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Fine-scale life-history structure in a highly mobile marine fish

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ABSTRACT

Background: A highly mobile marine fish, Atlantic cod (*Gadus morhua*), inhabits southern Norwegian coastal habitats that offer limited potential for individual dispersal and migration.

Questions: Do coastal populations of cod differ in life history? If so, is the variability spatially persistent and does it vary with time? What factors are responsible for life-history differences among the potential populations?

Method: Use long-term, fisheries-independent survey data to measure and compare life-history metrics among nine regions along the southern Norwegian coast. Conduct maturity analyses, using generalized linear mixed-effect models, where the probability of being mature is a function of fixed effects (length, age, weight, sex, and growing degree days) and random effects (location and year class nested within location).

Results: We detected that the probability of being mature has increased spatially (along an increasing longitudinal cline) and temporally (throughout a 30-year time-series). Neither of these trends could be fully explained by variation in sea temperature or population density.

Conclusion: Life-history variability in a highly mobile marine fish can be evident, and temporally persistent, at spatial scales considerably smaller than those encompassed by established fisheries management units and species recovery strategies. Our findings provide empirically defensible justification for studies on the ecological factors and evolutionary mechanisms responsible for producing and maintaining this variability.

Keywords: *Gadus morhua*, life history, maturity, Skagerrak, small-scale.

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INTRODUCTION

Life-history traits define the fitness of organisms and are thus fundamental for understanding evolutionary and ecological responses to natural and anthropogenic components of environmental change. In fish, basic life-history parameters such as growth and age and size at maturity are integral to the assessment of population status and, therefore, fisheries management. Namely, these are the key determinants of population growth rate, reproductive capacity, and biomass production (Kuparinen and Hutchings, 2012) and, therefore, they directly affect population resilience to fishing and ability to recover from overfishing.

In marine systems, there is widespread evidence for temporal shifts in fish life histories, typically showing a trend towards reduced individual growth rates and maturation at younger ages and smaller body sizes (Hutchings and Baum, 2005; Sharpe and Hendry, 2009). These changes can be caused by the environment or by human activities such as harvesting. For example, life histories can be modified through changes in temperature (Cox and Hinch, 1997; Rogers *et al.*, 2011), oxygen and salinity (Cardinale and Modin, 1999). Fishing can affect growth rates directly through density-dependent feedbacks associated with reductions in population size (Lorenzen and Enberg, 2002; Sinclair *et al.*, 2002). Alternatively, the selective removal of individuals with a certain set of life-history traits can also induce evolutionary changes in populations targeted by fishing (Hutchings, 2005; Swain *et al.*, 2007).

Distinguishing the key drivers of life-history change in marine systems remains a challenging task. First, most studies and available data sets focus on temporal changes in oceanic populations across relatively large spatial scales, whereas the spatial scale of true life-history structuring is likely to be much finer (Wright *et al.*, 2011). Averaging across differing populations can mask or obscure patterns manifest by individual populations and can make it difficult to link life-history trends to any particular factor, as the latter might vary considerably among locations. Second, several factors (e.g. climate and fishing) may co-vary in time, such that they cannot be readily disentangled (Heino and Dieckmann, 2008).

Identifying biologically meaningful spatial scales of life-history divergence in marine fish represents a substantial challenge for management and conservation (Conover *et al.*, 2006). Fisheries harvesting decisions and conservation-based recovery strategies are typically made at scales several orders of magnitude larger than the spatial scales at which life histories differ. The Atlantic cod (*Gadus morhua*) provides an example. Management units can extend more than 1000 km, yet differences in maturation and growth have been documented at distances of tens to hundreds of kilometres (Wright *et al.*, 2011; Kuparinen *et al.*, 2015). In light of these findings, the assumption that nearby populations, or even those considered part of the same 'unit', are similar is evidently not always well justified. When incorrect, this assumption can lead to over-exploitation of populations whose productivity is lower than the average for which fishing pressure is adjusted. At extreme levels, this can lead to the collapse of local populations and loss of locally adapted genotypes (Svedäng *et al.*, 2010). From an applied perspective, further understanding of the spatial scale of life-history variation and its potential drivers is integral for sustainable fisheries management and conservation of local populations. From an ecological and evolutionary perspective, the question arises as to how life-history variability can persist at spatial scales far smaller than the distances at which individuals are theoretically capable of dispersing, given that gene flow would be predicted to swamp such differences (Bradbury *et al.*, 2008).

Coastal systems represent an under-used opportunity for understanding drivers of life-history variations at small spatial scales. Here, demographic processes may occur within isolated local populations on comparatively small spatial scales and environmental gradients (e.g. temperature or density). The southern Norwegian coastal cod system provides a unique opportunity to examine Atlantic cod life-history traits at small spatial scales. These populations follow a longitudinal cline restricted northward by land and southward by the open ocean. While there are no physical barriers limiting gene flow, populations are genetically differentiated into separate populations at extremely fine spatial scales: from tens (Jorde *et al.*, 2007) to hundreds of kilometres (Knutsen *et al.*, 2003). Populations occupy small coastal areas in fjords and outer skerries, with movement between them being surprisingly limited: mark–recapture studies on local populations have estimated dispersal rates as low as 0.7% and 1.2% (Knutsen *et al.*, 2011; Rogers *et al.*, 2014). Egg density is also higher inside fjords, with levels falling outside the fjords, and especially dropping over sills or shallow areas outside the fjord (Knutsen *et al.*, 2007). Retention of eggs seems to be caused by circulatory patterns where eggs are generally located in the water layers with an average net flow in the fjords (Ciannelli *et al.*, 2010).

The combination of locally restricted movement, genetic differentiation, and coastal positioning results in a fine-scale spatial population structure along a longitudinal cline, an ideal candidate system for examining differences in life-history traits in cod at small spatial scales. Using a unique historic data set from coastal fisheries-independent surveys, our objectives are to: (1) examine the spatial and temporal variability of cod maturity across nine putative southern Norwegian coastal cod populations, and (2) explore whether observed differences can be predominantly explained by differences in local environments.

METHODS

Gill net survey data

Individual life-history data are available for 9414 cod sampled from nine locations along the southern Norwegian Skagerrak coast (Fig. 1, Table 1). Trammel nets were used to collect cod during annual late-autumn surveys (November–December) by the Institute of Marine Research Flødevigen. The survey, which began in 1984, continues to the present,

Table 1. Skagerrak coastal cod sampled during gill net survey: locations, sample sizes (*N*), years sampled, mean total body length (range), and mean age (range)

Sampling site	*N*	Years*	Length (cm)	Age (years)
Øygarden	151	2010	40 (20–83)	1.1 (0–5)
Farsund	742	2003–5, 2007–14	42 (16–90)	1.7 (0–8)
Korshamn	284	2003–5, 2007–8	44 (27–85)	1.4 (0–7)
Mandal	1311	2003–14	42 (17–88)	1.3 (0–7)
Høvag	2321	1985–2014	41 (17–88)	1.4 (0–8)
Flødevigen	1217	1984–2008	40 (13–105)	1.5 (0–10)
Jomfruland	1757	1984–2014	38 (14–95)	1.6 (0–10)
Hvasser	1187	1984–2014	36 (14–92)	1.3 (0–8)
Hvaler	444	2001–8, 2011	31 (14–75)	0.8 (0–4)

* No sampling was undertaken in 2009.

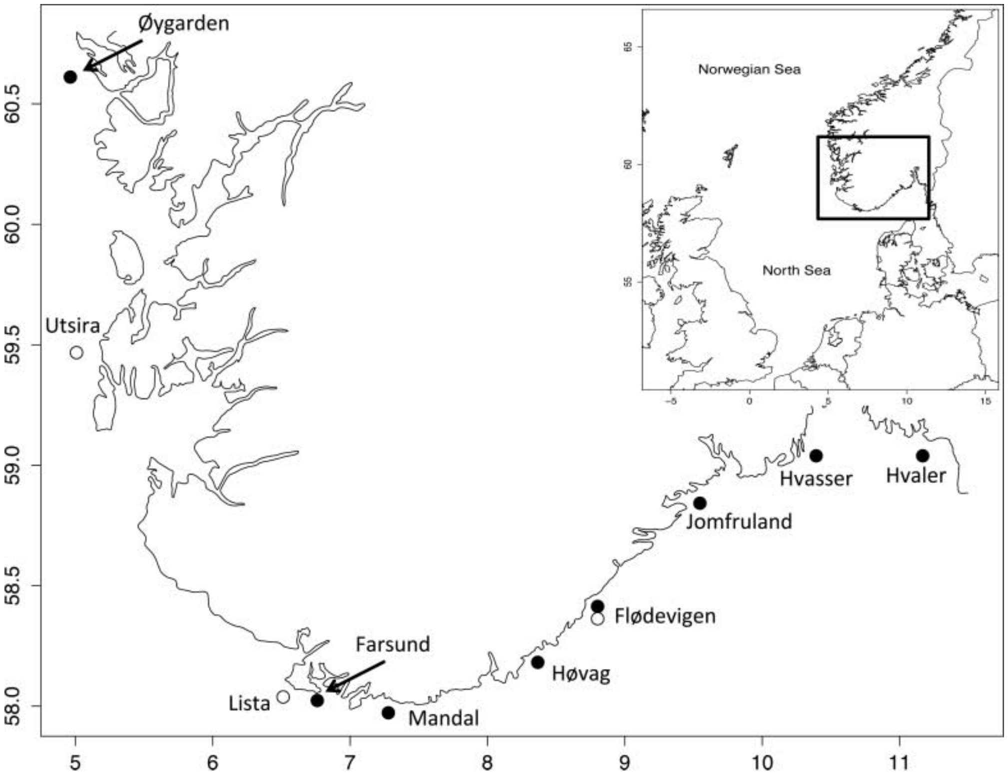

Fig. 1. Study area. Cod sampled from the Norwegian coast at nine locations. Solid circles represent gill net sampling locations. Empty circles represent fixed hydrographic stations.

consistently deploying the same sampling gear (45 mm mesh size) at well-defined sites. Data are available for an average of 11 years (range: 1–19 years) at each sampling location (Table 1). Nets were set in the evening and hauled the following morning, fishing for ~15 hours in shallow, near-shore waters (depth: 5–15 m). Upon collection, each individual was measured for total length (cm) and weight (g). Sex and maturity stage were determined via macroscopic inspection of the gonads. Otoliths were extracted for later age determination, following Dannevig (1933).

Temperature data

Temperature data were obtained from three fixed hydrographic stations along the Norwegian coastline: Utsira, Lista, and Flødevigen (Fig. 1). For more than 70 years, each station has recorded temperature at depths of 1 m and 19–20 m. Temperature is recorded bi-monthly at Utsira and Lista but daily at Flødevigen.

To obtain temperature estimates for each net-sampling location, we used the NorKyst-800 numerical ocean modelling system (Albretsen *et al.*, 2011). The NorKyst-800 applies the hydrodynamic model ROMS (Regional Ocean Modelling System: http://myroms.org), widely used by the scientific community, to provide data on coastal physical environmental variables, such as temperature, with a resolution of 800 m (horizontal grid cells at 20 m depth). The model was used to establish a relationship for temperatures at each net-sampling location relative to the nearest hydrographic station. The model was run for two years (2011–12), during which daily temperature estimates were extracted for coordinates at both sampling locations and hydrographic stations. For each sampling location, a linear model was then fit between the location and the nearest hydrographic station's respective temperature estimates. These location-specific relationships were then applied to the historic temperature data from the hydrographic stations nearest to each location, thus obtaining historic location-specific temperature estimates. These location-based temperature estimates were then used for all temperature analyses.

Temperature metric

To account for variability in the thermal environment that individuals experience at different locations and temporally, we used the metric 'thermal integral growing degree-days' (GDD). Using GDD is advantageous because it reflects the physiological age of an individual; thus it not only incorporates calendar time but any temporal and/or spatial variability in thermal environments (Neuheimer and Taggart, 2007; Neuheimer *et al.*, 2008). The GDD (°C-day) at day n was calculated for each individual, using the formula specified by Neuheimer and Taggart (2007):

$$\mathrm{GDD}(n) = \sum\nolimits_{i=1}^{n} (T_i - T_{Th})\Delta d, \qquad T_i \geq T_{Th}$$

where T_i is the interpolated mean daily temperature at day i and $i = 1$ at spawning, T_{Th} is the threshold temperature ($T_{Th} = 0$°C) and Δd is the time step, or days above the threshold temperature. The birth date of all individuals was assumed to be 1 April in the year that the fish were born, given that Norwegian coastal cod from this region generally reproduce in late winter/early spring (Dannevig, 1930).

Statistical modelling

Maturity analyses were conducted using generalized linear mixed-effect models, assuming that the maturity status data were binomially distributed. The first mixed-effect model fit included only sampled individual traits as fixed effects. In this model, the probability of being mature (M) was predicted as a function of the fixed effects (length, age, weight, and sex) and the random effects (location and year class nested within location):

$$\mathrm{M} \sim \mathrm{Length} + \mathrm{Weight} + \mathrm{Sex} + \mathrm{Age} + (1 \mid \mathrm{Location/Year\ class})$$

The second model was identical to the first in structure, although instead of including age – a metric-dependent calendar time that does not vary between locations or with time – the thermal integral GDD was included as a fixed effect:

$$\mathrm{M} \sim \mathrm{Length} + \mathrm{Weight} + \mathrm{Sex} + \mathrm{GDD} + (1 \mid \mathrm{Location/Year\ class})$$

Including GDD as a fixed effect will still account for age, although it will also represent an individual's thermal history, thus accounting for spatial and temporal differences in thermal regimes. Both age and GDD could not be considered in the same model owing to a strong correlation between the two variables. Model selection was performed following Zuur *et al.*

(2009), using the stepwise model reduction. To examine the robustness of the model selection and final models, stepwise forward model selection was also performed. The variance component, a measure that represents the amount of variance in the model associated with the random effect, was calculated for each of the random effect structures. Random effects from the final model were extracted and examined for trends to illustrate trends in maturity not explained by the fixed effects. All analyses were conducted with R v.3.1.0 (R Development Core Team, 2014).

RESULTS

Trends in length and age

There is no obvious temporal trend in the mean length or age of the fish sampled at most of the locations (see figures 1 and 2 at www.evolutionary-ecology.com/data/2979Appendix.pdf). The three populations that did exhibit temporal trends (Hvaler, Hvasser, Jomfruland) exhibited similar declines in both mean length and mean age. These three populations represent the most easterly of the sampling locations.

Model selection

For model A, which uses calendar time as a metric of age, weight – as a non-significant variable – was removed during model selection, leaving length, sex, and age as significant fixed effects (Table 2). For model B, which included the growth integral (GDD) as a proxy of physiological age (as opposed to calendar age), weight was again removed during model selection, leaving length, sex, and GDD as significant fixed effects (Table 2). For both models, the fixed effects of length, age, and GDD all have positive regression coefficients,

Table 2. Generalized linear mixed-effect models (assuming binomial distributions) for the probability of being mature in Norwegian coastal cod, where the binary response variable (adult = 1 and juvenile = 0) is a function of a combination of predictors including both fixed effects (length, age, sex, and GDD) and random effects (random intercept for both location and year class)

	Fixed effects		Random effects	
Model	Term	Estimate ± S.E.	Term	Var*
Model A	Probability of maturity ~			
	+ Length[#]	0.087 ± 0.005	+ Location	0.197
	+ Sex (Male)[#]	0.127 ± 0.05	+ Location/Year class	0.341
	+ Age[#]	0.555 ± 0.06		
Model B	Probability of maturity ~			
	+ Length[#]	0.081 ± 0.006	+ Location	0.186
	+ Sex (Male)[#]	0.125 ± 0.05	+ Location/Year class	0.344
	+ GDD[#]	0.019 ± 0.002		

* The proportion of total variance in the model associated with the random effect term.
[#] Significant predictor variable.

indicating that they have a positive additive effect on the probability of being mature. As for differences between the sexes, the male estimate was positive for both models, indicating that, everything else being equal, males have a higher probability of being mature than females. Model selection between A and B was performed using the deviance explained by the models. Model B, the one that incorporated the thermal integral GDD instead of age, was the superior model because it had a smaller residual deviance, indicating a better fit (Deviance: A = 9219.2 and B = 9195.7). Therefore, the results from model B were used in the following analyses.

Random effects

Location

The proportion of variance associated with the random effect 'Location' decreases from 0.197 to 0.186 when GDD is included in the model, representing the added value of the thermal growth integral in the model. After examination of the random effects for each location, there remains quite a bit of variation between locations (random effects ranging from −0.71 to 0.98). A positive random effect represents a location with a higher likelihood of being mature, while a negative random effect represents a location with less likelihood of being mature. When these random effects are plotted against their respective longitudes, a near-significant longitudinal trend emerges ($P = 0.075$, $r^2 = 0.31$) (Fig. 2). When an outlier location, Farsund, is excluded, the relationship becomes significant ($P = 0.002$ and $r^2 = 0.79$).

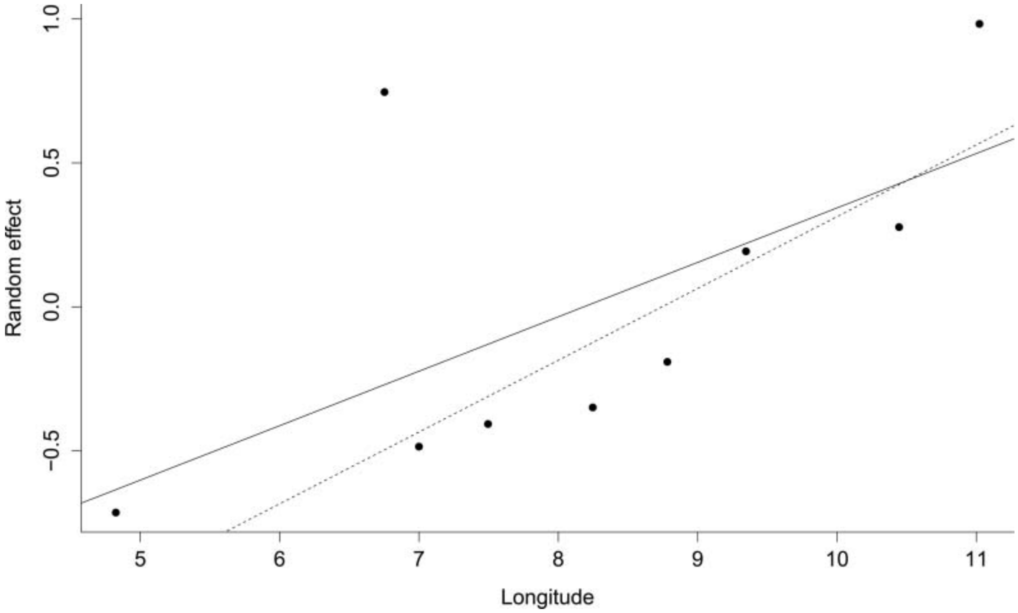

Fig. 2. Random effects of location versus longitude. Solid line represents linear model for all locations ($P = 0.075$, $r^2 = 0.31$). Dashed line represents linear model for all locations excluding the outlier Farsund ($P = 0.002$, $r^2 = 0.79$). Random effects extracted from model B.

Based on data from the survey, we are able to test the alternative hypothesis that density is responsible for the longitudinal trend in maturation. One would expect density to be inversely correlated with the random effects from our model: at lower densities, there are likely to be more resources available per individual who then experience faster growth and subsequently mature earlier [growth rate is negatively correlated with age at maturity in fish (Hutchings, 1993)]. The process resulting from a low density of fish would result in a positive random effect. To examine this hypothesis, we used the mean catch rate at each location as a proxy for density. The yearly catch rate was calculated as:

$$\text{Catch rate} = \frac{\text{Number of fish (45–55 mm)}}{\text{Number of nets}}$$

The mean catch rate was taken across available years at a location. When the random effect is plotted against the respective catch rate for each location, there is indeed a significant negative relationship ($P = 0.0342$, $r^2 = 0.42$) (Fig. 3).

Year class

The proportion of variance associated with the random effect of year classes at each location (Location/Year class) increases from 0.341 to 0.344 when GDD is included in the model, an indication that at each location GDD explains variation between year classes almost as well as age. After examining the random effects for year class at eight of the nine locations (Øygarden was excluded owing to insufficient data), it is evident that there is quite a bit of variation in the random effects (−1.84 to 1.61). In order to examine temporal trends in year-class random effects, we performed a linear analysis of the random effects versus year class (Fig. 4). Of the eight locations, four had near significant to highly significant

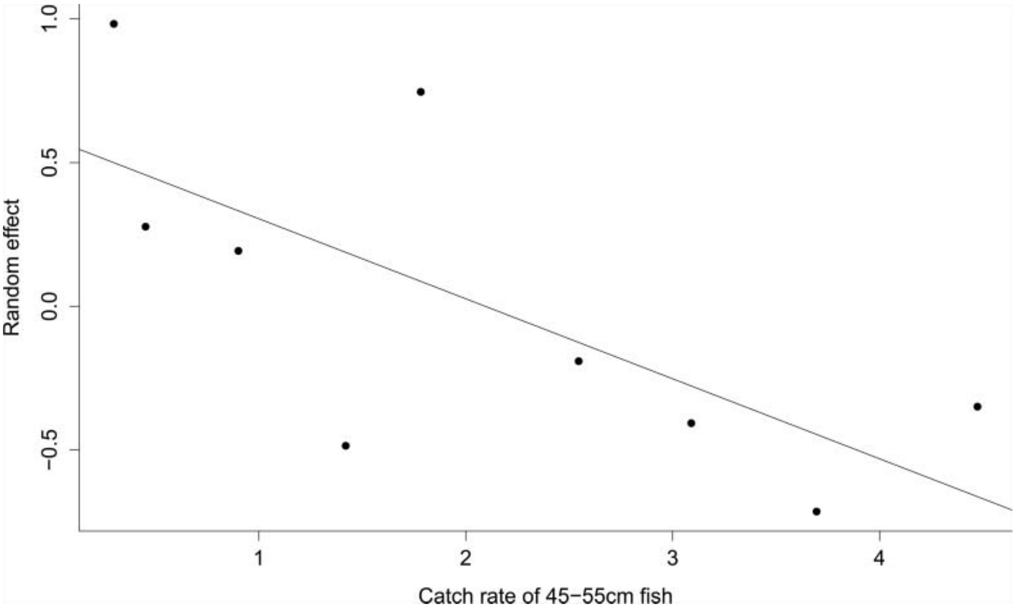

Fig. 3. Random effects of location versus catch rate of fish of 45–55 cm, a proxy for density ($P = 0.0342$, $r^2 = 0.42$). Random effects extracted from model B.

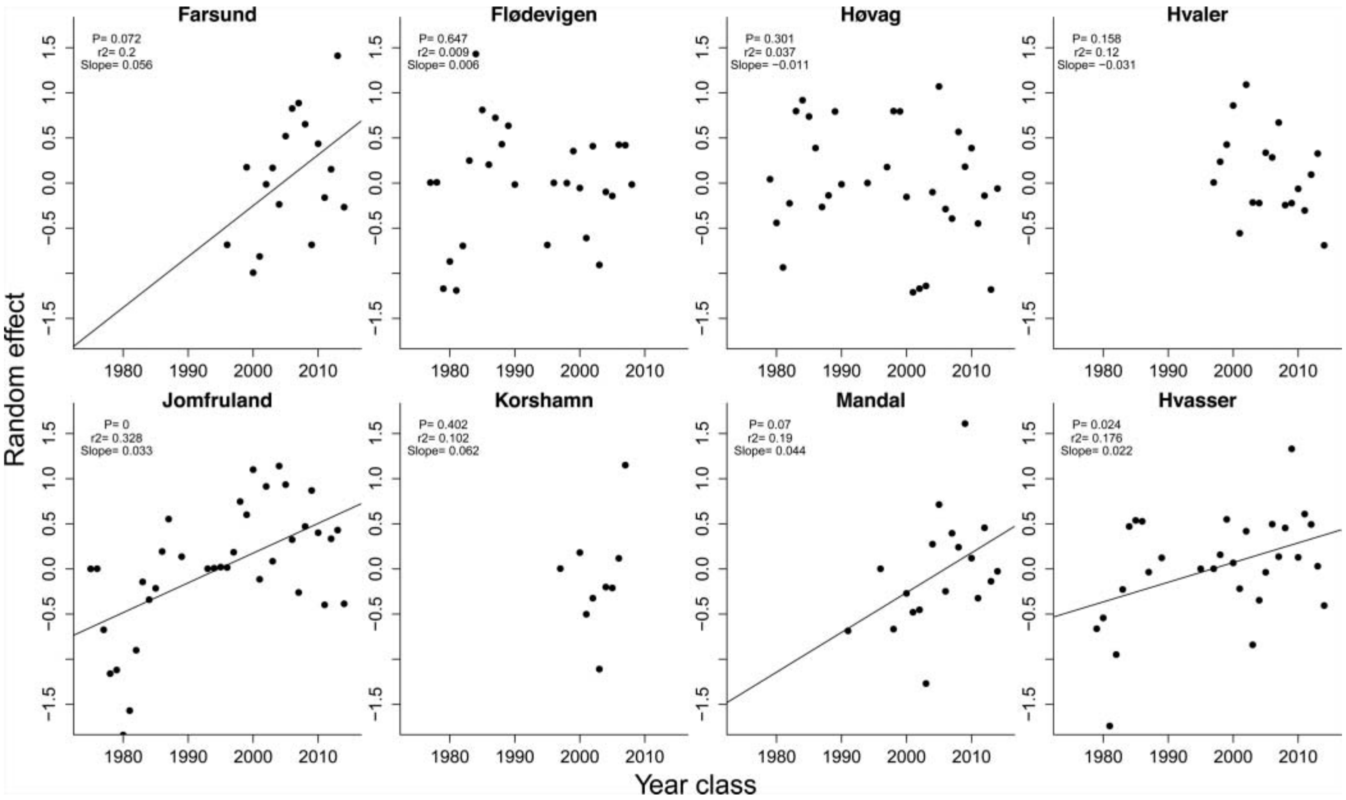

Fig. 4. Linear models of random effects of year class versus year class. The respective *P*-values (*P*), correlation coefficients (r^2), and slopes are shown in the upper left-hand corner of each panel. Random effects extracted from model B.

temporal relationships ($P < 0.10$): Farsund ($P = 0.07$), Mandal ($P = 0.07$), Jomfruland ($P < 0.001$), and Hvasser ($P = 0.02$), and all of the significant relationships had positive slopes, ranging from 0.022 to 0.056. This positive relationship indicates that the probability of being mature at those locations has increased temporally (Fig. 4).

To further investigate if the observed trends in maturity are density driven, we ran linear models plotting the density of location at the time of survey against the respective year-class's random effect (Fig. 5), the hypothesis being that density is inversely correlated with the year-class effect. Higher densities during the first year of a year class would be expected to result in a lower probability of being mature for the year class (or a negative random effect), as initial growth is poorer due to higher competition. Surprisingly, when density was plotted against the random effects of year class at each location, there were no significant relationships, suggesting that density does not explain the temporal variation in the probability of being mature at locations (note that no density data were available prior to 2001).

DISCUSSION

We examined life-history variability among nine southern Norwegian coastal cod populations and found an increasing temporal and longitudinal trend in the probability of being mature, both of which density and temperature failed to resolve. After accounting for variation in an individual's thermal environment, more eastern cod populations and recent year classes were found to have a higher probability of being mature. While subtle differences in thermal regimes explained some variation in life-history traits, they failed to resolve major spatial or temporal trends. We found that density correlated negatively with the random effect from each location, suggesting that density-driven processes are responsible for the observed spatial differences in maturity. If density is a key driver of fluctuations in maturity in this coastal system, then we would also expect to find temporal variations to be similarly correlated with fluctuations in density. However, while we found a temporal increase in the probability of being mature, density did not correlate with these increases or even fluctuations at any of the locations. Thus after accounting for variability in common key drivers, a positive longitudinal and temporal relationship remains in the probability of being mature.

Spatial variability in growth and length of cod along the southern Norwegian coast were first documented in 1933 (Dannevig, 1933) but remained largely unexamined until a recent resurgence of life-history studies (Lekve *et al.*, 2002; Olsen *et al.*, 2004, 2008; Rogers *et al.*, 2011; Kuparinen *et al.*, 2015). With the exception of Kuparinen *et al.* (2015), studies that have identified spatial variation in life-history traits have failed to detect any spatial patterns (Lekve *et al.*, 2002; Olsen *et al.*, 2004, 2008; Rogers *et al.*, 2011). Temporal trends in life history have also been noted previously in this coastal system, but in contrast to our findings they were related to environmental variables: spring-time temperature (Rogers *et al.*, 2011) and wind stress and density (Lekve *et al.*, 2002).

We suggest that density is unlikely to be a primary driver of maturity in this coastal system. First, density explained none of the temporal trends in maturity at any of the locations. If density were a key factor, we would have expected to observe temporal fluctuations in maturity correlated with local density. Second, in a comprehensive study that examined 91 years of age-0 cod growth data across the Skagerrak coastline, Rogers *et al.* (2011) found that although density did influence growth rate in age-0 cod, this effect was only

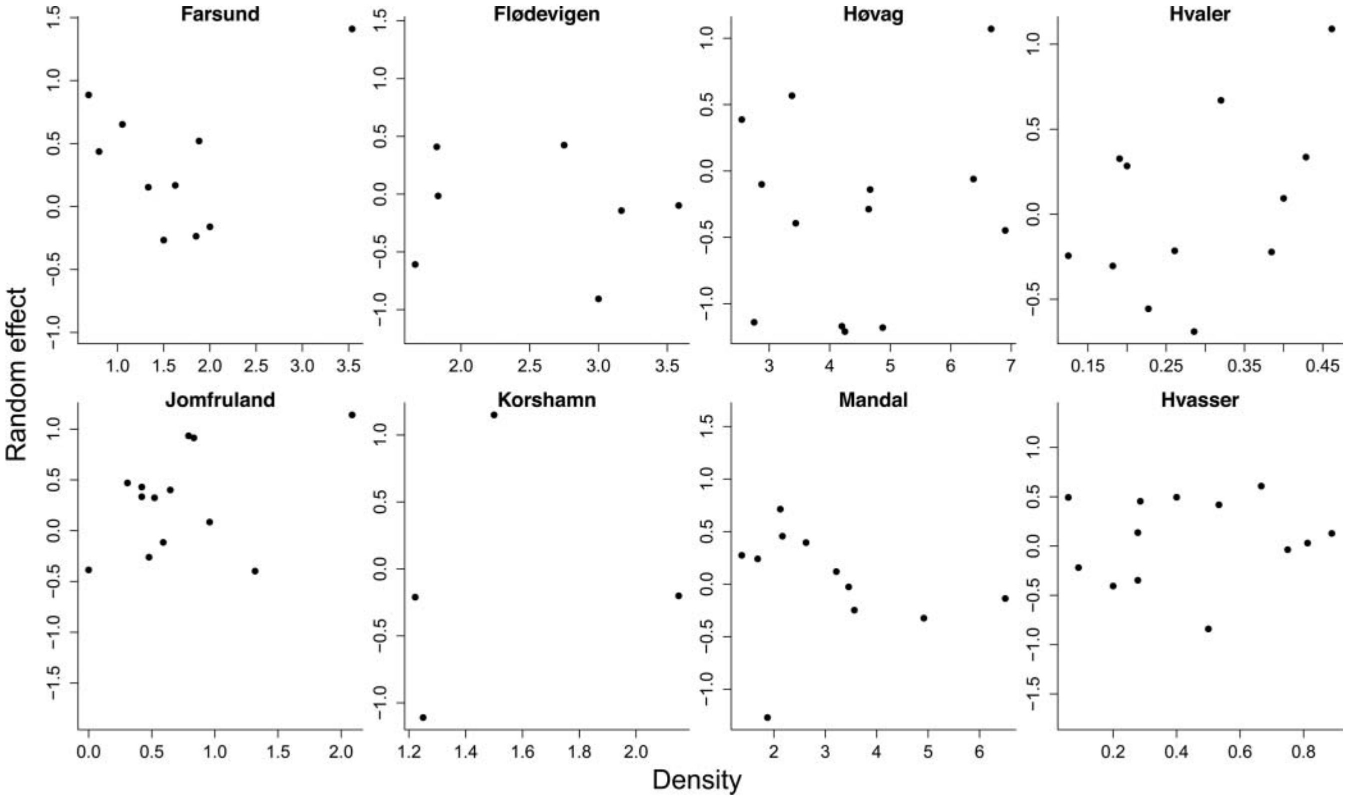

Fig. 5. Random effects of year class versus density in year of birth. No relationships were significant below a *P*-value of 0.10. Random effects extracted from model B.

detectable at uncharacteristically high densities. Throughout the near-century of data, with over 10,000 beach seine tows, only 5% of tows qualified as 'high density', and less than 1% in the past decade (Rogers *et al.*, 2011).

We cannot discount the possibility that other environmental variables that we were unable to account for are responsible for the spatial and temporal trends. For example, when Lekve *et al.* (2002) examined length dynamics in juvenile Skagerrak cod, they found that wind-stress events, which cause upwelling, correlated positively with growth. In contrast, Cardinale and Modin (1999) reported that length-at-maturity correlated negatively with oxygen and salinity, albeit for cod in the Baltic Sea, where oxygen levels and salinity can be unfavourable for cod. Although we controlled temperature from a physiological perspective, temporally increasing temperatures could have ecological or behavioural consequences that are not accounted for by growth integrals (Freitas *et al.*, 2015).

Another possible explanation for observed spatial and temporal trends is adaptation to local selective pressures. One widely postulated cause of human-induced evolution in fish populations is fishing mortality. While the southern Norwegian coast is not subject to large-scale commercial fisheries, it does experience substantial selective removals via recreational fishing (Julliard *et al.*, 2001), an activity postulated to yield selection intensities sufficiently high to generate evolution (Cooke and Cowx, 2004; Lewin *et al.*, 2006; Sutter *et al.*, 2012). For example, Kleiven *et al.* (2011) found recreational lobster traps contributed 65% of the total fishing effort (a proxy for fishing mortality) along ~200 km of the southern Norwegian coastline. Furthermore, results from a local mark–recapture study found that recreational fishing methods for a local cod population accounted for 71% of the total fishing mortality (Kleiven, *et al.* in press).

Natural mortality of age-1 and older Skagerrak coastal cod is around 10–30% per year, though generally less for the older and bigger cod (Fernández Chacón *et al.*, 2015). In addition to fishing, natural selection may therefore also play a role as a driver of life-history evolution. There is strong support from genetic studies that coastal Skagerrak holds a network of local fjord populations, where the habitats facing the open ocean seem to be affected more by an oceanic North Sea cod component (Knutsen *et al.*, 2003, 2004; Jorde *et al.*, 2007). However, it is unknown to what extent natural selection varies among the various populations of cod in Skagerrak, potentially driving the observed spatial and temporal trends in maturation. A mark–recapture study on cod from eastern Skagerrak found that a significant proportion of the fish migrated to the North Sea basin for a part of their life cycle (Svedäng *et al.*, 2007), while mark–recapture studies from western Skagerrak suggest that such offshore migrations are extremely rare (Rogers *et al.*, 2014). Thus, it is possible that changes in life-history traits of cod from eastern Skagerrak are more strongly influenced by offshore processes.

As with all life-history studies, there are inherent limitations to consider. First, the selectivity of fishing methods might influence how representative of the population the sampled fish are. However, this is unlikely to be an issue here because the same trammel net size has been used consistently throughout the survey period. Thus, any selectivity imposed by the trammel nets will have affected all locations similarly throughout the years of the survey. Second, any inaccuracies in initial ageing and determination of maturation could play a role in masking trends. Third, our estimates for temperature at each location were estimated, and thus are dependent on the relationship between sampling location and hydrographic location identified using the NorKyst-800 model. While we believe the model extracted sufficiently defensible relationships, it is possible that the failure of temperature to fully resolve temporal and spatial maturity trends could be attributable to a lack of *in situ* environmental data. Finally, when calculating the growing degree-day of an individual, we made two important assumptions: (1) individuals caught at a sampling location have been there throughout their lives [supported by low movement rates (Knutsen *et al.*, 2011)]; and (2) the temperatures experienced by individuals do not differ from those estimated at each sampling location.

Our work is part of a growing set of studies that together suggest that life-history variability in marine fish can be evident, and temporally persistent, at spatial scales considerably smaller than those encompassed by fisheries management units and species recovery strategies. This corpus of research provides empirically defensible justification for future work on the ecological factors and evolutionary mechanisms responsible for producing and maintaining this variability.

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