesbu, O. S. and Anderson, K. C. (2020). From gametogenesis to spawning: How climate-driven warming affects teleost reproductive biology. *Journal of Fish Biology*, **97**,607-632. <https://doi.org/10.1111/jfb.14439>
- Baudron, A. R. and Fernandes, P. G. (2014). Adverse consequences of stock recovery: European hake, a new “choke” species under a discard ban? *Fish and Fisheries*, **16**, 563–575.
- Baumann H., Jones, L.F. Murray, C.S., Siedlecki, S.A., Alexander, M. and Cross, E.L. (2022) Impaired hatching exacerbates the high CO2 sensitivity of embryonic sand lance *Ammodytes dubius*, *MEPS*, **687**, 147–162.
- Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., Kirby, R. R. *et al.* (2019). Prediction of unprecedented biological shifts in the global ocean. *Nature Climate Change*, **9**, 237–243. 10.1038/s41558-019-0420-1

- Bentley, J. W. (2020). Modelling the food web in the Irish Sea in the context of a depleted commercial fish community, Scottish Association for Marine Science, University of the Highlands and Islands.
- Bentley, J. W., Serpetti, N., Fox, C., Heymans, J. J. and Reid, D. (2020). Retrospective analysis of the influence of environmental drivers on commercial stocks and fishing opportunities in the Irish Sea. *Fisheries Oceanography*, **29**, 415–435. 10.1111/fog.12486.
- Bindoff, N. L., Cheung, W. W. L. and Kairo, J. G. (2019). Changing ocean, marine ecosystems, and dependent communities (ed. M. Barange and B. Seibel). IPCC Special Report on the Ocean and Cryosphere in a Changing Climate, Cambridge University Press, pp. 447–587.
- Carstensen, J. and Duarte, C.M. (2019). Drivers of pH Variability in Coastal Ecosystems. *Environmental Science and Technology*, **53**, 4020–4029.
- Clark, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003). North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, **9**, 1669–1680.
- Clements, J.F., Sundin, J., Clark, T.D. and Jutfelt, F. (2022). Meta-analysis reveals an extreme “decline effect” in the impacts of ocean acidification on fish behaviour. *PLOS Biology*, **20**(2), e3001511.
- Concannon, C. A., Cross, E. L., Jones, L. F., Murray, C. S., Matassa, C. M., McBride, R. S. and Baumann, H. (2021). Temperature-dependent effects on fecundity in a serial broadcast spawning fish after whole-life high CO₂ exposure. *ICES Journal of Marine Science*, **78**, 3724–3734. 10.1093/icesjms/fsab217
- Dahlke, F., Butzin, M., Wohlrab, S., and Pörtner, H.-O. (2022). Reply to: methodological inconsistencies define thermal bottlenecks in fish life cycle. *Evolutionary Ecology*, **36**, 293–298. 10.1007/s10682-022-10154-z
- Dahlke, F. T., Wohlrab, S., Butzin, M., and Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, **369**, 65–70. 10.1126/science.aaz3658.
- Dickey-Collas, M., Armstrong, M.J., Officer, R.A., Wright, P.J., Brown, J., Dunn, M.R. and Young, E.F. (2003). Growth and expansion of haddock (*Melanogrammus aeglefinus* L.) stocks to the west of the British Isles in the 1990s. ICES Marine Science Symposium 219, pp. 271–282.
- Esbaugh, A. J. (2017). Physiological implications of ocean acidification for marine fish: emerging patterns and new insights. *Journal of Comparative Physiology B*, **188**, 1–13. 10.1007/s00360-017-1105-6
- Faria, A. M., Lopes, A. F., Silva, C. S. E., Novais, S. C., Lemos, M. F. L., and Gonçalves, E. J. (2018). Reproductive trade-offs in a temperate reef fish under high pCO₂ levels. *Marine Environmental Research*, **137**, 8–15. <https://doi.org/10.1016/j.marenvres.2018.02.027>
- Fernandes, J. A., Frölicher, T. L., Rutterford, L. A., Erauskin-Extramiana, M., and Cheung, W. W. L. (2020). Changes of potential catches for North-East Atlantic small pelagic fisheries under climate change scenarios. *Regional Environmental Change*, **20**, 116. 10.1007/s10113-020-01698-3
- Frommel, A. Y., Maneja, R., Lowe, D., Malzahn, A. M., Geffen, A. J., Folkvord, A., Piatkowski, U. *et al.* (2012). Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Climate Change*, **2**, 42–46. 10.1038/nclimate1324
- Heath, M. R., Speirs, D. C., Thurlbeck, I., and Wilson, R. J. (2021). StrathE2E2: An R package for modelling the dynamics of marine food webs and fisheries. *Methods in Ecology and Evolution*, **12**, 280–287. <https://doi.org/10.1111/2041-210X.13510>
- Hill, C. E., Bentley, J. W., Serpetti, N., Fox, C., Angus, C., and Heymans, J. J. (2021). Modelling the trophic interaction, structure, and function of the northern North Sea food web. Ecopath Technical Report, Scottish Association for Marine Science, Report, 299, 115 pp. 10.13140/RG.2.2.11303.06561
- Ikpewe, E. I., VBaudron, A. R., Ponchon, A., and Fernandes, P. G. (2020). Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. *Journal of Applied Ecology*, **54**(7), 847–856. 10.1111/1365-2664.13807
- Kjesbu, O. S., Alix, M., Sandø, A. B., Strand, E., Wright, P. J., Johns, D. G., Thorsen, A. *et al.* (2022). Latitudinally distinct stocks of Atlantic cod face fundamentally different biophysical challenges under on-going climate change. *Fish and Fisheries*, n/a. <https://doi.org/10.1111/faf.12728>
- Lima, A. R. A., Garrido, S., Riveiro, I., Rodrigues, D., Angélico, M. M. P., Gonçalves, E. J., Peck, M. A. *et al.* (2022). Seasonal approach to forecast the suitability of spawning habitats of a temperate small pelagic fish under a high-emission climate change scenario. *Frontiers in Marine Science*, **9**, 10.3389/fmars.2022.956654.
- Lopes, A. F., Faria, A. M., and Dupont, S. (2020). Elevated temperature, but not decreased pH, impairs reproduction in a temperate fish. *Scientific Reports*, **10**, 20805. 10.1038/s41598-020-77906-1
- Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., and Stenseth, N. C. (2017). Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences*, **114**, 1952–1957. 10.1073/pnas.1621037114

- Maltby, K. M., Rutterford, L. A., Tinker, J., Genner, M. J., and Simpson, S. D. (2020). Projected impacts of warming seas on commercially fished species at a biogeographic boundary of the European continental shelf. *Journal of Applied Ecology*, **57**, 2222–2233. <https://doi.org/10.1111/1365-2664.13724>
- Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N. *et al.* (2021). Climate Change 2021: The physical science basis; summary for policymakers, Intergovernmental Panel on Climate Change, Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, 42 pp. <https://www.ipcc.ch/report/ar6/wg1/>
- Melzner, F., Gutowska, M. A., Langenbuch, M., Dupont, S., Lucassen, M., Thorndyke, M. C., Bleich, M. *et al.* (2009). Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences*, **6**, 1–19. www.biogeosciences.net/6/1/2009/
- Montgomery, D. W., Simpson, S. D., Engelhard, G. H., Birchenough, S. N. R. and Wilson, R. W. (2019). Rising CO₂ enhances hypoxia tolerance in a marine fish. *Scientific Reports*, **9**, 15152. [10.1038/s41598-019-51572-4](https://doi.org/10.1038/s41598-019-51572-4)
- Nagelkerken, I., Alemany, T., Anquetin, J. M., Ferreira, C. M., Ludwig, K. E., Sasaki, M. and Connell, S. D. (2021). Ocean acidification boosts reproduction in fish via indirect effects. *PLoS Biology*, **19**, e3001033. [10.1371/journal.pbio.3001033](https://doi.org/10.1371/journal.pbio.3001033)
- Núñez-Riboni, I., Taylor, M. H., Kempf, A., Püts, M. and Mathis, M. (2019). Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change. *ICES Journal of Marine Science*, **76**, 2389–2403. [10.1093/icesjms/fsz132](https://doi.org/10.1093/icesjms/fsz132)
- Oesterwind, D., Bobowski, B. T. C., Brunsch, A., Laptikhovsky, V., van Hal, R., Sell, A. F. and Pierce, G. J. (2020). First evidence of a new spawning stock of *Illex coindetii* in the North Sea (NE-Atlantic). *Fisheries Research*, **221**, 105384. <https://doi.org/10.1016/j.fishres.2019.105384>
- Pauly, D. (2021). The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances*, **7**, 18.
- Pinnegar, J.K., Garrett, A., Wouters, J., Kelly, R., Stiasny, M.H. and Marshall, C.T. (2023) Climate change impacts on fisheries relevant to the UK and Ireland. MCCIP Science Review 2023, 29pp, DOI: 10.14465/2023.reu11.fis
- Romagnoni, G., Kvile, K. Ø., Dagestad, K.-F., Eikeset, A. M., Kristiansen, T., Stenseth, N. C. and Langangen, Ø. (2020). Influence of larval transport and temperature on recruitment dynamics of North Sea cod (*Gadus morhua*) across spatial scales of observation. *Fisheries Oceanography*, n/a. [10.1111/fog.12474](https://doi.org/10.1111/fog.12474)
- Sadykova, D., Scott, B. E., De Dominicis, M., Wakelin, S. L., Wolf, J. and Sadykov, A. 2020. Ecological costs of climate change on marine predator–prey population distributions by 2050. *Ecology and Evolution*, **10**, 1069–1086. <https://doi.org/10.1002/ece3.5973>
- Schickele, A., Goberville, E., Leroy, B., Beaugrand, G., Hattab, T., Francour, P. and Raybaud, V. (2021). European small pelagic fish distribution under global change scenarios. *Fish and Fisheries*, **22**, 212–225. <https://doi.org/10.1111/faf.12515>
- Servili, A., Canario, A.V.M., Mouchel, O. and Munoz-Cueto, J.A. (2020). Climate change impacts on fish reproduction are mediated at multiple levels of the brain pituitary-gonad axis, *General and Comparative Endocrinology*, **291**, 113439.
- Servili, A., Leveque, E., Mouchel, O., Devergne, J., Lebigre, C., Roussel, S., Mazurais, D. and Zambonino-Infante, J.-L. (2023). Ocean acidification alters the acute stress response of a marine fish, *Science of the Total Environment*, **858**, Part 1, 159804.
- Spence, M. A., Griffiths, C. A., Waggitt, J. J., Bannister, H. J., Thorpe, R. B., Rossberg, A. G. and Lynam, C. P. (2021). Sustainable fishing can lead to improvements in marine ecosystem status: an ensemble-model forecast of the North Sea ecosystem. *Marine Ecology Progress Series*, **680**, 207–221.
- Sswat, M., Stiasny, M. H., Jutfelt, F., Riebesell, U. and Clemmesen, C. (2018). Growth performance and survival of larval Atlantic herring, under the combined effects of elevated temperatures and CO₂. *PLoS ONE*, **13**, e0191947. [10.1371/journal.pone.0191947](https://doi.org/10.1371/journal.pone.0191947)
- Stäbler, M., Kempf, A. and Temming, A. (2018). Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model. *Ocean and Coastal Management*, **165**, 280–297. <https://doi.org/10.1016/j.ocecoaman.2018.08.017>
- Stiasny, M. H., Mittermayer, F. H., Sswat, M., Voss, R., Jutfelt, F., Chierici, M., Puvanendran, V. *et al.* (2016). Ocean acidification effects on Atlantic cod larval survival and recruitment to the fished population. *PLoS ONE*, **11**, e0155448. [10.1371/journal.pone.0155448](https://doi.org/10.1371/journal.pone.0155448)
- Stiasny, M. H., Mittermayer, F. H., Göttler, G., Bridges, C. R., Falk-Petersen, I.-B., Puvanendran, V., Mortensen, A. *et al.* (2018). Effects of parental acclimation and energy limitation in response to high CO₂ exposure in Atlantic cod. *Scientific Reports*, **8**, 8348. [10.1038/s41598-018-26711-y](https://doi.org/10.1038/s41598-018-26711-y)
- Stiasny, M. H., Sswat, M., Mittermayer, F. H., Falk-Petersen, I.-B., Schnell, N. K., Puvanendran, V., Mortensen, A. *et al.* (2019). Divergent responses of Atlantic cod to ocean acidification and food limitation. *Global Change Biology*, **25**, 839–849. <https://doi.org/10.1111/gcb.14554>

- Thorpe, R. B., Arroyo, N. L., Safi, G., Niquil, N., Preciado, I., Heath, M., Pace, M. C. *et al.* (2022). The Response of North Sea Ecosystem Functional Groups to Warming and Changes in Fishing. *Frontiers in Marine Science*, **9**, 10.3389/fmars.2022.841909.
- Trifonova, N. I., Scott, B. E., De Dominicis, M., Waggitt, J. J. and Wolf, J. (2021). Bayesian network modelling provides spatial and temporal understanding of ecosystem dynamics within shallow shelf seas. *Ecological Indicators*, **129**, 107997. <https://doi.org/10.1016/j.ecolind.2021.107997>
- van de Wolfshaar, K. E., Barbut, L. and Lacroix, G. (2022). From spawning to first-year recruitment: the fate of juvenile sole growth and survival under future climate conditions in the North Sea. *ICES Journal of Marine Science*, **79**, 495–505. 10.1093/icesjms/fsab025
- van der Kooij, J., Engelhard, G. H. and Righton, D. A. (2016). Climate change and squid range expansion in the North Sea. *Journal of Biogeography*, **43**, 2285–2298. doi:10.1111/jbi.12847
- Villalobos, C., Love, B.A. and Olson, M.B. (2020). Ocean Acidification and ocean warming effects on pacific herring (*Clupea pallasii*) Early Life Stages, *Frontiers in Marine Science*, **7**.
- Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R. and Siepel, H. (2021). Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews*, **96**, 247–268. <https://doi.org/10.1111/brv.12653>
- Wakelin, S., Townhill, B., Engelhard, G., Holt, J. and Renshaw, R. (2021). Marine heatwaves and cold-spells, and their impact on fisheries in the southern North Sea. Copernicus Marine Service Ocean State Report, Issue 5. *Journal of Operational Oceanography*, **14** (Suppl. 1), s91–s96. 10.1080/1755876X.2021.1946240
- Williams, C.R., Dittman, A.H., McElhany, P., Busch, D.S., Maher, M.T., Bammler, T.K., MacDonald, J.W. and Gallagher, E.P. (2019). Elevated CO₂ impairs olfactory-mediated neural and behavioral responses and gene expression in ocean-phase coho salmon (*Oncorhynchus kisutch*). *Global Change Biology*, **25**, (3), 963–977.
- Wootton, H. F., Morrongiello, J. R., Schmitt, T. and Audzijonyte, A. (2022). Smaller adult fish size in warmer water is not explained by elevated metabolism. *Ecology Letters*, n/a. <https://doi.org/10.1111/ele.13989>.
- Wright, P. J., Pinnegar, J. K. and Fox, C. (2020). Impacts of climate change on fish, relevant to the coastal and marine environment around the UK, Marine Climate Change Impacts Partnership, 28 pp. 10.14465/2020.arc16.fsh