

# Drivers of body size changes in a *Pollachius pollachius* stock in NE Atlantic coastal waters

Alexandre Alonso-Fernández<sup>1,\*</sup>, Jaime Otero<sup>1</sup>, David Villegas-Ríos<sup>1,2</sup>, Rafael Bañón<sup>3</sup>

<sup>1</sup>Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas (IIM-CSIC), c/Eduardo Cabello 6, 36208 Vigo (Pontevedra), Spain

<sup>2</sup>Institute of Marine Research (IMR), Flødevigen Marine Research Station, 4817 His, Norway

<sup>3</sup>Servizo de Planificación, Consellería do Mar e Medio Rural, Xunta de Galicia, Rúa dos Irmandiños s/n, 15701 Santiago de Compostela (A Coruña), Spain

**ABSTRACT:** Fish body size is a key life history trait that influences population dynamics. Individual growth and size distribution are generally affected by both intrinsic and extrinsic factors. However, the drivers of body size changes are still poorly understood. The NW Iberian Peninsula is one of the most important fishing regions in Europe, where there is a special emphasis on artisanal fisheries. Despite the large contribution of small-scale fisheries to local communities, there is a lack of knowledge of the biotic and abiotic factors influencing the performance of coastal key species. In this study, we analyzed spatio-temporal changes in body size of *Pollachius pollachius* at the population level in response to a set of intrinsic and extrinsic factors. Generalized additive mixed-effects models were fit to a data set of ~11 000 records of individual body size of catch sampled by onboard observers during the last 13 yr in a complex multi-gear artisanal fishing fleet. Pollack body size showed strong spatio-temporal patterns, with an inshore–offshore geographic gradient where smaller fish were associated with shallower waters. Moreover, body size displayed a seasonal cycle, with larger individuals occurring mainly in winter months. This seasonality matches the annual reproductive cycle of the species. In addition, body size was affected by the interaction between population density and the temperature experienced by fish the year preceding the catch, with smaller individuals occurring at elevated temperatures and higher densities.

**KEY WORDS:** Generalized additive mixed model · Size-based indicators · Growth · Environmental drivers · *Pollachius pollachius*

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## INTRODUCTION

Body size of marine organisms plays a central role in the function, physiology and evolution of individuals and is involved in many ecological processes such as food web structure or energy flux (Hildrew et al. 2007). Moreover, changes in body size have broad implications for the fate and resilience of fish populations (Marshall & Frank 1999). Individual growth and size distributions vary within and among populations and are affected by both endogenous factors, which indicate that body size changes may be the result of

individual interactions, and exogenous forcing variables such as large-scale climatic changes and local variability in oceanographic conditions. Most importantly, both factors may operate in conjunction, resulting in complex ecological interactions (Jensen et al. 2000, Crozier et al. 2010, Ohlberger et al. 2013).

Body size influences fish population dynamics by affecting many life history traits. For instance, body size, together with growth trajectories, is a key determinant of reproductive potential (Trippel et al. 1997), modulating not only offspring quality and quantity (Berkeley et al. 2004, Birkeland & Dayton 2005, Lam-

bert 2008) but also reproductive timing (Trippel 1995, Wright & Trippel 2009) and sex change in hermaphroditic species (Hamilton et al. 2007, Molloy et al. 2007). Besides life history traits, fish behavior can also be driven by body size (Kaunda-Arara & Rose 2004, Jones 2005, Meyer & Holland 2005, Villegas-Ríos et al. 2013). Furthermore, size-selective mortality processes are common across fish species (Sogard 1997, Gislason et al. 2010) and are suggested to alter stock demography in commercial fish populations (Sinclair et al. 2002). Size-selective mortality processes were also postulated to generate evolutionary trends through genetic adaptation, ultimately affecting life history traits in exploited fish stocks (Olsen et al. 2004, Dieckmann & Heino 2007, Pérez-Rodríguez et al. 2013).

Intrinsic properties of a given species may determine the spatio-temporal patterns in body size distribution. For instance, on the one hand, spatial heterogeneity can be related to ontogenic processes such as size-specific segregation following a bathymetric gradient in *Pollachius virens* (Clay et al. 1989, Neilson et al. 2003) or the spawning migratory pattern in northeast Arctic cod (Bergstad et al. 1987). On the other hand, intrinsic biological cycles, such as reproduction, growth or recruitment, are among the main characteristics responsible for the temporal patterns of changes in body size across taxa (Willis et al. 1993, Blackwell et al. 2000). Density-dependent growth is also a widespread and important internal mechanism involved in the regulation of fish populations (Lorenzen & Enberg 2002). Decreases in fish body size have been associated with increased population densities in several fish species (Jensen et al. 2000, Crozier et al. 2010, Ohlberger et al. 2013) because of competition for food and cannibalism, further contributing to the regulation of fish populations (Jenkins et al. 1999, Bohlin et al. 2002).

In addition to studies on intrinsic effects, many efforts have been made to unravel the influence of environmental factors on fish growth in the wild. For instance, Wells et al. (2007) identified several forcing variables influencing body size in Chinook salmon, such as upwelling, sea level or curl conditions. However, the most outstanding driver of body size across ecosystems and species is temperature (Jensen et al. 2000, Rogers et al. 2011, Ohlberger 2013). In general, the tendency to find small organisms at warmer temperatures has been associated with well-known relationships. Bergmann's rule states that species found in colder climates (i.e. higher latitudes) have larger body sizes (Bergmann 1847). At the intraspecific level, smaller mean body sizes would be expected to

be found in warmer temperatures (i.e. James' rule, James 1970). Finally, the temperature–size rule predicts that size at a fixed age or developmental stage is smaller in warmer temperatures for ectotherms (Atkinson 1994). Although gathering evidence about the effects of temperature on body size concurs with those universal responses to current warming trends (Daufresne et al. 2009, Gardner et al. 2011, Ohlberger 2013), with often greater effects in aquatic compared to terrestrial ecosystems (Forster et al. 2012), many other field analyses have reported a variety of body size responses to warming (Jensen et al. 2000, Wells et al. 2007, Morrongiello et al. 2011, Gillanders et al. 2012, Neuheimer & Grønkjær 2012), concluding that there might be important exceptions to the ubiquitous temperature–size rules (e.g. Adams et al. 2013).

Fish body size is predicted to increase (decrease) as a response to environmental cooling (warming), yet this pattern might be truncated by harvesting (e.g. Fisher et al. 2010a). Moreover, recent model results suggest that assemblage-averaged maximum body weight of fishes is expected to shrink by 14 to 24% by 2050 because of changes in distribution, abundance and physiology, with larger effects at the tropics and intermediate latitudinal areas under the current global change scenario (Cheung et al. 2013). The modeling approach concluded that coastal areas are also expected to experience strong downsizing in fish weight. The joint effects of warming (Lima & Wetthey 2012) and cumulative anthropogenic pressures, such as those derived from overharvesting, that coastal marine ecosystems suffer (Halpern et al. 2008) could exacerbate this pattern. Indeed, regional climatic changes and commercial fishing have already been shown to alter fish community composition and body size-dependent responses (Genner et al. 2004, 2010). Therefore, it is crucial to understand the species-specific responses to shifts in temperature regimes and other abiotic and biotic factors that may help us to better anticipate the effects of the global warming scenario, under the current levels of exploitation, on the maintenance of coastal fish populations.

The NW Iberian Peninsula is at the northern boundary of the Iberian-Canary Current upwelling system. It is a highly productive region where coastal winds are seasonal, with northerly winds prevailing from March–April to September–October, promoting upwelling, and southerly winds predominating the rest of the year (Álvarez-Salgado et al. 2002). This region supports a large small-scale fishing sector with elevated levels of exploitation (Freire &

García-Allut 2000), and the upwelling strength is known to modulate the fate of the food web from plankton (Bode et al. 2009) to fisheries (Guisande et al. 2001, Otero et al. 2008) and aquaculture (Álvarez-Salgado et al. 2008). Recent analyses, however, revealed that coastal upwelling has weakened in this region, resulting in changes of an unprecedented nature (Pérez et al. 2010). Nevertheless, this negative trend in upwelling strength is still under scrutiny (Barton et al. 2013).

The objective of this study was to quantify the effects of a suite of biotic and abiotic variables on variations in body size of an exploited coastal population of *P. pollachius*, a species of increased interest to international bodies (European Union 2010) yet one for which there is a lack of basic biological and fishery knowledge (ICES 2010). Generalized additive mixed models (GAMMs) were fit to more than 10 000 individual records of pollack body size sampled by onboard observers off the Galician coast (NW Spain) during the last 13 yr. The questions posed by the modeling approach were 3-fold: (1) Is there an apparent spatio-temporal pattern in pollack body size that may be related to ontogenic processes? (2) Is there an influence of sea temperature conditions on growth performance that concurs with James' rule? (3) Are there any density-dependent effects on pollack growth?

## MATERIALS AND METHODS

### Study area and species

Galicia (NW Spain, Fig. 1) is one of the main fishing regions in Spain and Europe (Vázquez-Seijas 1998, Freire & García-Allut 2000), with a fleet of more than 4000 small fishing boats representing ~88% of the total fleet in this area. Galician waters are at the northern boundary of the Iberian-Canary Current upwelling system (Fraga 1981). Coastal winds at these latitudes (42° to 44° N) are seasonal; however, more than 70% of the total variability of coastal winds occurs during periods of less than 1 mo, so that the upwelling season appears as a succession of wind stress/relaxation cycles of periods lasting 10 to 20 d (Álvarez-Salgado et al. 2003).

*Pollachius pollachius* (Linnaeus, 1758) is a widely distributed species in the NE Atlantic ranging from northern Norway to North Africa (Cohen et al. 1990). Molecular studies have detected a weak but significant genetic differentiation among populations along the European coast, although the exist-

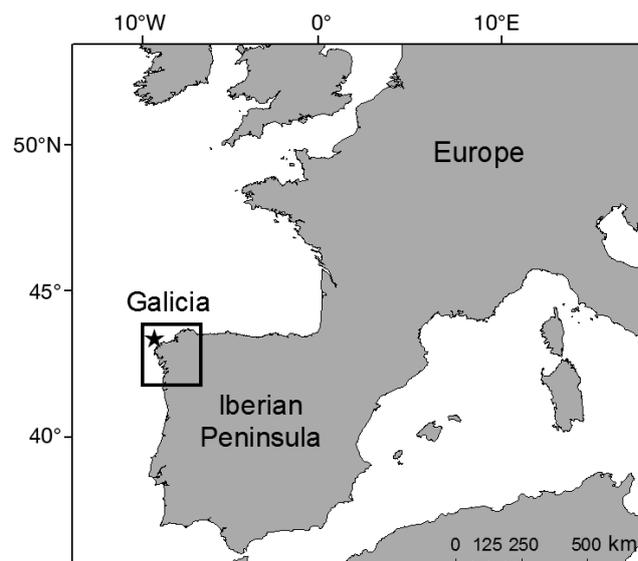


Fig. 1. Study area. Axes are in Universal Transverse Mercator (UTM) coordinates. Black star indicates the 2° × 2° cell centered at 43°N, 11°W used for computation of the upwelling index

tence of a high gene flow among spawning units is suggested (Charrier et al. 2006). Reproduction tends to be seasonal, and spawning aggregations are commonly found along its distribution at depths to 150 m (Quéro et al. 1984). In the study area, the spawning season spans over ~4 mo, from January to April, with a peak of reproductive activity in February (Alonso-Fernández et al. 2013). The species is mainly targeted by the artisanal fleet, using gillnets and hooks and lines deployed in coastal areas (depths to ~150 m) and is only occasionally caught as bycatch in offshore trawl fisheries (Rodríguez et al. 2011). In spite of its importance as a fishery resource throughout much of its distribution (ICES 2010), no analytical assessment of *P. pollachius* in NE Atlantic waters has been made, and biological information is scarce. This paucity in the data prevents any evaluation of the stock status; thus, a compilation of biological data has been requested (ICES 2010).

### Biological data

Sampling was undertaken off the Galician coast (NW Spain), between the mouth of the Eo River (43°32' N to 7°01' W) and the Miño River estuary (41°50' N to 9°40' W), comprising ICES Divisions IXa and VIIIc (Fig. 1). The body size of *P. pollachius* was obtained from the historical (1999 to 2012) artisanal fishing sampling program run by the Unidade Téc-

nica de Pesca de Baixura (UTPB, Technical Unit of Artisanal Fisheries) of the Xunta de Galicia (Galician autonomous government). UTPB observers on board fishing vessels randomly selected from within the artisanal fishing fleet recorded the total length (TL,  $\pm 0.1$  cm) of both retained and discarded *P. pollachius*. In total, 11049 measured individuals were obtained from 1981 hauls conducted by 445 fishing vessels using 27 different artisanal gears during the period January 1999 to December 2012. The sampling program covers the full set of multiple artisanal gears used in Galician waters (hooks and lines, traps and nets). This design has 2 advantages. First, it might reduce the likely bias in the aggregate catch of each fishing gear due to differences in catchability; second, this fishery-dependent approach provides a wider spatio-temporal coverage than a fishery-independent survey. Thus, this data set is assumed to be a random sampling of the studied fish population that is well balanced among the different artisanal fishing gears, seasons and spatial coverage.

In addition to the onboard survey, 622 individuals were sampled from fish markets along the western coast of Galicia (Fig. 1) on a monthly basis, from November 2009 to October 2010, to ascertain the main biological cycle of the species. For each individual, we recorded TL ( $\pm 0.1$  cm), total weight (TW,  $\pm 0.01$  g), eviscerated body weight (EW,  $\pm 0.01$  g), gonad weight (GW,  $\pm 0.01$  g), stomach weight (SW,  $\pm 0.01$  g) and maturity stage. Further sampling details can be found elsewhere (Alonso-Fernández et al. 2013). Two somatic indices were estimated using the above morphometric parameters, the gonadosomatic index (GSI):

$$\text{GSI} = \frac{\text{GW}}{\text{EW}} \times 100 \quad (1)$$

and the stomach index (STI):

$$\text{STI} = \frac{\text{SW}}{\text{EW}} \times 100 \quad (2)$$

### Environmental data

To evaluate the role of environmental variables on *P. pollachius* body size, we compiled data on sea

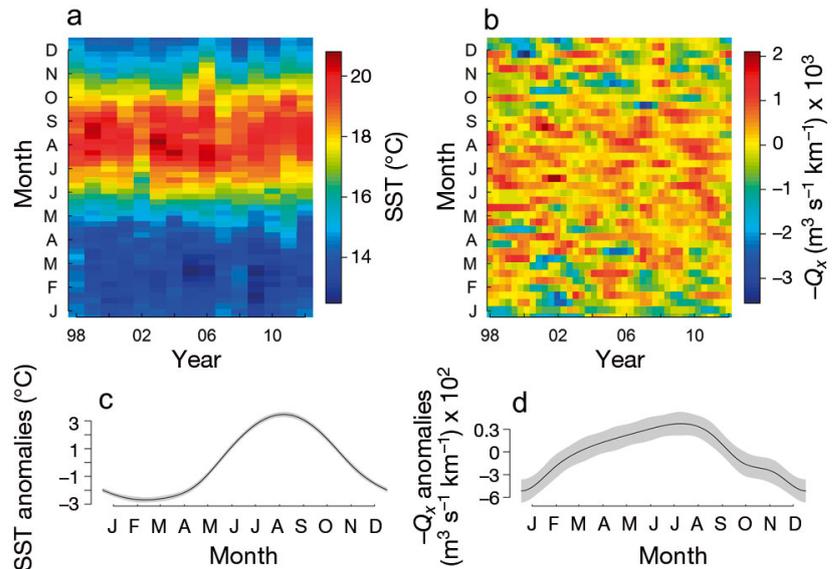


Fig. 2. Temporal (seasonal and annual) variation of environmental variables used in the current analysis. Distribution of (a) sea surface temperature (SST) and (b) upwelling index ( $-Q_x$ ) for Galician waters during the study period 1998 to 2012. Fitted seasonal generalized additive mixed model for (c) SST and (d)  $-Q_x$ . Light grey shaded areas represent 95% confidence intervals around the main effect

surface temperature (SST, in  $^{\circ}\text{C}$ ) and upwelling intensity ( $-Q_x$ , in  $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$ ). First, optimum interpolation SST data available at weekly  $1^{\circ}$  latitude  $\times$   $1^{\circ}$  longitude grid resolution from a combination of satellite and *in situ* measurements (Reynolds et al. 2002) were obtained from the NOAA Earth System Research Laboratory ([www.esrl.noaa.gov/psd/](http://www.esrl.noaa.gov/psd/)) for the period 1998 to 2012 (Fig. 2a). Sea temperature at the latitude of the study area undergoes different seasonal cycles at the surface and bottom layers (see Fig. S1a,b in the Supplement at [www.int-res.com/articles/suppl/m511p223\\_supp.pdf](http://www.int-res.com/articles/suppl/m511p223_supp.pdf)). However, once removed, the annual and long-term trends of both patterns are correlated (Fig. S1c); thus, SST can be assumed as a valid proxy for depicting the changes occurring in the pollack's habitat conditions. Second, the upwelling intensity was computed in a  $2^{\circ} \times 2^{\circ}$  cell centered at  $43^{\circ}\text{N}$ ,  $11^{\circ}\text{W}$  (Fig. 1) from geostrophic winds calculated from the surface atmospheric pressure fields analyzed every 6 h by the Fleet Numerical Meteorology and Oceanography Center ([www.usno.navy.mil](http://www.usno.navy.mil)) and following the method described by Bakun (1973). Data were obtained for the period 1998 to 2012 (Fig. 2b) and downloaded from [www.indicedeafloramiento.ieo.es/](http://www.indicedeafloramiento.ieo.es/). Positive values of  $-Q_x$  indicate upwelling-favorable offshore Ekman transport. Conversely, negative values indicate downwelling-favorable onshore Ekman transport.

## Data analyses

### Environmental data

At the latitude of our study site, both environmental variables (temperature and upwelling) showed a seasonal pattern (Fig. 2). Therefore, to avoid co-variability and potential confounding effects and interpretations, SST and  $-Q_X$  were deseasonalized and detrended using a generalized additive mixed model (GAMM, Wood 2006), as follows:

$$Y_{t,i} = \alpha + f_1(\text{DoY}_{t,i}) + f_2(\text{Days}_{t,i}) + \varepsilon_{t,i} \quad (3)$$

where the response variable  $Y_{t,i}$  would be SST or  $-Q_X$  recorded at day  $t$  and year  $i$ .  $\alpha$  is an intercept, and the  $f_{ns}$  are 1-dimensional non-parametric smoothing functions describing the effect of DoY (day of the year) and Days (consecutive days from 1998 to 2012). The smoothing functions were fit by a penalized cyclic cubic regression spline and a cubic regression spline for DoY and Days, respectively. Observations were made sequentially over time; thus, errors ( $\varepsilon_{t,i}$ ) might not be independent. Therefore, a correlation structure was added to the formulation following an auto-regressive model of order 1 allowing for within-year autocorrelation between the residuals, as follows:

$$\varepsilon_{t,i} = \phi \varepsilon_{(t-1),i} + \eta_{t,i} \quad (4)$$

where  $\eta_{t,i}$  are independent and identically distributed errors.

### Body size data

Body size records were obtained from many boats that might use different fishing gears deployed several times per day. This implies potential correlation among body size records within hauls, boats and gears. Thus, to include both fixed and random effects, account for the lack of independence and allow for non-linearities, the data were analyzed using a GAMM (Wood 2006), as follows:

$$\begin{aligned} \text{TL}_{ihbg} = & \alpha + \beta_1 \text{SST}_{ihbg} + \beta_2 \text{Den}_{ihbg} \\ & + \beta_3 (\text{SST}_{ihbg} \times \text{Den}_{ihbg}) + \beta_4 Q_{Xihbg} + \beta_5 (Q_{Xihbg} \times \text{Den}_{ihbg}) \\ & + f_1(\text{Depth}_{ihbg}) + f_2(\text{DoY}_{ihbg}) + f_3(\text{Year}_{ihbg}) \\ & + g_1(\text{Lon}_{ihbg}, \text{Lat}_{ihbg}) + a + b + c + \varepsilon_{ihbg} \end{aligned} \quad (5)$$

where TL is the total length of fish  $i$  caught in haul  $h$  by boat  $b$  and gear  $g$ . Exploratory analyses revealed that SST,  $-Q_X$  (upwelling intensity) and Den (*P. pollachius* abundance) did not present non-linear effects;

thus, these explanatory variables were introduced in the models as parametric terms, with  $\beta_{ns}$  representing the linear coefficients.  $\alpha$  is an intercept, and  $f_{ns}$  and  $g$  are 1- and 2-dimensional nonparametric smoothing functions describing the effect of DoY, Year (year), Depth (soak depth) and site location at longitude (Lon) and latitude (Lat). The deseasonalized and detrended environmental covariates SST and  $-Q_X$  (denoted in the models as  $Q_X$  for simplicity) were averaged along the year preceding the day of catch and assumed to account for individual effects on growth conditions. The covariate Depth was assumed to account for the vertical behavior of *P. pollachius* associated with ontogenic shifts in the species distribution. Moreover, including a function of longitude and latitude would act as a 'catchall' proxy for other factors that vary spatially and were not taken into account in the formulation. The covariate Den was the ln-transformed total number of *P. pollachius* caught in the corresponding haul and assumed to account for the density-dependent effects. Finally, intra- and inter-annual variation in length was represented by covariates DoY and Year, respectively. The smoothing functions were fit by penalized cubic regression splines and a thin plate regression spline with 3 and 8 knots for the 1- and 2-dimensional functions, respectively (Wood 2006), with the exception of DoY, which was fitted by penalized cyclic cubic regression splines with 4 knots.  $a$ ,  $b$  and  $c$  are random effects allowing for variation between gears, between boats within gears, and between hauls within boats within gears, respectively. Random effects were assumed to be normally distributed with mean 0 and variances  $\sigma_a^2$ ,  $\sigma_b^2$  and  $\sigma_c^2$ . The residuals  $\varepsilon_{ihbg}$  were assumed to be normally distributed random error, with mean 0 representing within-haul, gear and boat variation. However, the variance in residual length ( $\sigma^2$ ) was further modeled as a function of the covariates included in Eq. (5); for example:

$$\text{var}(\varepsilon_{ihbg}) = \sigma^2 \exp(2\delta \text{Depth}_{ihbg}) \quad (6)$$

where  $\delta$  is a parameter to be estimated that describes the estimated change in variance with Depth. Other variance structures were tested further.

Prior to model development, all explanatory covariates summarized in Table S1 (Supplement) were inspected for collinearity using variance inflation factors (VIF, Zuur et al. 2010). Model selection was then performed iteratively. First, with all fixed effects included in the model, appropriate random effects structure and variance models were selected using Akaike's information criterion (AIC). Model parameters were estimated using restricted maximum likeli-

hood (REML). Then, the optimal fixed effects were determined using maximum likelihood and comparing AIC in favor of the most parsimonious model among the candidate model set. Models with a difference in AIC ( $\Delta\text{AIC}$ ) smaller than 2 were considered as equivalent; then, the simpler model was selected (Burnham & Anderson 2002). Finally, parameters for the optimal model were estimated by REML (Zuur et al. 2009). To further assess the robustness of the model structure and stability of the patterns at the level of sampling, a bootstrap was performed by randomly leaving out 20% of the original data and resampling the remaining 80% in each of the iterations of 1000 runs. Because of computational limitations, the bootstrapping exercise was carried out by fitting a GAM, keeping the fixed structure from the optimal GAMM. Graphical inspection of the partial effects of smooth terms and histograms of estimated coefficients for the parametric terms was used to critically evaluate the adequacy of the data set.

#### Morphometric indices

It has been previously shown that *P. pollachius* exhibits clear seasonal variation in several biological indices (Alonso-Fernández et al. 2013). For the purpose of this study, the seasonal variation of somatic indices, GSI and STI, was investigated using a GAM as follows:

$$Y = \alpha + f_1(\text{DoY}) + \varepsilon \quad (7)$$

where the response variable  $Y$  would be the somatic index, GSI or STI;  $\alpha$  is an intercept; and  $f_1$  is a 1-dimensional non-parametric smoothing function (fitted using a cyclic cubic spline with a maximum of 4 knots) describing the effect of DoY.

All analyses and treatment of data were performed using R (R Development Core Team 2013) and the 'mgcv 1.7-13' (Wood 2006) and 'nlme 3.1-103' (Pinheiro et al. 2014) packages.

## RESULTS

### Environmental data

SST and the upwelling index described a seasonal pattern, with maximum values during summer months (Fig. 2). The seasonal trend explained 95% of the variation in SST (Table S2 in the Supplement), while it explained less than 10% in the case of the upwelling index (Table S3). In both cases, no signifi-

cant year trend was detected during the 1998–2012 period. Nevertheless, the resulting deseasonalized and detrended SST and  $-Q_x$  were subsequently used as covariates (see above) in the body size models. Notably, the temporal model for  $-Q_x$  explained a small percentage of the total variability as compared to SST. However, we decided to maintain this approach for  $-Q_x$  to remove any remaining temporal pattern that might cause collinearity issues and confounding interpretations.

### Body size models

Average TL was  $36.73 \pm 10.93$  cm (mean  $\pm$  SD). Calculation of VIF among all candidate variables (Table S1) revealed no signs of collinearity with all VIF values below a cutoff level of 3. Model selection favored the inclusion of all 3 nested random effects, that is, gear type, fishing boat and haul (Table S4), imposing a correlation between 2 observations from the same grouping factor. Moreover, model performance was better when including a residual variance model (Table S4). In particular, a combination of variance structures allowed for both an exponential increase in residual body size with Depth and an exponential decrease with Den as variance covariates. Regarding the fixed effects (Table 1), the optimal model showed that body size was larger in the southern coast of the study area (Fig. 3a) and also in offshore deeper waters (Fig. 3b). Furthermore, TL showed a clear seasonal pattern, with minimum values during summer months (Fig. 3c), but a not significant year trend. Finally, body size showed a positive correlation with temperature when densities were low but turned to be negative at high densities (Fig. 3d). Upwelling index was not significant. The patterns of the relationships found were stable at the level of sampling, as shown by the bootstrapping (Figs. S2 & S3 in the Supplement). The final GAMM fits the data reasonably well, though a slight deviation at larger body sizes was apparent (Fig. 4). Normalized residuals did not show any departures from normality or further heterogeneity issues (Fig. S4). Random effects were also reasonably normally distributed (Fig. S5).

### Morphometric indices

The average GSI of *Pollachius pollachius* sampled during the period 2009 to 2010 in Galician waters was  $2.30 \pm 2.80$ , with maximum values in February ( $6.56 \pm$

Table 1. *Pollachius pollachius* body size model results. Summary of the optimal model fitted to pollack total weight. Shown are the parameter estimates and statistical significance for the parametric and smooth terms included in the model. CI = 95% confidence interval; edf = estimated degrees of freedom; SD = standard deviation; SE = standard error

| Effect                   | Estimate | SE   | CI           | t-value | edf  | F-value | p-value |
|--------------------------|----------|------|--------------|---------|------|---------|---------|
| <b>Fixed</b>             |          |      |              |         |      |         |         |
| <b>Parametric</b>        |          |      |              |         |      |         |         |
| Intercept                | 37.81    | 1.58 | 34.71; 40.92 | 23.88   |      |         | <0.0001 |
| $\beta_1$                | 5.74     | 1.63 | 2.54; 8.94   | 3.51    |      |         | 0.0004  |
| $\beta_2$                | -0.10    | 0.18 | -0.41; 0.20  | -0.66   |      |         | 0.5101  |
| $\beta_3$                | -3.46    | 0.91 | -5.24; -1.68 | -3.82   |      |         | 0.0001  |
| <b>Smoother</b>          |          |      |              |         |      |         |         |
| $f_1$                    |          |      |              |         | 1.98 | 271.52  | <0.0001 |
| $f_2$                    |          |      |              |         | 1.96 | 46.50   | <0.0001 |
| $g_1$                    |          |      |              |         | 6.18 | 7.08    | <0.0001 |
| <b>Random (SD)</b>       |          |      |              |         |      |         |         |
| $\sigma_a$               | 7.00     |      | 4.93; 9.69   |         |      |         |         |
| $\sigma_b$               | 3.32     |      | 2.85; 3.86   |         |      |         |         |
| $\sigma_c$               | 3.80     |      | 3.49; 4.14   |         |      |         |         |
| $\sigma$                 | 5.78     |      | 5.54; 6.04   |         |      |         |         |
| <b>Variance function</b> |          |      |              |         |      |         |         |
| $\delta_{\text{Depth}}$  | 10.33    |      | 9.68; 10.98  |         |      |         |         |
| $\delta_{\text{Den}}$    | -0.22    |      | -0.24; -0.21 |         |      |         |         |

4.10) and a minimum in September ( $0.38 \pm 0.29$ ). The STI averaged  $4.95 \pm 2.55$ , and maximum and minimum values were opposite to the GSI pattern, reaching  $3.55 \pm 1.26$  in February and  $7.41 \pm 4.04$  in September. Both somatic indices showed significant seasonal cycles, with minimum values of GSI in summer months (Fig. 5a, Table S5), mirroring the modeled cyclic pattern in body size (Fig. 3c). By contrast, STI showed an inverse pattern, with maximum values during summer (Fig. 5b, Table S6).

### DISCUSSION

Fish body size is a central trait that influences multiple ecological processes such as population abundance, geographical distribution or ecosystem functioning (Fisher et al. 2010b).

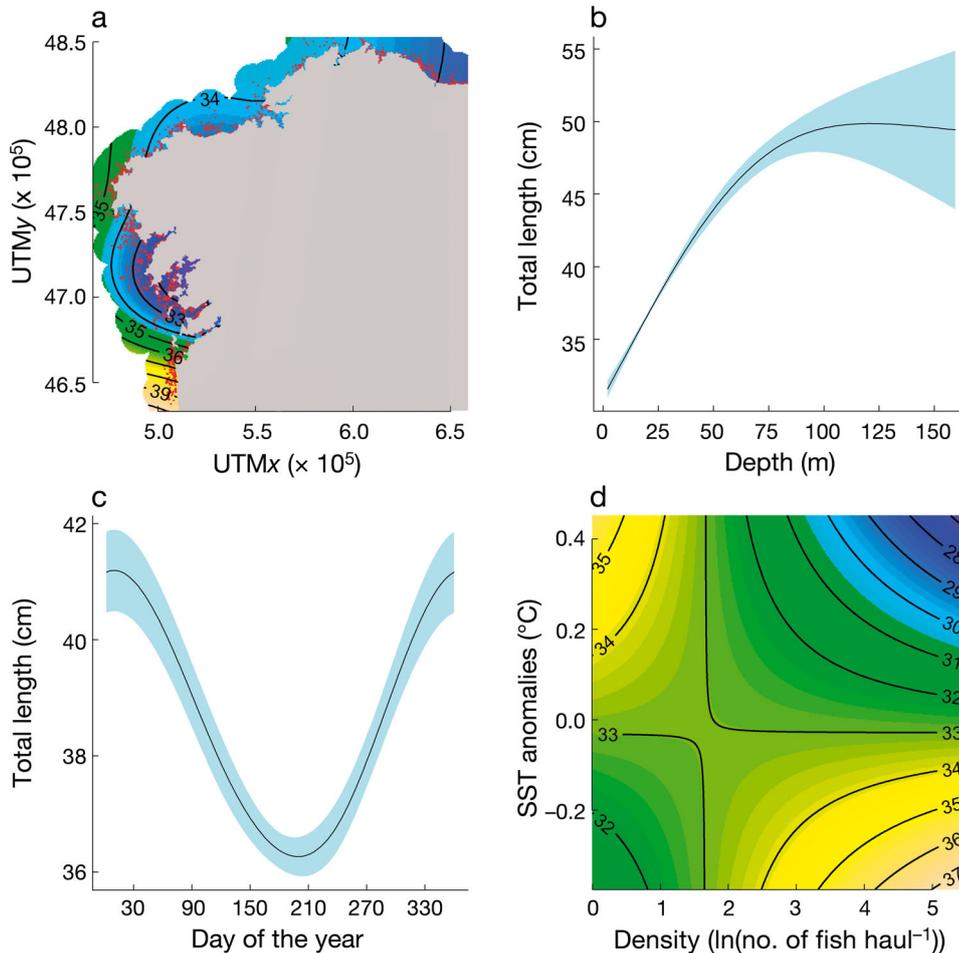


Fig. 3. *Pollachius pollachius* generalized additive mixed model terms for total fish length monitored off the Galician coast from 1999 to 2012. (a) Smooth function of geographical distribution (UTM coordinates), (b) smooth curve of depth of catch, (c) smooth function of day of the year and (d) first-order interaction between deseasonalized and detrended sea surface temperature (SST) averaged over the year preceding the catch and ln-transformed fish density. Red dots in (a) indicate the sampling points. Blue-shaded areas in (b) and (c) represent 95% confidence intervals around the main effects

At the species level, many biological processes that affect survival, maturation or reproduction are also body size dependent. Moreover, size distribution of fish is sensitive to fishing, which is often a size-selective activity. Therefore, the trait weight/length of the population has been proposed as one of the

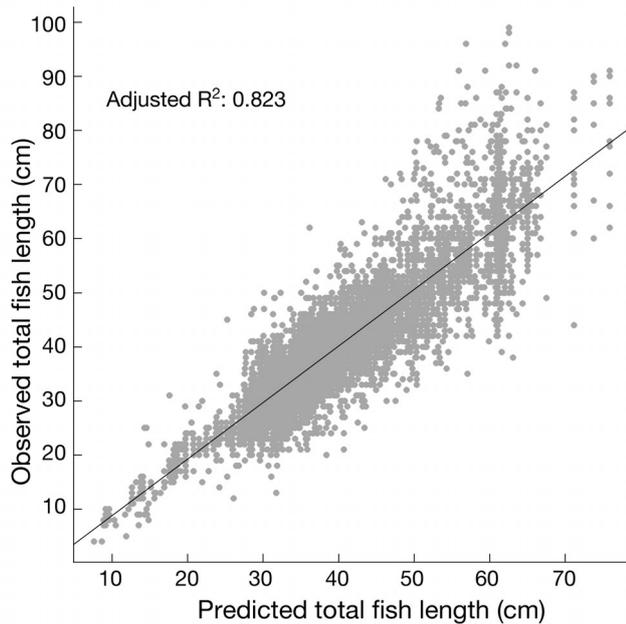


Fig. 4. Scatterplot of observed total fish length and model predictions for the entire data set obtained from the optimal model

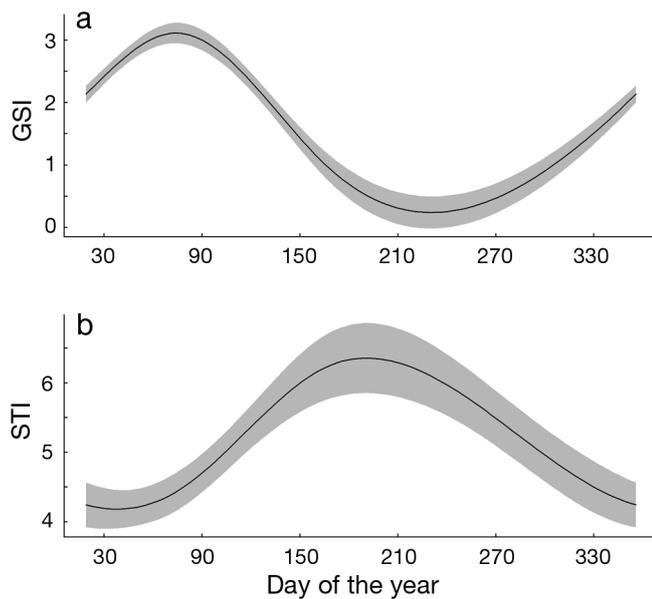


Fig. 5. Generalized additive model smoothing curves for day of the year of the (a) gonadosomatic index (GSI) and (b) stomach index (STI). Light grey-shaded areas represent 95% confidence intervals around the main effects

size-based indicator (SBI) metrics that might be used to assess the status of harvested ecosystems (Shin et al. 2005). These indicators are commonly used to describe the fate of fish populations and relate their variability to different abiotic and biotic constraints in part because SBIs should be integrative metrics that are not only sensitive to anthropogenic impacts such as fishing but also to the environmental forcing and internal dynamics of the population (Shin et al. 2005). Our study provides compelling evidence for a variation in *P. pollachius* body size at the population level in response to both intrinsic and extrinsic factors.

Despite the frequent use of aggregated catch-dependent size data in the absence of other detailed information (e.g. Cheung et al. 2013), one of the main concerns regarding the analyses of body size is the lack of information on age structure, as was the case here. Data on age classes are desirable to separate differences in growth from population composition when determining relationships with biotic and abiotic factors, as has been frequently shown for both marine (e.g. Rogers et al. 2011) and freshwater (e.g. Ohlberger et al. 2013) aquatic systems and terrestrial species (e.g. Gardner et al. 2014). The intention of our modeling approach was to minimize the potential biases caused by the lack of information on age structure by taking into account the uncertainty usually associated with the use of pooled fisheries statistics to study species-specific ecological responses.

We found that pollack body size increased in offshore waters and towards lower latitudes, with larger individuals peaking at the southern boundary of the studied area. Body size was also related to depth, with average size increasing in deeper waters. Moreover, size variability was also higher when depth was greater. Spatial heterogeneity is a common feature in fish populations. For instance, Fromentin et al. (1997) reported on divergences in spatial structure for juvenile gadoid species, including pollack, along the Norwegian Skagerrak coast and concluded that this variability was associated with species-specific habitat preferences, intrinsic dynamics and environmental changes (Fromentin et al. 1998). Spatial patterns are also apparent in pollack adults that form spawning aggregations along the European coast (Quéro et al. 1984). This variability in space is also evident for other members of the same family such as *P. virens*, which perform offshore-inshore migrations because of differing affinities to feeding grounds (Armannsson et al. 2007). Bathymetric gradients in body size are also common and have been previously reported for both *P. pollachius* (Moreau 1964) and *P. virens*

(Neilson et al. 2003) as a result of ontogenic changes, with older fish inhabiting deeper waters. Our results also provided evidence for spatial variation through an apparent strong affinity of larger individuals for offshore deeper waters along the Galician coast. This segregation pattern could suggest that smaller individuals would inhabit shallower waters because their conspicuousness would result in a competitive disadvantage in feeding (Ward & Krause 2001). In addition, the increase in body size spread with depth may be a consequence of this ontogenic shift in fish distribution; that is, a higher number of different cohorts would occur at deeper waters compared to shallower waters. Clay et al. (1989) also found that younger cohorts of *P. virens* were restricted to inshore waters.

Seasonality is a ubiquitous feature in fishes, especially in relation to reproduction (Munro et al. 1990), and *P. pollachius* is no exception. Gonad development for this species occurs during winter, and spawning extends until early spring (Alonso-Fernández et al. 2013). This concurs with our finding of maximum body sizes and GSI values during autumn and winter months. By contrast, the minimum of reproductive activity matched a different biological cycle for the species, namely feeding, with maximum STI values peaking during summer after the end of the spawning season. Seasonal changes in fish body size, however, can be a mixture of responses to variations in reproductive timing, recruitment and/or growth (Shin et al. 2005). We suggest that the observed cyclic pattern would point to an offshore-inshore migration related to the reproductive timing of the species. Larger individuals would migrate from deeper waters towards the coast for spawning in autumn and winter. The occurrence of a spot of larger body sizes in SW Galicia would reinforce this interpretation. Nonetheless, more detailed ecological studies are required to test this later explanation for geographic aggregations. Alternatively, high recruitment pulses of juveniles during the summer period may reduce the average fish size of the population, masking the former hypothesis. In any case, both processes can act simultaneously, and the analysis of trends in abundance would facilitate the interpretation (Shin et al. 2005).

Environmental conditions influence body size through multiple mechanisms. One of the most pervasive variables with a strong theoretical setting for interpreting shifts in body size is temperature (Gardner et al. 2011). Recent analyses in the context of Bergman's rule concluded that current warming will lead to reductions in body size across ecosystems and taxa (Daufresne et al. 2009), including fishes (Che-

ung et al. 2013). However, body size responses to temperature changes are strongly species specific and will be a function of the thermal requirements defined by the species' thermal sensitivity curve (Angilletta 2009). Hence, the direction and magnitude of body size responses to warming can be heterogeneous and will depend on the optimal temperature ranges for growth and size-dependent feedbacks at the population and community levels (Gardner et al. 2011, Ohlberger 2013). Regarding fishes, smaller mean body sizes at age in response to warmer water conditions have been reported for several species (e.g. Todd et al. 2008, Xu et al. 2010, Rogers et al. 2011). However, positive relationships between growth and temperature have also been found (e.g. Morrongiello et al. 2011, Gillanders et al. 2012, Neuheimer & Grønkvær 2012). The reason for this disparity may be that the temperature-size responses in ectothermic organisms seem to be linked to tolerance limits in fish growth (Neuheimer et al. 2011). Whereas positive relationships are common in the middle of a species' geographical range (Gillanders et al. 2012), the detrimental effects of temperature become apparent at warmer edges of their distribution, close to the tolerance thermal limit (Neuheimer et al. 2011). Rearing experiments with pollack showed a fast growth potential for the species, with juveniles attaining up to 400 g in 2 yr at temperatures ranging from 9 to 18°C (Suquet et al. 1996). Person-Le Ruyet et al. (2006) further reported maximum growth rates for pollack juveniles at a narrower range of 12 to 15°C. These studies, however, were carried out at constant photoperiod, aeration and feeding conditions and thus did not consider variations in food availability and other constraints such as interactions and feedbacks.

Environmental conditions, together with inter- and intra-specific interactions such as predation or competition, are primary determinants of phenotypic changes in a variety of life history traits including growth (Edeline et al. 2013). Therefore, the environmental responses will further depend on population density levels and would be especially apparent in species that shoal. In the particular case of *P. pollachius*, given the correlation among individuals within hauls, it is reasonable to think that each haul catches individuals that aggregate, likely belonging to the same cohort. Taking all of this together, our data showed a significant interaction between individual thermal regime (sea temperature during the last year of life) and an index of fish density. Although temperature showed a positive effect on fish size at lower fish densities, an increase in fish density resulted in a

negative response of body size to thermal conditions. Moreover, changes in body size occurred at a faster rate at a high-density regime. Therefore, our results concur with James' rule only at elevated densities. Interacting effects of density and temperature on individual fish performance, i.e. strengthened negative density-dependent processes at warmer temperatures, have been suggested previously for several species (e.g. Crozier et al. 2010, Xu et al. 2010). Population density is widely recognized as a common driver of changes in body size; that is, an increase in density induces a reduction in body size because of competition for habitat and food resources among others, which decreases individual growth performance (Jensen et al. 2000, Xu et al. 2010, Rogers et al. 2011).

Density-dependent growth is generally circumscribed to the recruitment phase and found as a key mechanism for the regulation of population dynamics (Lorenzen & Enberg 2002). However, density effects are neither limited to early life stages (Jenkins et al. 1999, Bohlin et al. 2002) nor so influential (Brander 2007). In any case, a complete understanding of body size responses to thermal variation requires considering ecological interactions such as competition or predation (Edeline et al. 2013). Temperature-size responses are determined not only by changes in individual growth but also by size-dependent population feedbacks and community interactions, and this is especially true in aquatic systems (Forster et al. 2012). We are aware that our findings have some limitations mainly because of the lack of age information and because the population density used here is a rough index of abundance. However, the modeling approach tried to overcome these flaws by accounting for most of the variation in fish abundance, thus minimizing the potential biases in population structure and density. For instance, the inclusion of random effects in the model formulation shows the strong correlation and decreased variability among individuals caught at the same haul. Detailed information on weight or length at age is not always available; thus, fishery-dependent size data could be used instead to better understand ecological responses and derive valid inferences at the population level.

Upwelling dynamics is a key variable in determining the productivity of the study area (Álvarez-Salgado et al. 2002) and has been identified as an important factor affecting, for instance, the fate of recruitment in *Sardina pilchardus* (Guisande et al. 2001) and *Octopus vulgaris* catches (Otero et al. 2008) in the region. Few studies, however, have analyzed the influence of upwelling in body size varia-

tion. Regarding the present work, our model failed to detect any significant relationship between body size and upwelling strength. This might be because the upwelling index did not properly capture the variability in environmental conditions other than temperature, or the influence of this factor might be restricted to a specific life stage (i.e. larval phase), not taken into account here given the lack of age structure data, that would allow us to evaluate reliable time lags. A positive relationship between body size and upwelling has been detected, for instance, in the early growth of Chinook salmon *Oncorhynchus tshawytscha* (Wells et al. 2007) and size of the California market squid *Doryteuthis opalescens* (Jackson & Domeier 2003).

In conclusion, body size of *P. pollachius* catch in NW Spain was influenced by both extrinsic and intrinsic factors. After accounting for spatial effects, size increased with depth and showed a seasonal pattern related to the species' biological cycles, which conditioned the population structure along the Galician coast. Furthermore, we detected an interaction between temperature and fish density, suggesting that growth for the species would be density dependent only in warmer waters. Therefore, this work evidences the usefulness of a size-based indicator obtained from fishery-dependent data to better understand the factors that drive the spatio-temporal patterns of a key life history trait in exploited fish stocks.

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