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In Focus. Staying out of the heat: how habitat use is determined by local temperature

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In the marine environment species distributions are closely linked to temperature gradients, but how individual behaviour is affected by local temperatures is less well understood. Frietas *et al.* (2016) tracked Atlantic cod within a Norwegian fjord using electronic acoustic tags. They showed that when surface waters were warm, cod occupied the cold deep non-vegetated habitats. However, when surface waters cooled, fish moved into shallow seagrass and macroalgae beds that were previously out-of-bounds. The study provides a clear example of how thermal regimes determine habitat use over fine spatial and temporal scales, with potential implications for population dynamics under climate warming.

To ensure peak physiological performance animals should occupy an optimal temperature regime. Sub- or supra-optimal temperatures will result in a lower physiological efficiency and be energetically expensive. At extreme critical temperatures, core aerobic physiological processes will fail, ultimately leading to death (Pörtner & Farrell 2008). Due to these major effects that temperature can have on animals it is perhaps not surprising that thermal tolerance is a one of the major drivers of species distributions (Sunday *et al.* 2012). However, life is never simple, and temperature alone does not determine species ranges. Instead species ranges are also determined by the availability of essential resources, such as food and shelter, and the distributions of natural enemies. Thus, the need for optimal thermal habitat can conflict with the need to spend time in other locations (van Beest *et al.* 2012). Animals may benefit when moving from thermally optimal habitats if the costs of staying become too high. Such movement can in principle be determined by how temperature changes over daily, seasonal, or even interannual cycles.

Atlantic cod is one of the most commercially important species of fish, with recent (2013) estimates of fisheries landings in excess of 1.3 million tonnes per year (FAO 2015). The species has a broad distribution across the boreal waters of the northern Atlantic from northern Europe to Iceland, Greenland and North America (Mieszkowska *et al.* 2009). Many fished populations have historically been decimated by overharvesting, but there are also strong indications that populations have been negatively affected by climatic warming (Brander 2010). Decades of study by fisheries biologists have provided key information on how temperature affects reproduction, growth and longevity in the species (Taylor 1958; Pörtner *et al.* 2001; Kling *et al.* 2007; Righton *et al.* 2010). Moreover, several studies with tagged Atlantic cod have identified temperature as an important factor affecting depth distributions (Neat & Righton 2007; Frietas *et al.* 2015), suggesting an influence of the local temperature regime on individual behaviour. Against this background, it is clear that the species provides useful opportunities to investigate how natural temperature changes affect patterns of habitat use and population demography.

Freitas *et al.* (2016) tagged individuals within an Atlantic cod population in a Norwegian fjord with acoustic transmitters. Then, using a comprehensive array of receivers they were able to compile information on the location and depth of these fish to the remarkable spatial resolution of less than 5m. Uniquely they coupled location data with high quality habitat maps and sea temperature information from underwater data loggers, enabling tests of how habitat use alters with changing temperature. The authors discovered that when temperatures in surface waters were cool (<16°C), cod entered the shallows to use eel grass and macroalgae beds where they are presumed to feed. However, when surface waters were warm (>16°C), the cod descended into non-vegetated rock and sand habitats characteristic of deeper waters. These results suggest that these fish avoid warmer waters, and only when the surface temperatures cool past a thermal threshold can they use their favoured habitat. It seems that sea surfaces temperatures directly determine the seasonal time window when cod can use shallow water resources.

The work of Freitas *et al.* (2016) highlights the link between temperature and habitat use in fish, but the underlying reasons for the correlation can be complex. Warmer waters have lower dissolved oxygen, so rising temperatures can lead to a mismatch between oxygen demand and availability (Pörtner & Knust 2007; Pörtner & Farrell 2008). Thermal shifts may also affect the behaviour and abundance of prey, predator and competitor species of Atlantic cod (Brander *et al.* 2010), perhaps making shallower waters less profitable environments in warmer periods. Due to this complexity a full understanding of how thermal change drives behavioural and abundance changes in populations and communities will be major undertaking, but perhaps the cool-water fjord ecosystem studied by Freitas *et al.* (2016) will be a valuable system in which to undertake such future study.

Evidence of temperature-dependent habitat selection from Frietas *et al.* (2016) helps to interpret earlier work that shows that Atlantic cod often use thermal habitat that is less than optimal for growth (Neat & Righton 2007). It appears likely that cod are capitalising on resource rich habitats that are thermally tolerable, but less than ideal for growth. Although further work is needed to establish this concept firmly, the results are indicative of fish distributions being dependent upon requirements for both suitable thermal habitat and essential ecological resources. The combination of these needs may be the driver of the spatial patterns of population substructure often seen in cod from both tagging (Neat *et al.* 2014), and genetic studies (Knutsen *et al.* 2011).

Sea surface temperatures in the North Sea region are projected to rise by 1.8°C over the next 50 years (Rutterford *et al.* 2015). Projections of the impacts of such climate change on marine fish distributions to date have been primarily based on bioclimate envelope modelling approaches that extrapolate existing thermal occupancy patterns to projected future environments (Cheung *et al.* 2010). By necessity such methods overlook more subtle effects of temperature on populations, such as thermally-driven migrations or shifts in competitive ability (Milazzo *et al.* 2013). It is becoming increasingly clear that population-level responses of marine fishes to climate change may not necessarily always involve active wholesale movement of populations to optimal thermal regimes (Simpson *et al.* 2011; Rutterford *et al.* 2015). Instead we may expect marine climate change to lead to differences in recruitment and survivorship of established local populations that are co-located with the essential resources they need.

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Figure legend

Figure 1. Atlantic cod (*Gadus morhua*) and the Tvedestrand fjord Norwegian Skagerrak coast studied by Freitas *et al.* (2016). Photos by Øystein Paulsen (left), and Institute of Marine Research, Norway (right).