



Original Article

Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units

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Kuparinen, A., Roney, N. E., Oomen, R. A., Hutchings, J. A., and Olsen, Esben M. Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units. – ICES Journal of Marine Science, 73: 286–292.

Received 28 August 2015; revised 13 September 2015; accepted 18 September 2015; advance access publication 9 October 2015.

A basic challenge to successful management and conflict resolution is to correctly identify the spatial scale at which strategies for harvesting are developed. For commercially exploited marine fish, distributional boundaries of many stocks are based on the premise that productivity is similar at spatial scales that represent a small fraction of an individual's potential migration distance. Within such confined geographic regions, differences among individual life history traits—primary determinants of population productivity—are assumed to be negligible. The empirical basis for these assumptions bears re-examination for some widely distributed species, such as Atlantic cod (*Gadus morhua* L.), for which there is evidence that life history structuring is evident at much finer scales than previously thought. Here, we focus on a unique system in the Norwegian Skagerrak, divided into inner and outer fjord habitats between which cod movement across distances of a few kilometres is limited and populations show signals of genetic differentiation. Based on back-calculated length-at-age data, cod in the inner fjord are systematically smaller at young ages (1–5 years) and are characterized by shorter asymptotic body lengths than cod in the outer fjord. Our work on growth and life history supports genetic analyses which indicate that productivity and resilience of widely distributed marine fish are likely to differ at considerably smaller spatial scales than those delineated by traditional stock management boundaries.

Keywords: asymptotic body size, *Gadus morhua*, growth, length-at-age, otolith, Skagerrak, von Bertalanffy.

Introduction

Fisheries management is based on the premise that life history variation within species is negligible for fish inhabiting the same geographic region, i.e. spatial scales considerably smaller than the potential migration distance of individuals. Within these management units (stocks), individuals are assumed to grow, mature, and reproduce similarly, and population projections and fishery reference points are considered applicable for the entire unit (Hilborn and Walters, 1992). From an evolutionary perspective, life histories in nearby populations are generally thought to be similar because of shared environmental selective pressures and gene flow between

reproductive entities, whereas distant populations are more likely to show life history differences because of genetic drift, environmental differentiation, and local adaptation (Slatkin, 1993; Roff, 2002). For example, the well-known Bergmann's rule suggests that differences in temperatures will manifest through differences in body size and growth rate (Bergmann, 1847; Atkinson, 1994), and such body size patterns along latitudinal gradients have been demonstrated in many ectotherms (e.g. Angilletta *et al.*, 1997; Fisher *et al.*, 2010). However, the perception that meaningful differences in life history are manifest only at long distances is inconsistent with evidence of life history differences at relatively small spatial

scales, such as that reported for Atlantic salmon, *Salmo salar* L., inhabiting the same river system (Vähä *et al.*, 2007) and along comparatively narrow depth gradients for Atlantic cod, *Gadus morhua* L., in Iceland (Árnason *et al.*, 2009).

Atlantic cod, an iconic species that has experienced massive depletions throughout most of its range, has been studied for the potential role that life history changes can play in contributing to population collapse and recovery ability (Hutchings and Rangeley, 2011; Kuparinen *et al.*, 2014). While a substantial body of research has focused on detecting temporal trends in cod life histories (e.g. McIntyre and Hutchings, 2003; Olsen *et al.*, 2004; Swain *et al.*, 2007), it has also been demonstrated on both sides of the Atlantic that there exist differences in life histories at unexpectedly small spatial scales, that is, within management units (e.g. Olsen *et al.*, 2008; Oomen and Hutchings, 2015). For example, age and size at maturation vary among North Sea cod substocks (Wright *et al.*, 2011) and similar within-stock differences have also been detected in Icelandic cod life histories (Pardoe *et al.*, 2009). If cod substocks with different life histories are viewed as one entity, variation in the relative abundance of the substocks can either mask temporal trends in life histories occurring across substocks or give false indications of such (Wright *et al.*, 2011; Pukk *et al.*, 2013). Similarly, vulnerability of different substocks to fishing can substantially differ due to differences in their renewal ability stemming from life history differences. Therefore, identifying fine-scale life history structuring is a key to managing fisheries in a sustainable manner and to detecting substocks of particular conservational concern.

The Skagerrak between Norway and Denmark (Figure 1) is among the southern Eastern Atlantic cod habitats. Cod in this area are vulnerable to warming temperatures and increasing human impacts (Stige *et al.*, 2006; Rogers *et al.*, 2011). In the present study, we focus on life history differences in cod within a unique fjord system in Skagerrak. The Risør fjord is divided into inner and outer fjord areas with separate larvae nursery areas and between which cod dispersal is rare: a capture–mark–recapture study ($n = 2427$) conducted in 2005–2007 detected 1.2% dispersal from inner fjord to outer fjord and 0.7% dispersal in the opposite direction (Knutsen *et al.*, 2011). Cod also show signs of genetic differentiation between the inner and outer fjord areas (Knutsen *et al.*, 2011). The study area, limited to 20 km², is orders of magnitude smaller than the areas among which cod life history differences have previously been reported. That said, earlier studies have indicated that cod in the inner fjord are typically smaller than outer fjord cod (Dannevig, 1949; Lekve *et al.*, 2006; Gjørseter and

Danielssen, 2011). Such a pattern is likely to be more general across the Skagerrak coastline, as in many fjord systems, cod juveniles have been found to be smaller in the inner fjord than in outer fjord habitats (Dannevig, 1949; Lekve *et al.*, 2002).

Here, we examine whether cod growth differs substantially between the inner and outer Risør fjord areas. To this end, we sample adult cod in the two areas and back-calculate their growth trajectories from otoliths. Survival analyses based on the capture–mark–recapture programme mentioned above indicate that there are no significant differences in cod survival between the inner and outer fjord areas or between cod grouped according to their body size (Fernández-Chacón *et al.*, 2015). Therefore, mortality patterns shaping the demographic structure of a cod cohort from birth to adulthood appear to be similar in the two areas, and differences found among life histories are likely to predominantly reflect phenotypic differences between the two cod populations.

Material and methods

Age determinations

Atlantic cod were sampled with fykenets in Sørfjorden (inner fjord habitat) and Østerfjorden (outer fjord habitat) in the Risør area on the Norwegian Skagerrak coast from late November 2013 to early January 2014 (Figure 1). The fykenets (mesh size: 20 mm) were not baited and were set in shallow (1–5 m) water with a soak time of up to 1 week. Coastal Atlantic cod often visit such near shore habitats during night, presumably to feed (Espeland *et al.*, 2010), and the fykenets are known to capture a broad range of cod size classes (range: 15–93 cm; Rogers *et al.*, 2014). The same locations distributed across each study area were sampled by the same researchers and commercial fishers following the same sampling protocol throughout the sampling period. Sampling locations were those thought to provide the highest catch rates to allow sampling to be conducted within as short a time frame as possible. To avoid biases in the growth histories arising from potentially differing demographic structures of the populations and to provide a conservative insight into the potential differences in growth between the two populations, our sampling was designed to collect mature cod (>45 cm) of similar sizes from both populations. Focusing on mature fish, for whom interannual growth has begun to decrease, was essential to reliably estimate asymptotic body sizes. To these ends, we included captured fish that were above 45 cm and roughly below 65 cm in length, until the desired sample sizes were achieved. The upper boundary was set to catch fish with similar

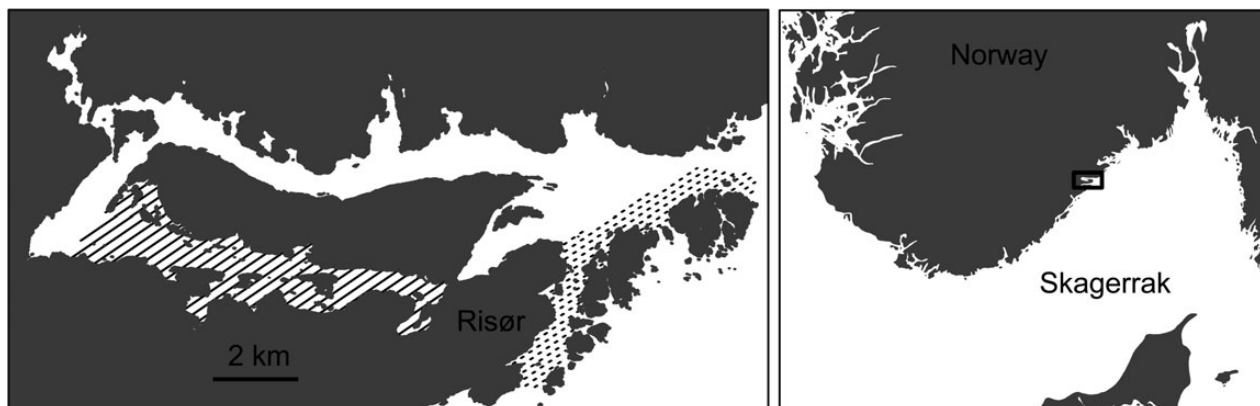


Figure 1. Study area. Atlantic cod was sampled from the inner (lined area) and outer (dashed area) Risør fjord on the Norwegian Skagerrak coast.

body sizes in both the populations, as in the inner fjord population cod are typically below 65 cm. Altogether, we sampled 35 fish each from the outer fjord [21 females, 14 males; mean body length (\pm SD): 57.8 cm (\pm 4), range: 51.0–66.1 cm] and the inner fjord habitats [20 females, 15 males; mean body length (\pm SD): 54.2 cm (\pm 3), range: 48.6–59.9 cm]. Given that the ranges of the sampled fish did not completely overlap, we checked the robustness of the results by restricting between-population comparison to individuals between 51.0 and 59.9 cm.

For length-at-age estimation, one otolith from each individual was embedded in a black polyester resin and transversally sectioned with a high-speed sectioning saw at the Otolith Research Laboratory at the Bedford Institute of Oceanography, Canada. For detailed information on the equipment and protocol used in this standard procedure, refer to the following: http://www.bio.gc.ca/otoliths/methods-methodes/annuli_age-ageanneaux-en.php. Images of sectioned otoliths were then obtained under reflected light, using an Axiocam Mrm camera mounted to a Zeiss SteREO Lumar v12 stereomicroscope. Before measuring interannual distances, all images were processed to enhance local contrast between the opaque and translucent zones. Relative interannual distances were then measured along a transect through the ventral plane of the otolith, starting from a landmark at the centre of the nucleus and then to each subsequent annulus along the transect. All image processing and measurements were performed using the open-source image analysis program Fiji (Schindelin et al., 2012). Lengths-at-age were back-calculated from relative distances, using the biological intercept method (Campana, 1990):

$$L_a = L_c + (O - O_c)(L_c - L_i)(O_c - O_i)^{-1},$$

where L_a is the estimated length-at-age a , L_c the length at capture, O the distance from the centre of the nucleus to the outer edge of the opaque annulus corresponding to age a , O_c the distance from the centre of the nucleus to the outer edge of the otolith, and L_i and O_i are the fish length and otolith length at the biological intercept. Biological intercepts used in this study (fish length = 2.44 mm, otolith length = 0.44 mm) were initially published by Sinclair et al. (2002) and have since been used in studies for a variety of Atlantic cod stocks [e.g. Gulf of St Lawrence (Swain et al., 2007), Arctic cod (Hardie and Hutchings, 2011), and Norwegian coastal cod (Li et al., 2008)]. This method is generally considered to provide more accurate back-calculation estimates as it uses a biologically determined intercept value as opposed to traditional methods that statistically estimate intercepts (e.g. Fraser–Lee; Campana, 1990; Campana and Jones, 1992). To check for robustness of the results with respect to the back-calculation method, the analyses were repeated with lengths-at-age back-calculated using the traditional Fraser–Lee method.

Growth analyses

Age-specific lengths were initially compared between sexes within populations and then between populations. As differences between sexes or populations can be age-dependent, the lengths at each age were compared separately, using Student's two-sample t -test. The normality of the samples was confirmed through visual comparison of the sample and the normal distribution quantiles, plotted against each other (qq-plot).

Back-calculated growth trajectories were summarized through von Bertalanffy growth (VB) curves $L(t) = L_\infty - (L_\infty - L_0)e^{-kt}$, where t is the age of a fish, $L(t)$ is the length of a fish at age t , L_∞

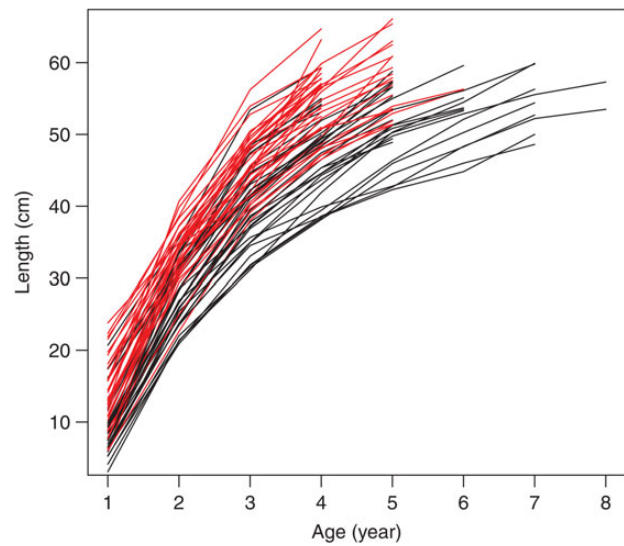


Figure 2. Individual Atlantic cod growth trajectories back-calculated from otoliths. Inner fjord cod are drawn with black lines and outer fjord cod with red lines.

the asymptotic length, L_0 the average length at $t = 0$, and k the intrinsic growth rate, i.e. the rate at which an individual reaches its L_∞ (von Bertalanffy, 1938). VB curves were fitted to each back-calculated growth trajectory through non-linear least-squared regression (L_0 , L_∞ , and k were treated as free model parameters; Pardo et al., 2013). Between-population differences in VB parameters were tested using Student's t -test or Wilcoxon's test, depending on the normality of the samples, and k was log-transformed for the sake of normality.

Results

The otoliths provided ample evidence of growth differentiation between the inner and outer fjord populations. If the populations experienced similar growth patterns, the age structures of similarly sized fish sampled from both populations should also be similar, given that both populations experienced similar mortality. But outer fjord cod were, on average, 1 year younger for a given length than inner fjord cod, indicating that growth was slower among inner-fjord cod relative to those in the outer fjord. Back-calculated growth trajectories revealed that lengths of cod of the same age from the inner fjord area were systematically smaller than those of cod from the outer fjord area (Figures 2 and 3a–e). There was no evidence of length differences between sexes within either of the populations ($p > 0.05$ for each t -tests for age-specific lengths between sexes). Thus, comparisons between populations were conducted with males and females pooled within each population. Age-specific length differed significantly between inner and outer fjord fish, such that the outer fjord fish were on average 4.6, 5.6, 5.6, 7.1, and 7.1 cm longer at ages from 1 to 5 years, respectively (Figure 3a–e; $p < 0.05$ in each t -test). For older ages, comparison was not possible, as there were no outer fjord fish older than 5 years. In contrast, the oldest inner fjord fish were 8 years old (Figure 2). If the Fraser–Lee back-calculation method was used instead of the biological intercept method, the age-specific differences were on average 4.8, 5.5, 5.5, 6.8, and 6.8 cm for 1- to 5-year-old fish, respectively, and t -tests revealed these differences to be significant ($p < 0.05$ in each t -test).

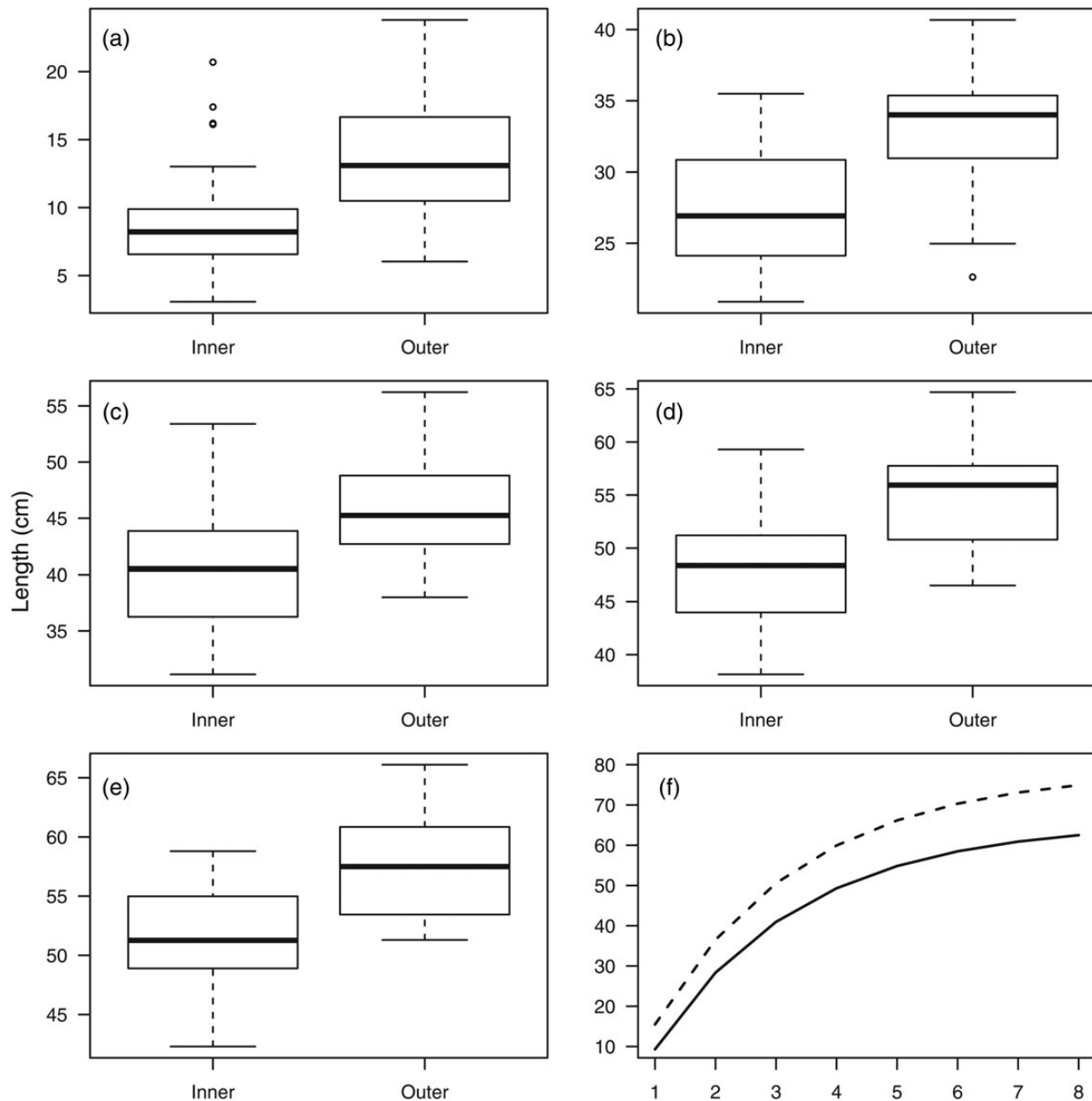


Figure 3. Comparison of age-specific lengths between inner and outer fjord cod at ages from 1 to 5 years (a–e, respectively). Medians are indicated bold horizontal lines, boxes span the inter-quartile range, and whiskers encompass values < 1.5 box lengths away from the box. Outliers are marked with open circles. Average von Bertalanffy growth trajectories of inner (solid line) and outer fjord (dashed line) cod are shown in f.

VB curves were successfully fitted to all back-calculated growth trajectories (R^2 ranged between 98.5 and 99.9%). Differences observed in the raw back-calculated length-at-age data were reflected by the VB curves (Figure 3f), such that estimated L_∞ was on average 65.6 cm (s.e.: 1.4 cm) for inner fjord fish and 78.6 cm (s.e.: 3.9 cm) for outer fjord fish and the difference was significant based on both the t -test ($t = -3.1$, d.f. = 43.7, $p = 0.003$) and the Wilcoxon's test ($W = 392$, $p = 0.009$). The average k was 0.413 (s.e.: 0.02) for cod in the inner fjord and 0.406 (s.e.: 0.02) for those in the outer fjord, and they did not differ significantly (t -test on log-transformed k : $t = 0.72$, d.f. = 57.5, $p = 0.47$). Robustness of the results with respect to one potential outlier value of L_∞ was tested; if this observation was removed, average

L_∞ for outer fjord was 76.2 cm and the difference with inner fjord remained significant (t -test: $t = -3.0$, d.f. = 47.2, $p = 0.004$; Wilcoxon's test: $W = 392$, $p = 0.014$).

The detected difference between the inner and outer fjord L_∞ was robust with respect to the back-calculation method. When using length-at-age data back-calculated using the Fraser–Lee method, the average L_∞ was 65.6 cm for inner fjord and 78.6 cm for outer fjord ($t = -3.1$, d.f. = 43.7, $p = 0.003$; $W = 392$, $p = 0.009$). Exclusion of the potential outlier decreased the average L_∞ in outer fjord to 76.2 cm, but the difference remained significant ($t = -3.0$, d.f. = 47.3, $p = 0.004$; $W = 392$, $p = 0.01$).

If data were restricted to fish with strictly overlapping size range (51.0–59.9 cm), the results were analogous: lengths-at-age were

systematically higher in the outer fjord population ($p < 0.05$ each t -test). L_{∞} was 67.2 cm in the inner population and 74.2 cm in the outer population, though the difference remained near-significant ($t = -1.8$, d.f. = 35, $p = 0.08$).

Discussion

Investigation of Risør fjord cod growth histories revealed that cod growth can substantially differ within a distance of 10 km or less. These differences in growth have considerable potential to produce dramatic differences in female egg production, as cod fecundity is well known to positively correlate with body length (Buzenta and Waiwood, 1982; Kjesbu *et al.*, 1996; McIntyre and Hutchings, 2003). In the outer fjord area, lengths-at-age 4 and 5 years were typically 7 cm longer than in the inner fjord, a difference that would correspond to a $\sim 25\%$ increase in individual fecundity in Newfoundland's northern cod (Kuparinen *et al.*, 2012), whereas in North Sea cod, the fecundity increase would be as high as 40–50% (Oosthuizen and Daan, 1974). Similar length–fecundity relationships are not available for Skagerrak cod, but there is no reason to believe that the reproductive benefit would not be in the same order of magnitude and, as indicated by the differences in asymptotic body size L_{∞} , the discrepancy is expected to further increase among older age classes.

In accordance with well-established life history invariants, the differences in L_{∞} documented in the present study likely reflect differences in the age and length at maturation (Charnov, 1993). Thus, the life history differences documented here suggest that cod fitness landscapes and their renewal ability might differ considerably within the same fjord region (e.g. Risør), which will likely translate into differences in the vulnerability of the local populations to fishing and their ability to recover from disturbances and cope with environmental variability. Similar observations made along the Skagerrak coast in cod juveniles (Dannevig, 1949; Lekve *et al.*, 2002) suggest that the pattern documented here reflects a broader pattern of life history differences between the two coastal habitat types. Indeed, also in the western Atlantic, smaller cod body size and genetic differentiation has been detected in Gilbert Bay, Labrador, when compared with offshore cod and an inshore population at a distantly southern location in Trinity Bay, Newfoundland (Ruzzante *et al.*, 2000). These observations underline the potential for substantial differences in environmental conditions, reproductive capacity, and even local adaptations among inshore and offshore cod at a variety of spatial scales within the same regions.

As with any life history study, potential biases in sampling can affect the interpretations. First, differences in mortality patterns experienced by populations can affect the phenotypic distributions of the sampled fish. In the present study, this is not likely to be the case: survival analyses based on an extensive capture–mark–recapture programme suggest that year-to-year survival (1–total mortality) does not significantly differ between inner and outer fjord cod populations or depend on the body sizes of the marked fish (Fernández-Chacón *et al.*, 2015). Early in life, body size has likely affected larval and juvenile survival, but there are no reasons to suggest that the size-dependence of larvae and juvenile survival differed between the two populations: broad meta-analyses across fish species and populations have detected a consistent strong, positive relationship between body size and early life survival (Perez and Munch, 2010). Therefore, it is unlikely that size-selectivity of the early life mortality had so largely differed between the populations that the differences in body size and growth documented later in life would arise from those. Moreover, the detected life history

differences represent the spawning stocks of the inner and outer fjord cod populations. Given the isolation of these populations and given that quantitative life history differences are typically moderately heritable (heritability ~ 0.2 – 0.3 ; Mousseau and Roff, 1987), if the documented life history differences have any genetic basis, it is reasonable to assume that they might be passed to future cod generations.

Second, virtually every fishing method is selective in one way or another, such that the distribution of fish observed through fisheries captures reflects that part of the population selected by the applied gear. However, for between-population comparisons, such as that undertaken in the present study, the most relevant thing is that the populations are sampled similarly. Indeed, the same size-selective sampling design was used for both populations in our study, resulting in similar size ranges of mature individuals sampled from both populations. Our sampling was not intended to detect underlying length-at-age distributions of the two populations, but rather demonstrate that fish of similar sizes have arrived at their current sizes through completely different growth trajectories, depending on whether cod were sampled from the inner or outer Risør fjord. Importantly, given that we intentionally used similarly sized fish in our work, the detected differences in growth are likely to be very conservative. Had cod smaller than 45 cm from the inner fjord population and cod larger than 65 cm from the outer fjord population been included in the samples, the differences in growth would have been even more pronounced. This is well illustrated by the ages of the sampled fish: no 6- to 8-year-old fish smaller than 65 cm were evident in the outer fjord samples, whereas in inner fjord, there were several such individuals (Figure 2).

The primary objective of the present study was to determine whether growth differs substantially between cod inhabiting inner and outer sections of a single fjord. Given our results, the question arises as to what the causal mechanisms for such intra-fjord differences in growth might be. It is notable that body size differences were already established by the age of 1 year, well before fish were exposed to fishing. On the other hand, inner fjord cod are not able to compensate for the size differences later in life, as would be expected if the reason for slower growth was only temporary and not present throughout life. Inner fjord temperatures are slightly higher than temperatures in the outer fjord (on average by 0.6 and 1.4°C higher at 5 and 10 m depths, respectively; Supplementary material), which might cause additional stress for cod already close to the edge of its species range. Indeed, warmer summer temperatures have been found to reduce the occupancy of cod in optimal shallow feeding habitats (e.g. eelgrass beds) in a neighbouring fjord in Skagerrak (Freitas *et al.*, 2015). Therefore, growth conditions in the inner fjord might be poorer due to worse feeding opportunities and increased stress.

In addition to being the result of a plastic response to environmental differences inside and outside the fjord, population differences in life histories could result from adaptation to differing local selective pressures. Returning to Bergmann's rule (Bergmann, 1847; Atkinson, 1994), smaller body sizes might be adaptive inside the fjord, where water temperatures are generally higher. Further, within sill fjords such as Risør, the water temperature is stratified (Dannevig, 1933), while exposed areas along the coast experience more vertical mixing (Supplementary material; Dahl *et al.*, 1983). Coupled with the fact that the negative impact of temperature on diel vertical migratory feeding behaviour of Tvedestrand cod was more pronounced for larger individuals (Freitas *et al.*, 2015), such differences in thermal regimes would be expected to select for slower growth rates inside

the Risør fjord. Local adaptation at such a microgeographic scale would be remarkable, although studies capable of disentangling genetic from environmental effects (e.g. common-garden experiments) are needed to identify it. Nonetheless, evidence of homing by spawning cod at remarkably small spatial scales within fjords (Skjærraasen *et al.*, 2011) suggests that local adaptation at similarly small spatial scales is possible.

The present study indicates that Atlantic cod life histories can differ substantially among groups at very small geographic scales (20 km²), and that the differences are likely to translate into differing reproductive capacity and fitness landscapes of the local populations. These findings are consistent with an emerging body of knowledge which indicates that marine fish, such as cod, are often managed as excessively large reproductive units (Hutchinson *et al.*, 2001; Jonsdottir *et al.*, 2007; Knutsen *et al.*, 2011). If spatial mismatches between management units and biological or evolutionary units are not resolved, management will not be able to successfully adopt the strategies necessary to mitigate the impacts of fishing and climate change. This can have long-term socio-economic and biological consequences. Catch levels set at an inappropriately large spatial scale will result in higher fishing mortality and a greater risk of overfishing and depletion for comparatively small stocks relative to comparatively large stocks. For example, for Risør cod, if population productivity is predicted based on population parameters of cod sampled in the outer fjord or central Skagerrak and fishing mortality limits are set accordingly, a mortality level that is sustainable for larger outer fjord cod could lead to a collapse of the population of small inner fjord cod. Nonetheless, this population is commonly targeted by recreational fisheries and is therefore of considerable economic value for coastal villages through tourism. From a climate-change perspective, a spatial mismatch between management units and biological units will reduce the ability of management agencies to effectively adapt fisheries management practices at spatial scales appropriate to the spatial scales of adaptation by cod to climate change. If smaller body sizes of inner Risør cod indeed resulted from local adaptation to higher temperature, preserving these genotypes would be vital for cod adaptation to increasing temperatures in the future. To this end, fishing in the inner fjord should be drastically limited, and even assisted migration could be considered as a way to promote local adaptation of other coastal or nearby populations to increasing temperatures (Aitken and Whitlock, 2013).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

The study was funded by the Academy of Finland (AK), Canada's Natural Sciences and Engineering Research Council (Discovery Grant to JAH and Canada Graduate Scholarships to NER and RAO), and the Norwegian Research Council (HAVKYST Grant to JAH and Mobility Grant to RAO).

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Handling editor: Sarah Kraak