Spatial, interannual, and generational sources of trait variability in a marine population

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ABSTRACT

Life history traits of individuals in marine populations exhibit large sources of variability. In marine fish, variation of individual size at a given age has three main components: *1. spatial*, correlated with the location in which individuals are caught, *2. temporal*, correlated with the time when individuals are caught, and *3. generational*, correlated with the year of birth of the examined individuals. These variations, if present, have practical implications for individual fitness as well as for sampling, survey design, and population assessment. Disentangling these variations and understanding their sources is hard, given the potentially correlated nature of their effects on individual traits. This study examines the size-at-age relationship of the Bering Sea Pacific cod -- an economically and ecologically important groundfish. We used extensive records spanning 1994 to 2016 (inclusive) of 25,213 observations of both environmental variables and catch lengths and ages. We found that the average size of individuals of the same age could differ in size up to 7 cm. Notably, we found that the cohort composition of the sampled population explained > 75% of the year effect, and that individuals caught in the northwest and shallower portion of the sampling area were on average 5 cm smaller than individuals caught in the southern and deeper portion. We further found that northwest movement of young cod (age 1-5) as a result of warming places individuals in areas where we predict them to have smaller size-at-age. Smaller and less conditioned individuals are less fecund and may not be able to perform long migrations to return to their distant spawning grounds. Both the spatial distribution and water temperature experienced by Pacific cod in the Bering Sea are changing, and this study provides a mechanism for how these changes affect Pacific cod life-history-traits and individual fitness.

KEY WORDS: traits, cohort, spatial ecology, phenotypic plasticity, growth, Bering Sea, size-at-age

INTRODUCTION

Life history traits of individuals in marine populations exhibit large sources of variability. Trait variability affects individual fitness (Webb et al. 2010) and the assumptions necessary to sample the population (Puerta et al. 2019). Growth rate is one of such traits that results in individuals having vastly different body sizes at a given age. In turn, body size and growth rate have well-known fitness consequences, which for marine fish are especially evident during early life stages (Sogard 1997, Houde 2008). Observed variability of individual growth rates originates from multiple processes, including heterogeneous environmental conditions experienced by different individuals (Matta et al. 2010), long-lasting environmental effects experienced during early life history stages (Hurst et al. 2012), complex genetic structures (Spies 2012), density-dependence (Stige et al. in press), or size-selective predation (Bailey and Houde 1989). As a result of these multiple and interacting processes, individual size at a given age may be grouped according to three main patterns of variability: *1. spatial*, correlated with the location in which individuals are caught, *2. temporal*, correlated with the time (e.g., year in multi-year sampling programs) when individuals are caught, and *3. generational*, correlated with the year of birth of the examined individuals.

Decomposing trait variability among the three main patterns can lead to new insight on the processes that generate such variability and on their potential consequences to management of the population and fitness of individuals. However, identifying patterns and processes driving growth variability in marine fish is challenging due to their correlated nature. For example, temporal growth variability could be driven by spatial variability, if the distribution of the individuals changes over time. Likewise, temporal variability could be driven by a generational effect, if the proportion of individuals from different cohorts changes over time. A typical approach to discern different sources of growth variability is that of using common garden experiments, where individuals from different geographic origins are exposed to similar experimental conditions (e.g., Hutchings et al. 2007); however, these approaches are hard to conduct in adult individuals with long life span and slow growth rate (Germino et al. 2019). Retrospective analyses of field data are a valid alternative (Thorson and Minte-Vera, 2016), but require large sample sizes spanning over environmentally contrasting periods .

Pacific cod (*Gadus macrocephalus*) is a marine groundfish widely distributed across the Bering Sea, Gulf of Alaska, and Aleutian Islands area (Thompson, 2016). It is one of the most important species for commercial fishing off of Alaska. In addition, Pacific cod is ecologically significant as both a predator and prey species. It serves as prey for multiple marine mammals, including the endangered Steller sea lions (Calkins, 1998). Gaichas and Francis (2008) found that Pacific cod is the most interconnected species in the Gulf of Alaska food web, making it one of four critical groundfish species, together with walleye Pollock (*Gadus chalcogrammus*), Pacific halibut (*Hippoglossus stenolepis*), and arrowtooth flounder (*Atherestes stomias*). Having an accurate model of size-at-age is necessary for managing sustainable fisheries, in which regulations for total allowable catch are made based on a stock assessment (Thompson, 2016). For Pacific cod, the stock assessment estimates both the age structure of the population and the overall population size (Methot and Wetzel, 2013). Therefore, it is important to have both accurate ageing techniques and representative sampling criteria from which population demographic variables are derived.

In this study, we use abundance, length, and age data collected during a long-term fishery monitoring program, to identify patterns of variability (i.e., temporal, spatial and generational) and processes correlated with these patterns in the Pacific cod size-at-age of the Bering Sea. The analysis is applied to 23 years of standardized collections spanning a period of highly contrasting environmental conditions. The data that we analyze and the ensuing results are instrumental in characterizing patterns and isolating drivers of individual trait variability in wild populations, providing a level of understanding that is necessary to sample and sustainably manage these commercially important populations (Puerta et al. 2019), and to predict individual fitness in a changing climate.

Data and Methods

Sampling area and field collections

We used individual size and age data collected during National Oceanic and Atmospheric Administration (NOAA), Alaska Fisheries Science Center (AFSC) groundfish surveys. The survey obtained catch samples from a standardized set of stations in the Eastern Bering Sea every year from 1982 to 2016 (Fig. 1). Due to a potential bias in age determinations from the first part of the time series, the size-at-age data for this analysis only includes samples from 1994 onwards (Roberson et al, 2005, Matta and Kimura, 2012). At each station, there is a record of the position (latitude and longitude measurements), date and time of haul, weight of fish caught, number of fish caught, duration and distance of haul. Additionally, the surface and bottom temperatures and depth have been recorded at each station (Conner and Lauth, 2018). For a subsample of the hauls, there are measurements of size and age of a subsample of the fish caught, with age determined by otolith analysis. Over time, there has been an increase in both the number of stations containing Pacific cod in the sample (min: 21, mean: 94, max: 257) and fish sub-sampled for ageing (min: 571, mean: 1126, max: 1819). The years 2015 and 2016 had the most stations containing Pacific cod in the sample (231 and 257, respectively) and numbers of fish sub-sampled for ageing (1819 and 1624, respectively), because two parallel sub-sampling strategies were implemented (Puerta et al. 2018). All samples from 2015-16 were included in the current analyses because of the limited differences in size-at-age functional relationships estimated from the parallel strategies (Puerta et al. 2018). The total sample size in the full data set was 25,213.

Analyses on full data set

We applied different formulations of Generalized Additive Models (GAMs) to the available size-at-age data. GAMs are a nonlinear regression technique that does not require *a priori* specification of the form of the relationship between a set of covariates and a response (Wood, 2017). The models represented different levels of complexity, as shown in Table 1, and they all regressed fish length (in mm) as a function of the intervening factors and covariates. Hereon we use *covariate* when referring to numerical variables that are included in the regression analyses as continuous and smooth effects (i.e., age, water temperature, latitude and longitude of sampling). We instead use *factor* when referring to numerical and categorical variables that are included in the regression analyses as either a random or fixed effects, altering the model intercept (i.e., year of sampling, year of birth, individual sex).

The *reference model* only included age of the fish as a covariate, and was used to test the null hypothesis that there are no spatial, temporal, and generational patterns of variability in cod-size-at-age. The successive five models fitted to the full data set included covariate and factors to differentiate sources of variability among the *spatial* (latitude and longitude), *interannual* (year of capture), and *generational* (year of birth) components, and to account for the effect of environmental conditions (i.e., bottom temperature at the sampled location) and sex (males vs females) on individual size-at-age. However, these five models differ in the way covariates and factors are assumed (or not) to interact with each other. Specifically, in model 2, all covariates and factors examined, except year of birth, are assumed to have a fixed and additive effect on fish size. In model 3, we added an interaction between age and bottom temperature, assuming different effects of temperature on age. In model 4 we added an interaction between temperature with age and sex, assuming different effects of temperature on different age groups and sex levels. Because of collinearity, year of birth and year of sampling could not be included as fixed terms in the same models. Thus, these factors were either included in separate models (model 5 is similar to model 4 but with year of birth instead of year sampled), or one as fixed (year sampled) and the other as a random (year of birth) term (model 6).

The selection of the best model among those implemented was based on the lowest Akaike Information Criterion (AIC), Generalized Cross-Validation (GCV), and highest percentage of variance explained (R^2). Once the best model was determined, we inspected the residuals for potential violation of the model assumptions, particularly with regard to normality, constant variance, and independence (Zuur et al, 2009).

Effect of water temperature on cod distribution

We found significant variability of Pacific cod size-at-age correlated with the location of capture (spatial effect). Previous work (Ciannelli and Bailey 2005) and preliminary analyses (Fig. 1) indicate that bottom water temperature is a strong driver of Pacific cod spatial distribution. Therefore, we conducted an additional analysis on the full data set (1992 to 2016) to determine the age-specific effect of bottom temperature on Pacific cod distribution using variable coefficient models (Ciannelli et al. 2012). Namely, the predicted catch per unit effort (*cpue*, number of individuals ha^{-1}) of Pacific cod for a given location (*lat, lon*), year, and age group is modeled as follows:

$$\ln\left(cpue_{age,\,lat,lon,year} + 1\right) = \delta_{age,year} + s_{1,age}(lat,lon) + \beta_{\mathrm{age,\,lat,lon}}\left(Temp_{lat,lon}\right)$$

where $\delta_{age,year}$ is the model intercept capturing the age-specific interannual variability of Pacific cod cpue, $s_{age,1}(lat,lon)$ is a smooth function capturing the age specific spatial variability of Pacific cod cpue, $\beta_{\mathrm{lat,lon}}$ is a spatially variable linear coefficient determining the variation of Pacific cod cpue due to a unit variation of bottom temperature at the corresponding location. Model error was assumed to be log-normally distributed, and stations with zero catches were removed from the analyses.

Cohort analyses

The analyses conducted on the full data set indicated that there is a significant amount of variability in cod size-at-age that is correlated with the year of birth (cohort effect) of the examined individuals. Therefore, we conducted additional analyses, which we refer to as *cohort analyses*, to examine the mechanisms driving this variability. Cohort analyses were conducted on a restricted data set that only included individuals of age-1 to age-5, and cohorts that were fully represented in this age range (i.e., from age-1 to age-5). This operation resulted in a trimmed data set of 16,236 observations, including the 1993 to 2011 cohorts. We restricted the analyses on individuals from age-1 to age-5 because these are the stages when individuals experience fast growth, and when even subtle differences in growth rate at an early age may cause large variations in size-at-age at later ages.

All models implemented in the cohort analyses include location of capture (latitude and longitude), bottom temperature at the capture location, and sex (males vs females), as these covariates and factors were found to be statistically significant when tested in the full data set. Additional factors included in the models are year of birth and year sampled, which were necessary to partition between interannual and generational sources of size-at-age variability and to establish the correlation between them. We also included environmental covariate and factors aimed at discerning between an effect of *early environmental exposure* and/or *genetic origin* on the generational variability of cod size-at-age. Specifics of all the models and associated hypotheses tested follow (Table 2).

As a first step to the cohort analyses, we determined whether the year effect was correlated with the cohort composition of the population, and if so, to what extent. Accordingly, models 1 and 2 are used to quantify interannual and generational sources of variability and to establish the correlation between the two (Appendix S1: Section S1 *Correlation between year and cohort effects*). We then proceeded to test for both the *early environmental exposure* and the *genetic hypotheses*, by (1) using temperature experienced by each cohort during the age-1 stage as an index of early-life environmental exposure (Model 3), and (2) location (center of distribution) of the cohort during the age-1 stage as an index of the relative spawning origin of the cohort (Model 4). See Appendix S1: Section S2 *Determining temperature and location of the age-1 groups* for additional details on these analyses. Models 5 and 6 include both temperature and location of the age-1 cohorts and therefore simultaneously test for both hypotheses. However, because both of these variables vary in relation to the cohort, their estimated effects would compete if they are included as covariate in the same model. Thus in model 5 temperature during the age-1 stage is included as continuous and smooth effect, while cohort location is included as a factor with two levels separating eastward- versus westward-located cohorts (Appendix S1: Section S2 *Determining temperature and location of age-1 groups*). In model 6, cohort location is a smooth effect and temperature during age-1 is a factor separating warm versus cold cohorts. The breakpoint between the two levels (east-west or cold-warm) was determined by minimizing the model AIC across a range of values that leave at least 20% (4 cohorts) in either level. Similarly to the analyses implemented on the full data set, the selection of the best model was based on AIC, GCV, and R^2.

All models were fit using the mgcv package 1.8-23 in R version 3.4.3. All data and R code are available via GitHub: https://github.com/lciannel/Cod-size-at-age

Sensitivity analyses

In 2011 the Alaska Fisheries Science Center underwent a study to estimate potential bias in Pacific cod otolith readings (Kastelle et al. 2017). Across all ages, the study found that the probability of correctly determining otolith age was 61%. The probability of overestimating age by 1 year was 25%, and that of underestimating by 1 year was 13%. A two-year error (over- and under-estimating) was very unlikely (<1%). We used these probabilities to assess the sensitivity of the year effect (interannual variability) to the ageing bias (Appendix S1: Section S3 *Sensitivity analyses*).

Results

During the time considered in this analysis, the average temperature of the Bering Sea middle shelf (> 50 m and < 100 m depth) has varied between -0.13 ^{o}C in 2012 and 3.72 ^{o}C in 2016. Prior to 1999, cold and warm years alternated on a yearly basis. After 1999, warm and cold years came as stanzas, with warm periods from 2002-2005, cold from 2006-2013, and warm again after 2013 (Fig. 1). Overall, Pacific cod is widely distributed across the Bering Sea shelf. However, the distribution is influenced by water temperature. Cod tend to avoid extremely cold (e.g., < 0^{o} C) and extremely warm (e.g., > 6 ^{o}C) water. This is evidenced by the sharp differences in distribution between one of the coldest (1999) and one of the warmest (2003) years on record (Fig. 1). There are also differences in the distributions of the various age groups. In general, younger individuals are more abundant in the inner (<50 m depth) and middle shelf, while older and larger individuals are more abundant in the middle and outer shelf (Appendix S1: Fig. S1). The interannual consistency of habitat use (quantified by the percentage of variance explained by a GAM that only includes spatial coordinates to estimate cod abundance) is greatest in younger individuals (age-1 and age-2) and progressively declines in older and larger individuals (Appendix S1: Fig. S1). Spatial distributions of males and females were visually very similar across the years, although unsexed individuals were more clustered near the coast due to their younger age.

Analyses on full data set

Table 1 summarizes the AIC (d-AIC), Generalized Cross Validation (GCV), and R^2 values for six different GAMs of length as a function of age and other environmental variables fitted to the full data set. The reference GAM, obtained by simply correlating individual size with individual otolith age, explains more than 90% of the variability in individual size-at-age. This result confirms that otolith age is indeed the primary predictor of fish size; but, as evidenced by the scatterplot of fish age vs fish size (Fig. 2), there is also biologically and statistically significant left-over variability. We extracted the raw residuals from the reference model and plotted their average value by each location to determine if there are spatial variations of cod size at age. We found that residuals in the inner and northwest portions of the sampled area are consistently smaller than those from the outer shelf (Fig. 2), and thus confirmed that in the reference GAM there are unexplained sources of spatial variability in cod size-at-age.

Longitude, latitude, and bottom temperature were all found to be significant covariates, and the year of catch, birth year, and sex were all significant factors. The inclusion of environmental covariates, in addition to fish age, resulted in models with lower AIC and GCV compared to the reference model. Different combinations of environmental covariates also resulted in slight improvement of model performances, but to a lower extent. The best model that did not include birth year as a factor was the 4th formulation in Table 1, and included an interaction between fish age, water temperature, and individual sex (males vs females). Visual inspection of the residual variogram by year did not indicate the presence of spatially structured patterns, implying that the fixed part of the intervening model is sufficient to capture the spatial patterns of cod size. Figure 3 shows the spatial effect estimated from this model (i.e., 4th formulation in Table 1), as predictions of fish length at a reference age (age-3 in this example). In agreement with the residual pattern of the reference model (Fig. 2), we found that the predicted fish size-at-age is consistently smaller in the inner than outer shelf (Fig. 3). Bottom temperature at the sampled location had a slight positive effect on fish size from 0^{o}C to about 2^{o}C, to then revert to a slightly negative effect at higher temperature values (Appendix S1: Fig. S2). However, because the 4th model contains an interaction between age and temperature, by sex, the relative predictions indicate that older females (>age 7+) achieve statistically significantly larger sizes than similarly aged males from the same temperature environment (Appendix S1: Fig. S2). The inclusion of birth year as a random effect in addition to year of capture as a fixed effect resulted in lower AIC and GCV of all examined models (Table 1, Model 6). This particular formulation estimates that the cohort-to-cohort standard deviation is about one third of the residual error standard deviation, and therefore is an important source of variability of cod size-at-age. The fixed effects of Model 6 were similar to those shown for Model 4.

Effect of water temperature on cod distribution

In situ values of bottom temperature are important drivers of fish distribution across all age groups, but particularly so for age groups from 1-5 (see Fig. 4). Consistent with previous studies (e.g., Ciannelli and Bailey 2005, Stevenson and Lauth 2018), we found that cod abundance increases in the northwest region of the sampled area when temperature also increases. The effect is such that, when local bottom temperature increases by 1^{o}C, cod catches can double in the said region. Particularly for the age groups 1-5, an increase in temperature can result in more biomass in the areas where we estimated lower individual size (compare Figs. 3 and 4).

Cohort analyses

A simple image of the distribution of each cohort during the age-1 stage, overlaid on the bottom temperature, revealed that cohorts differ in term of the temperature and east-west location experienced during the age-1 stage (Appendix S1: Fig. S3). For example, the average temperatures experienced by the 1998 and 2005 cohorts during the age-1 stage were -0.18 ^{o}C and 1.02^{o}C respectively, while those of the 2001 and 2002 cohorts were 4.07^{o} C and 4.23^{o} C respectively. Further, the center of distribution of the 2005 cohort during age-1 stage was about 294 km to the west of the 2011 cohort. Temperature and location during the age-1 stage are not linearly correlated with each other (Pearson correlation = -0.10).

The first two GAMs applied on the restricted data set were intended to quantify the variability associated to the sampled year and birth year terms (Fig. 5). The model that contains sampled year (Table 2, Model 1) slightly outperforms the model that contains birth year (Table 2, Model 2). We found that the population cohort composition, weighted by the respective cohort effects, explains about 75% of the year-to-year variability in average cod size at age (Appendix S1: Fig. S4). Therefore, we conclude that the cohort composition is the primary driver of the estimated year effect.

The next four models (Models 3-6 of Table 2) are meant to investigate the possible drivers of the cohort effect, and therefore include environmental variable in lieu of the sample year or year of birth. Both the temperature and location experienced by each cohort during its first year of life significantly correlate with the size-at-age that individuals from the respective cohorts experience up to age-5. The best cohort model is achieved when age-1 temperature is a smooth continuous effect, and location is a factor, separating eastward vs. westward cohorts (Model 5 in Table 2). The estimated shapes and magnitudes of these effects are shown in Fig. 6. Notably, cohorts that during the age-1 stage are exposed to intermediate values of bottom temperature (~ 2^{o} C) are about 3 cm larger than cohorts exposed to either the lowest (~ 0^{o} C) or highest (~4^{o} C) range of bottom temperature. Also, westward cohorts tend to be 1.5 cm smaller than eastward cohorts, up to age-5. The boundary between westward and eastward cohorts is estimated at about 231 km from the northwest origin of the least square lines through the age-1 center of distribution (Appendix S1: Fig. S5). The combined additive effect of location and age-1 temperature are on the order of 5 cm, in agreement with the estimated magnitude of the cohort effects from Model 2 (Table 2).

Sensitivity analyses

The inclusion of an age determination error in the raw data set resulted in Pacific cod size-at-age to be underestimated by an average of 11.02 mm for an individual of age-3 during the period 1994-2011. While this is a statistically significant bias, the ensuing estimate of cod size-at-age interannual variability does not visibly change from the one estimated with the uncorrected data (Appendix S1: Fig. S6).

Discussion

By performing a retrospective analysis of cod size-at-age we can see definite variation across the Bering Sea region and over time. The best-performing model – where length is described as a function of longitude and latitude, year of sampling, and age interacting with temperature by sex -- predicts an overall pattern of larger fish farther offshore. In separate models, we found additional sources of variability correlated with the year of birth, and confirmed that the cohort composition of the sampled population drives the estimated interannual variability. The geographic origin and the average water temperature experienced by the cohort have long lasting effects on the individual traits, and significantly contribute to cod size-at-age variability in the eastern Bering Sea. Identifying and quantifying these sources of trait variability have important implications for ecology and management of marine species, especially in light of the abrupt changes in abundance and spatial distribution that several species of the Bering Sea have recently undergone (Stevenson and Lauth 2019).

Interannual variation of Pacific cod size-at-age can result in individuals differing by as much as 6-7 cm in size at a given age. Other authors have found interannual variations of growth parameters in marine fish (Thorson and Minte-Vera 2016), however, there is no clear understanding as to what drives such variation. At a first examination (compare Fig. 5 upper panel with Fig. 1 lower panel), the variability associated with sample year that we have identified seems to align with the warm-cold stanzas of the eastern Bering Sea: size-at-age anomalies are lowest and negative during the warm period 2000-2006, and highest and positive during the cold period 2007-2013. However, after 2013, size-at-age anomalies continued to increase, even though the eastern Bering Sea entered a (very) warm regime (Stabeno et al. 2017). Thus we find unlikely that the annual average size-at-age is driven by a direct and plastic effect of the Bering Sea temperature on cod growth. Instead, based on the fact that about 75% of the observed interannual variability of cod size-at-age is correlated with the relative cohort composition of the surveyed population, we find more likely that cohort effects drive the temporal variability of cod size at age. Cohort-related effects could be driven by both long lasting plasticity of the fish reaction norm in relation to conditions experienced early in life (*early environmental exposure* hypothesis), and/or a genetic effect (*genetic* hypothesis). The evidence gathered in this study lends support to both hypotheses.

With regard to environmental exposure we found that the size-at-age of Pacific cod is highest through age-5, when the age-1 cohorts experience average temperature of 1.5 to 2.5^{o}C (Fig. 6). Hurst et al. (2018) found that age-0 cod in the eastern Bering Sea experience higher potential for growth during cold than during warm years. They proposed that different prey compositions and temperature, that in certain coastal locations may exceed the maximum for growth (11.6^{o} C), reduce growth. Hurst et al. (2012) suggested that variation of water temperature experienced during the year of birth alter the phenotype of the individuals at later ages. Collectively, these studies indicate that cod experiencing low temperatures during the age-1 stage may have a growth advantage, provided that temperature continue to stay low in later years. The range of average ambient temperature for maximum cohort growth that we have identified in our analyses (1.5 to 2.5^{o}C) includes the most frequently occurring ambient temperature experienced by age-1 groups (median = 2.31^{o}C), and is likely to explain the growth advantage conferred even at later ages. With regard to genetic origins, we found that eastward cohorts experience slightly (1-2 cm) but statistically significantly larger size-at-age than westward cohorts. Spies (2012) has shown that, based on neutral markers, there is genetic isolation between the spawning aggregations of Unimak and Pribilof Islands. While differentiation of neutral markers does not necessarily imply adaptive selection, the presence of such isolation underscores a genetic difference among spawning sub-populations that could result in the observed patterns of size-at-age.

The location of capture had a large contribution to cod size-at-age variability, with individuals of all ages being on average about 5 cm smaller near the coast than at the edge of the Bering Sea shelf. This strong spatial variation may be attributed to environmentally driven phenotypic plasticity, which is either trophically and/or thermally driven. The Bering Sea habitat is heterogeneous in temperature and prey/predator distribution, all of which could affect cod growth and distribution. For instance, sea ice melt interacts with local topography (Stabeno et al, 2012) to cause water stratification that results in a cold pool across the middle of the region during summer months. This thermal barrier restricts the movement of fish populations in the region and can determine ecosystem interaction (Ciannelli and Bailey 2005, Mueter and Litzow 2008). Visually, the region of lower-than-average size-at-age identified in this study overlaps with the area of the cold pool, which is located in the northwest region of the sampled area (Fig. 1). Assuming that cod inhabit the near-bottom portion of the water column (Nichol et al. 2007), individuals in the low size-at-age area would then be exposed to temperatures < 2° C. Hurst et al. (2010) conducted experimental studies to characterize Pacific cod growth in relation to water temperature and found that post-settlement juveniles grew 2.9 (growth in mass) and 3.7 (growth in length) times faster at 9° C than they did at 2° C. We are unaware of similar experiments conducted on older Pacific cod stages, but it is highly likely that growth is impaired at low temperatures even in post age-0 stages. Therefore, there is support to the hypothesis that the observed spatial patterns of cod size-at-age are caused by thermally-driven phenotypic plasticity.

The spatial effects identified in this study include individuals from multiple cohorts and age groups. While horizontal and vertical mobility may be limited during the first year of life, adult and subadult cod are known to move extensively across the Bering Sea shelf (Shimada and Kimura 1994). Therefore, smaller individuals caught in the northwest sampled area may be from cohorts that were not originated in the same area. If this assertion were correct, then one would expect that the residual patterns observed in Fig. 1 becomes progressively stronger as individuals from younger cohorts are excluded from the analyses. We thus separately plotted the residuals of the reference model (Table 1, Model 1) by age groups, and found that the spatial pattern of residuals is visually prominent for the older (i.e., age-3+), but not in younger age groups (i.e., age 1-3, Appendix S1: Fig. S7), confirming that the spatial effect is mostly associated with phenotypic expression of older individuals.

Variation in size-at-age can affect individual fitness through two main processes: reproductive success and size-selective predation. With regard to reproductive success, variation in size-at-age and body condition are linked to maturity and fecundity (i.e., number of eggs, Jung et al. 2009) and to swimming abilities and migratory performances during the spawning season (e.g., Slotte and Fiksen, 2000). In the Bering Sea, the size at which a cohort is 50% mature is around 58 cm, which corresponds to individuals of about age-5. However, there is large variability, and individuals can mature as early as age-3 (Stark 2007). Potential fecundity (PF, number of eggs in ovary) varies allometrically with size, with length (cm) exponent equal to 4.48 ($PF = 0.0133 \times Length^{4.48}$

$PF = 0.0133 \times Length^{4.48}$, Jung et al. 2009). With these relationships, small body size variations, on the order of those observed in our study (i.e., 5 cm), can result in a decrease/increase of about 25-30% of the number of eggs produced at a given age.

Pacific cod in the Bering Sea is also known to conduct extended seasonal migrations from summer feeding grounds, primarily in the shelf area, to spawning grounds, primarily in the slope area (Shimada and Kimura 1994, Rand et al. 2014). Although there are no direct estimates for Pacific cod migratory performances in relation to individual traits, several studies have shown that migration performance and swimming abilities in other temperate and sub-arctic fish species are linked to fish size and condition (Slotte and Fiksen 2000, Sundby and Nakken 2008, Opdal 2010). Therefore, it is likely that the reproductive success of Pacific cod in the Bering Sea is affected by their size-at-age also via altering migration performances, especially on younger and newly matured individuals. Of note is a series of apparently unprecedented northward migration of Pacific cod in recent warm years (Stevenson and Lauth 2018), which correspond to areas where we estimate lower than average size-at-age. In such a scenario, we predict that younger and smaller-than-average reproductively mature individuals may no longer be able to complete their spawning migration, and therefore fail to reproduce.

Fitness consequences of reduced size-at-age can also be mediated through size-selective predation (e.g., Ottersen and Loeng 2000, Stige et al., in press). Size-selective predation is particularly impactful on fish from high latitudes, given the strong seasonality of sub-polar environments, during the first winter of life (Sogard 1997), and during the transition from pelagic to benthic environments (Stige et al. in press). All of these conditions apply to age-0 Pacific cod in the Bering Sea. However, in our study, the first age group monitored is the age-1, and survivors may have already gone through the dominant processes that regulate year class strength via predation pressure. Thus, we do not expect additional predation on age-1 and older individuals to be a driver of Pacific cod year class strength in the Bering Sea.

From a management perspective, by not accounting for additional covariates (i.e., spatial, temperature, year of birth) in estimates of fish size-at-age, there is the risk of assigning fish to wrong age groups. This has consequences on estimates of numbers at age obtained from an age-structured stock assessment. In a recently published study Puerta et al. (2019) conducted a sampling strategy evaluation to quantify the effect of different sampling strategies (i.e., random vs length-stratified) and assumptions about age-length relationships (e.g., with and without spatial terms) on the estimates of the cod population age structure (i.e., numbers of individuals at any given age) in the eastern Bering Sea. From these analyses, we found that not accounting for spatial effects in the age-length relationships results in misidentifying age by at least one year in 7.85% of the individuals in the population. Including spatial effects results in age misidentification in 5.00% of the individuals. The spatial term is not the only factor affecting fish age (sex, water temperature, year of sampling and year of birth also affect fish size-at-age), so our calculations are conservative. In the model without spatial terms, most of the individuals assigned to the wrong age group were age 1-3. Considering that these are the most abundant groups in a population, the error can have significant contribution in recruitment estimates.

In this study, we have analyzed an extensive data set of individual size-at-age that spans over a period of 23 years. The analyses have uncovered previously unknown spatial, temporal, and generational patterns of size-at-age variation that are correlated with both the geographic origin and the early environmental exposure of the fish. Recent studies predict progressive warming of the eastern Bering Sea shelf (Hermann et al. 2016). Our study demonstrates that northwest movement of young cod (age 1-5), as a result of warming, places individuals in areas where we predict them to have smaller size-at-age. Smaller and less conditioned individuals are less fecund and may not be able to perform long migrations to return to their spawning grounds, which are primarily located at the southern edge of the sampling area (Neidetcher et al. 2014). Both of these effects are likely to negatively influence recruitment.

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Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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DATA AVAILABILITY

Data and code for the analyses are available on Zenodo: http://doi.org/10.5281/zenodo.3463664

TABLES

Table 1. Statistical comparison among the Generalized Additive Models (GAM) implemented to estimate the expected Pacific cod size (*l*) of individual *i* as a function of the following variables: otolith age (*age*), individual sex (*sex*, male or female), geographic coordinates of the site of capture (lat,lon, latitude and longitude), bottom

temperature at the site of capture (*Temp*), year of capture (*year*), and year of birth (*cohort*). The coefficients β are intercept parameters that vary according to the year of capture (*year),* or the individual year of birth (*cohort*). The coefficient δ is an intercept parameter that varies according to the individual sex. The symbol *I* is an indicator variable for the individual sex. The parameter η_{cohort} represents normally distributed variability associated to the individual year of birth. The symbols *s* represents unidimensional or two-dimensional smooth functions of the respective variables. For each model, AIC is the Akaike Information Criteria, d-AIC is the difference between the target model and the one with the lowest AIC tested, GCV is the generalized cross validation, and R^2 is the proportion of variance explained. The sample size for all of the models listed was 25,213. The models represented differ by i. the number of covariate included (1st vs all others), ii. whether the environmental variables are included additively (1st and 2nd) or non-additively (all the others), and iii. whether the year of birth is included as a fixed (5th) or random (6th) effect.

Model	Equation	AIC (*d-AIC*)	GCV	R^2
1	$l_{i,,cohort,lat,lon,year} = \beta + s_1(\mathrm{age}_\mathrm{i})$	276557 (*6696*)	3397	0.909
2	$l_{i,cohort,lat,lon,year} = \beta_{year} + \delta_{sex} + s_1(age_i) + s_2$ $(lat,lon) + s_3(Temp_{lat,lon})$	270531 (*670*)	2675	0.929
3	$l_{i,cohort,lat,lon,year}) = \beta_{year} + \delta_{sex} + s_1(age_i,Temp_{lat,}$	270346 (*485*)	2655	0.929
4	$l_{i,cohort,lat,lon,year} = \beta_{year} + I_{sex} * s_1(age_i,Temp_{lat,lon})$	270133 (*272*)	2633	0.930
5	$l_{i,cohort,lat,lon,year} = \beta_{cohort} + I_{sex} * s_1(age_i,Temp_{lat,lo}$	271097 (*1236*)	2736	0.927
6	$l_{i,cohort,lat,lon,year} = \beta_{year} + \eta_{cohort} + I_{sex} * s_1(age_i,Te$ $\eta_{cohort} \sim N(0,var = 13.68^2)$	269861 (*0*)		0.927

Table 2. Statistical comparisons of GAM models applied to the restricted data set, used to assess the mechanisms that drive a cohort effect on individual size at age (*l*). The restricted data set only includes individuals from age 1 to age 5, and the 1993 to 2011 cohorts. All the models are additive, and they differ by i. whether year of capture (1st) or year of birth (2nd) is included, ii. whether the cohort effect is hypothesized to covary with the bottom temperature experienced by the cohort at age-1($Temp_{age=1}$, 3rd), iii. whether the cohort effect is hypothesized to covary smoothly with the average location experienced by the cohort at age-1($lon_{age=1}$, 4th), iv. by an additive and smooth combination of both variables (5th), iv. or by an additive and smooth effect of temperature and a threshold effect of location (6th). All symbols and table notations are explained in Table 1.

Model	Equation	AIC (*d-AIC*)	GCV	R²
1	$l_{i,cohort,lat,lon,year} = \beta_{year} + \delta_{sex} + s_1(age_i) + \ s_2($	*171635* (*0*)	*2283*	*0.900*
2	$l_{i,cohort,lat,lon,year} = \beta_{cohort} + \delta_{sex} + s_1(age_i) + \ s_2$	*172123* (*488*)	*2353*	*0.897*
3	$l_{i,cohort,lat,lon,year} = \delta_{sex} + s_1(age_i) + \ s_2(lat,lon)$	173279 (*1644*)	2526	0.889
4	$l_{i,cohort,lat,lon,year} = \delta_{sex} + s_1(age_i) + \ s_2(lat,lon)$	173602 (*1967*)	2577	0.887
5	$l_{i,cohort,lat,lon,year} = \delta_{sex} + lon_{age=1} + s_1(age_i) +$	173070 (*1435*)	2494	0.890
6	$l_{i,cohort,lat,lon,year} = \delta_{sex} + Temp_{age=1} + s_1(age_i)$	173250 (*1615*)	2521	0.889

FIGURE LEGENDS

Figure 1. Top two panels: maps of the eastern Bering Sea shelf area with locations of sampled stations. The maps show the distribution of Pacific cod during a cold (1999, left)

and a warm (2003, right) sampling year. Bubble size is proportional to natural log of the catch per unit effort (number of individuals ha^{-1}) plus 1, at the sampled location. Grey scale image indicates bottom water temperature at time of sampling (units: ^{o}C). Bottom panel: time series of eastern Bering Sea middle shelf (50-100 m depth) average temperature from 1994 to 2016.

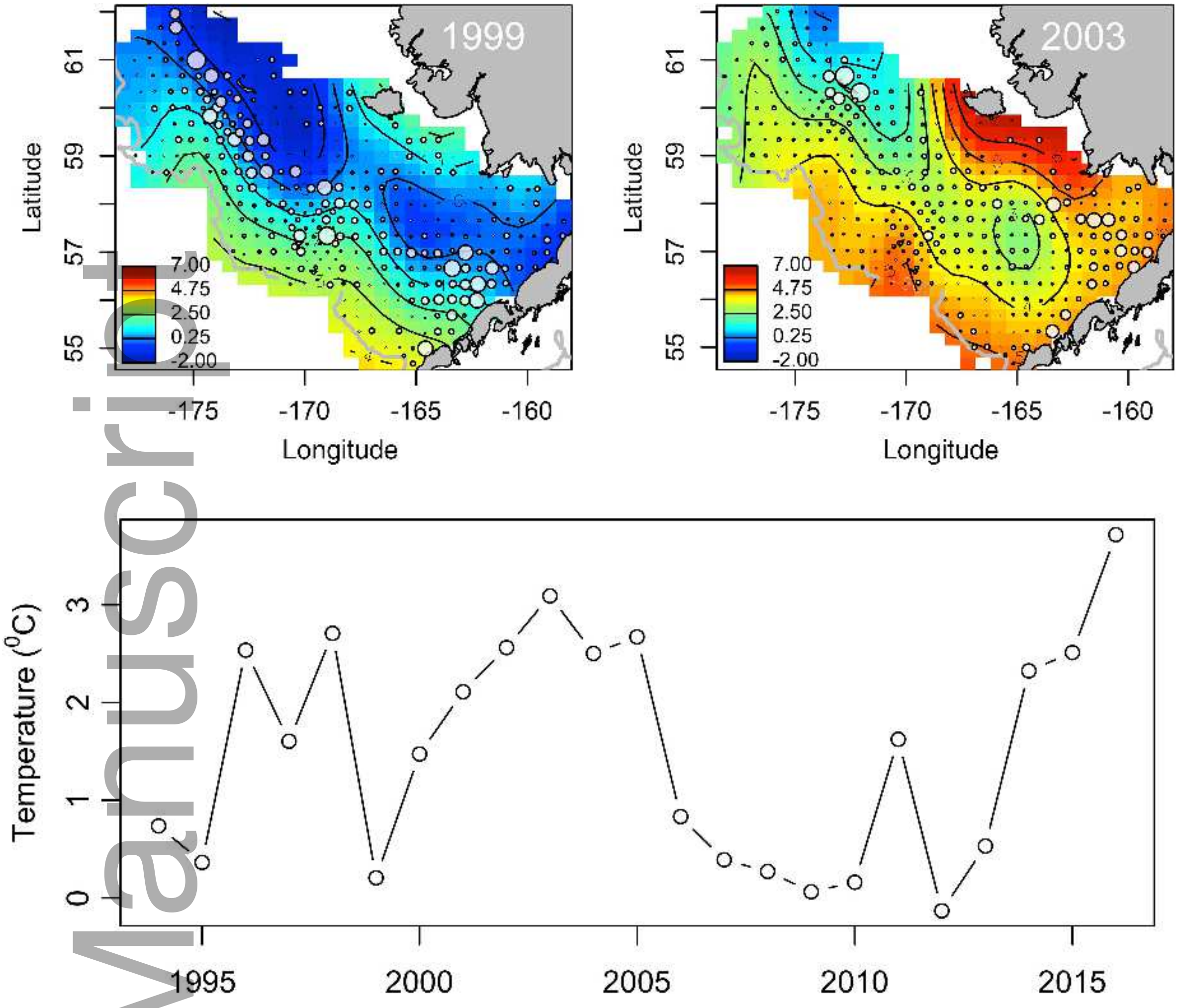
Figure 2. Predicted relationship between fish size and otolith age derived from the reference GAM model (Table 1, first row). Model residuals are shown in black if they are negative and grey if they are positive (left panel) and their average values at each location are displayed on a map of the sampled area (right panel). Also shown are bottom temperature isolines: 0, 1, 2, 3 ^{o}C.

Figure 3. Predicted length of 3-year-old males (left) and females (right). Isolines indicate the standard length of the fish (mm) from Model 4 in Table 1.

Figure 4. Effect of bottom water temperature on Pacific cod spatial distribution for different age groups. The grey-tone image indicates the estimated abundance (ln[1+n ha^{-1}]), and the red bubbles indicate the increase of cod abundance due to 1^{o}C variation of bottom temperature at the target location.

Figure 5. Upper panel: anomalies of cod size at age in relation to the sampled year, included as a factor in the Model 1 of Table 2. Lower panel: similar anomalies, but in relation to cohort (birth year), included as a factor in the Model 2 of Table 2. Anomalies are in reference to the 1994 year of sampling or 1993 year of birth. All analyses are conducted on the restricted data set, which only includes age groups from 1 to 5 and cohorts that are fully represented within the examined age range (1993 to 2011).

Figure 6. Estimated effects of location (left panel) and average temperature experienced by each cohort during age-1 stage (right panel) on Pacific cod size-at-age. Effects are shown as the average size (mm) of an age 3 individual, and are estimated from Model 5 in Table 2. See Fig. S5 for separation between east and west cohort locations.



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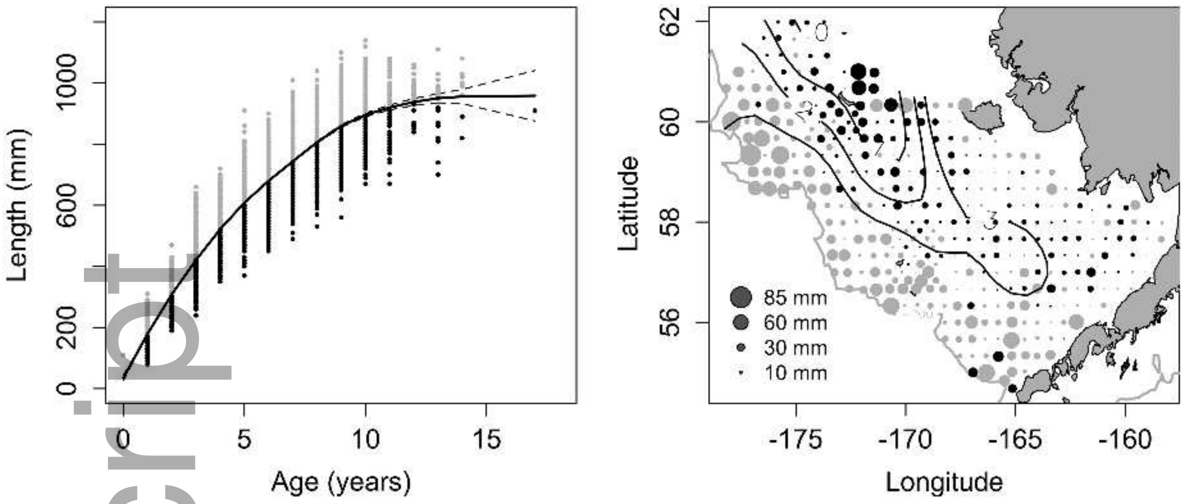

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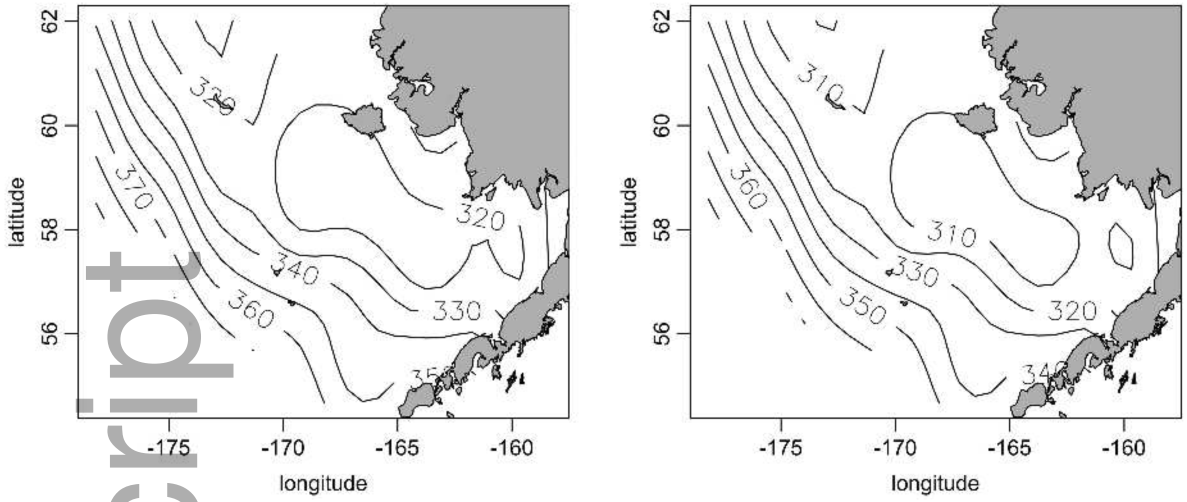

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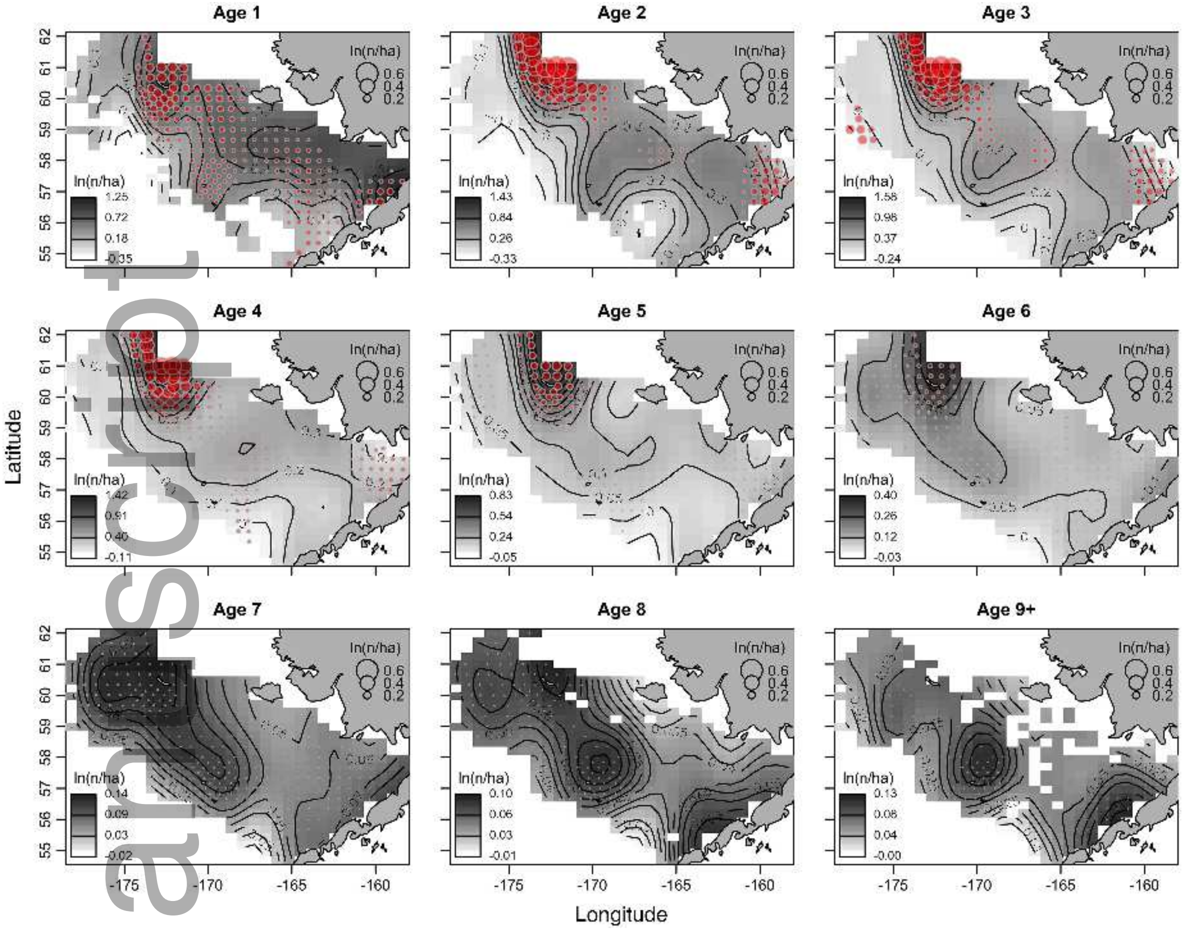

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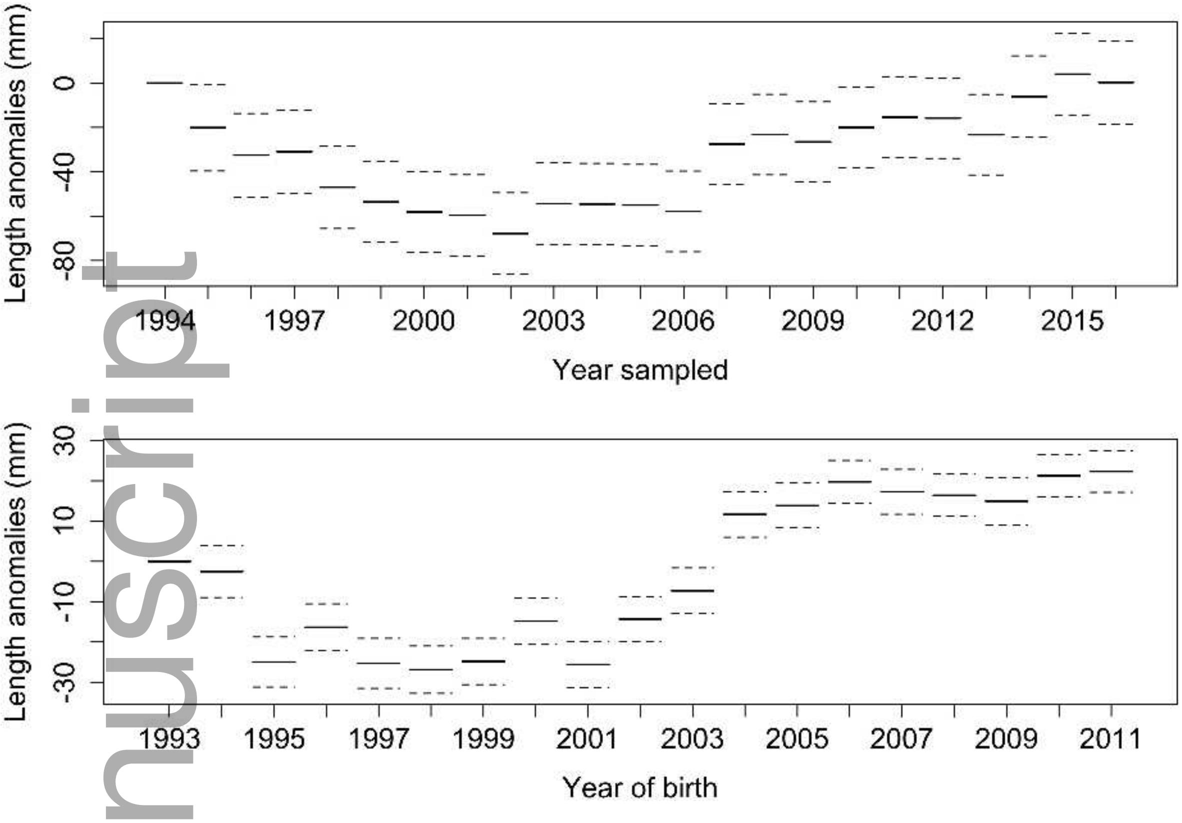

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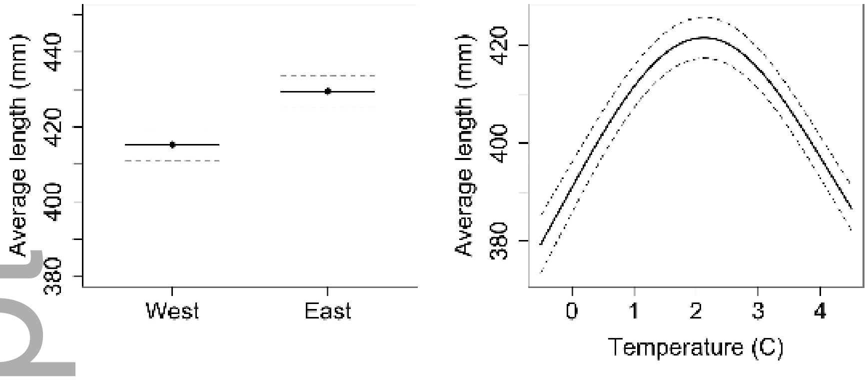

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