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Research Paper

Distribution and timing of spawning Faroe Plateau cod in relation to warming spring temperatures

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ABSTRACT

The Faroe Plateau cod stock has been in a poor state since 2005, while temperatures in the region have been increasing. However, the importance of distributional changes in contribution to the poor stock size and the mechanisms that drive the distribution of spawning Faroe Plateau cod are still not clear. Density dependent processes and temperature limitations imposed due to the narrow thermal niche for cod during spawning are two potential drivers for the geographical distribution of spawning cod. We analyse the changes in the geographical location, spawning area, timing of spawning and realised temperature niche in relation to abundance and temperature. Distributions were modelled using generalized additive models (GAM) based on CPUE and bottom temperature data from Spring Bottom trawl survey. We can clearly separate the two main spawning areas of the Faroe Plateau cod and show that there are no indications of density dependence effects on the distribution within these spawning areas. However, we found both a geographical shift in the north-eastern direction and a shift in the timing of spawning in the northern area, while no changes in distribution or timing of spawning were found within the western spawning area. Both shifts were significantly correlated with temperature, leading us to conclude that temperature plays a key role in the spatial and temporal dynamics of the Faroe Plateau cod. However, due to the limited data of this study, future studies should re-examine the mechanisms controlling the distribution of spawning cod when a longer timeseries is available.

1. Introduction

Environmental change has been predicted to cause irreversible changes in the spatial distribution, behaviour and productivity of species, potentially leading to invasions, extinctions and a decrease in the fisheries catch potential (Pörtner et al., 2014). Understanding the mechanisms that determine the spatiotemporal distribution of a species in an ecosystem can be seen as a key first step to predicting and projecting such future changes, and thereby adapting to these changes.

The Faroe Plateau cod (*Gadus morhua* L.) is one of the most commercially important species of the Faroe Islands (Steingrund et al., 2005). However the state of this stock has been poor since 2005 (ICES, 2016). Meanwhile the mean temperature at the Faroe Plateau during spawning season February to May has increased from 6 °C in 1994 to 6.5 °C in 2016 with a maximum mean temperature of 7.4 °C in 2003 (Faroe Marine Research Institute, unpublished) (Fig. 1). Cod spawn in two main spawning areas, one north and one west of the Islands (Fig. 2) (Jákupstovu and Reinert, 1994; Joensen et al., 2005; Steingrund and Mouritsen, 2009; Tåning, 1943). Conventional tagging has shown that Faroe Plateau cod show a strong site fidelity to their spawning area with 93% of the tagged cod returning to the same spawning area as they were tagged at the year before (Steingrund et al., 2009; Steingrund and Mouritsen, 2009; Tåning, 1940) why they are classified as 'accurate homers' (Robichaud and Rose, 2004). Further, the spawning areas are located where the concentration of copepod (*Calanus finmarchicus*) eggs, the main food source for cod larvae, is highest (Gaard and Steingrund, 2001). However, a quantitative definition of the spawning areas, the spatial distribution of spawning cod within these areas and the mechanisms controlling this distribution, are still unknown.

Abundance is one driver potentially causing changes in the distribution. The relationship between species distribution and abundance can be explained by density dependence where the occupied area expands and includes less optimal areas as abundance increases (Blanchard et al., 2005; Swain and Sinclair, 1994; Swain and Wade, 1993). For adult Faroe Plateau cod, density dependence has been shown to affect the distribution (Steingrund et al., 2005; Steingrund and Ofstad, 2010), while the role of density dependence for spawning Faroe Plateau cod is unknown.

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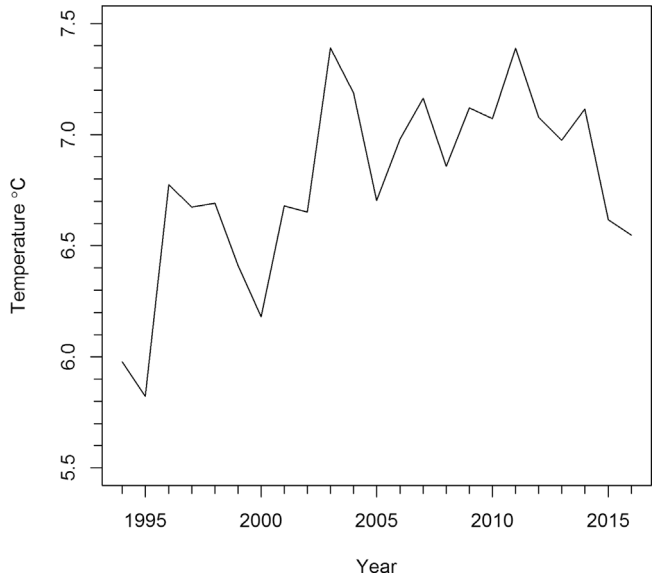

Fig. 1. Mean temperature measured in the spawning season from February to May at Oyragjógv coastal station.

Another driver is temperature. For fish, increasing temperatures in the ambient environment directly affect physiological processes as growth rate (Brander, 1995, 1994) and, via their thermal tolerances and preferences, defining their geographical distribution (Pörtner et al., 2014). However thermal limitations are species specific: for cod, while the thermal niche is between −1.5 and 19 °C (Righton et al., 2010), oocyte growth of cod has been shown to be highly influenced by temperature suggesting that the temperature is critical during spawning (Kjesbu et al., 2010; Righton et al., 2010). However the breadth of temperature niche during spawning is not clear: while Rose (2005) proposed an optimal spawning temperature of 0–6 °C, warmer temperatures of between 1 and 8 °C were suggested by Righton et al. (2010) based on tagging data and Van Der Meeren and Ivannikov (2006) showed that cod spawned successfully at temperatures up to 9.6 °C in rearing experiments.

Both changing abundance and temperatures in the environment can affect the realised niche of a species driving a geographical shift. For cod, geographical shifts are already well documented (Hedger et al., 2004; Opdal and Jørgensen, 2015; Perry et al., 2005; Rindorf and Lewy, 2006; Sundby and Nakken, 2008) although the mechanisms for the reported shifts are not uniform. The spatial shifts of spawning habitats of the Northeast Arctic cod have been linked directly to increasing temperature (Sundby and Nakken, 2008), fishing mortality causing changes in demographic composition or evolution of the cod stock (Opdal and Jørgensen, 2015) and warm and windy winters for the North Sea cod (Rindorf and Lewy, 2006). Other studies have shown that the geographical shift in cod in the North Sea mainly were juveniles while adult cod staying in temperature above optimal rarely shifted to areas with lower temperature (Neat and Righton, 2007; Rindorf and Lewy, 2006).

Changing temperatures also affect the timing (phenology) of key events in the life cycle, via impacts mediated by both development rates and behavioural responses (Pedersen, 1984; Poloczanska et al., 2013; Pörtner et al., 2014; Wieland, 2000). In the case of cod, the timing of spawning has been shown to be linked closely to local environmental conditions (Hutchings and Myers, 1994; Kjesbu et al., 2010; Neuheimer and MacKenzie, 2014). Changes in the timing of spawning have been hypothesized to have impacts on the recruitment of a fish stock, via the so-called “match-mismatch hypothesis”, where the agreement, or lack thereof, in space and time between larvae and their prey is critical in determining their survival (Cushing, 1990; Platt et al., 2003). Furthermore, in cases where a species migrates to its spawning location, the interplay between the timing of observations and changes in the timing of migration can falsely give the impression of distributional

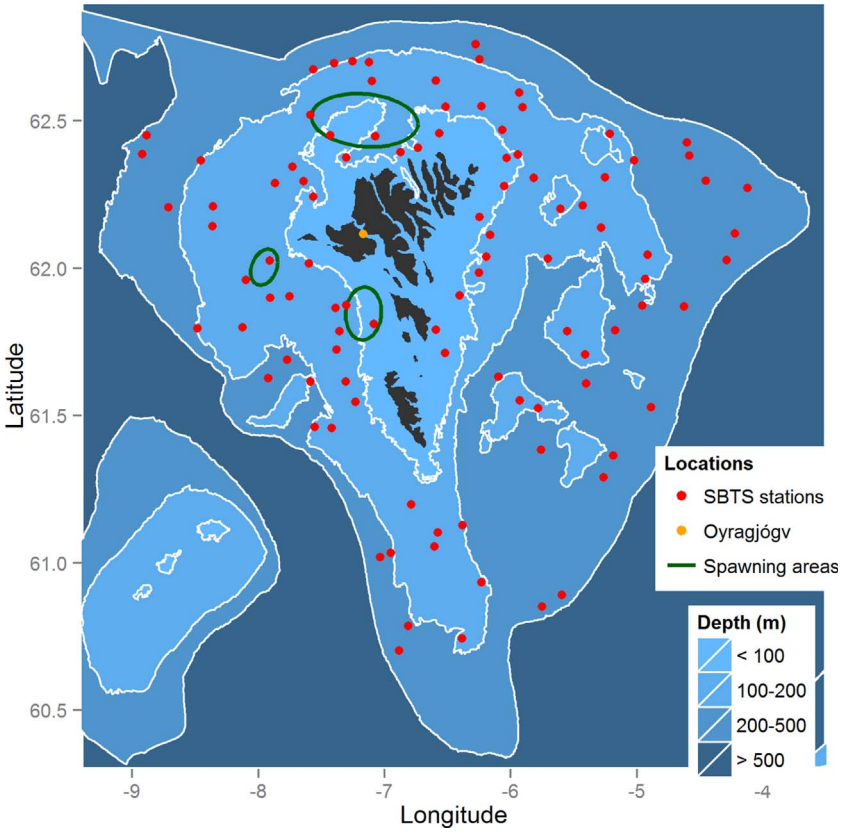

Fig. 2. Stations covered by the Spring Bottom trawl survey on the Faroe Plateau (red), Oyragjógv coastal station (orange) and main spawning areas (green ellipses). Contour lines indicate depths of 100, 200 and 500 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)