

Contrasting evolutionary demography induced by fishing: the role of adaptive phenotypic plasticity

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Abstract. Mounting evidence now shows that fishing activity modifies both heritable life-history traits and ecological processes in harvested populations. However, ecological and evolutionary changes are intimately linked and can occur on the same time scale, and few studies have investigated their combined effect on fish population dynamics. Here, we contrast two population subunits of a harvested fish species in the Northeast Atlantic, the European hake (*Merluccius merluccius*), in the light of the emerging field of evolutionary demography, which considers the interacting processes between ecology and evolution. The two subunits experienced similar age/size truncation due to size-selective fishing, but displayed differences in key ecological processes (recruitment success) and phenotypic characteristics (maturation schedule). We investigate how temporal variation in maturation and recruitment success interactively shape the population dynamics of the two subunits.

We document that the two subunits of European hake displayed different responses to fishing in maturation schedules, possibly because of the different level of adaptive phenotypic plasticity. Our results also suggest that high phenotypic plasticity can dampen the effects of fisheries-induced demographic truncation on population dynamics, whereas a population subunit characterized by low phenotypic plasticity may suffer from additive effects of ecological and life-history responses. Similar fishing pressure may thus trigger contrasting interactions between life history variation and ecological processes within the same population. The presented findings improve our understanding of how fishing impacts eco-evolutionary dynamics, which is a keystone for a more comprehensive management of harvested species.

Key words: contemporary evolution; demographic erosion; European hake; evolutionary demography; fisheries conservation; fishing-induced effects; *Merluccius merluccius*; phenotypic plasticity.

INTRODUCTION

Understanding how fishing modifies the natural mechanisms that regulate fish populations' productivity is of serious concerns for fisheries ecologists (Rose et al. 2001, Lorenzen and Enberg 2002). This understanding is a prerequisite for designing stock-specific conservation strategies and for better predicting the future functioning of marine ecosystems (Fisher et al. 2010). Particularly, natural mechanisms of regulation can be modified by the disproportional removal of older and larger individuals due to fishing activity (Law 2000). The view embodied in fisheries science is that variation of adult density is the main factor regulating the juvenile

survival, while changes in phenotypic characteristics of adults have been investigated as independent processes (Lorenzen and Enberg 2002). However, phenotypic variation can have an essential role in the population regulation of harvested species (Goodwin et al. 2006, Marshall et al. 2010).

The effects of size-selective fishing on both population dynamics and life history have been documented worldwide (for a review, see Jørgensen et al. [2007], Hsieh et al. [2010]). For instance, the erosion of the age structure makes populations more dependent on younger age classes (i.e., demographic erosion; Ottersen 2008), which tightens the link between population and environmental variability (Anderson et al. 2008). Size-selective exploitation also affects population dynamics through diminishing maternal influences, which reduces the positive effect of size-related reproductive traits (fecundity, quality of eggs, or bet-hedging strategies) on the offspring survival (Venturelli et al. 2010). Furthermore, there is accumulating evidence that selective

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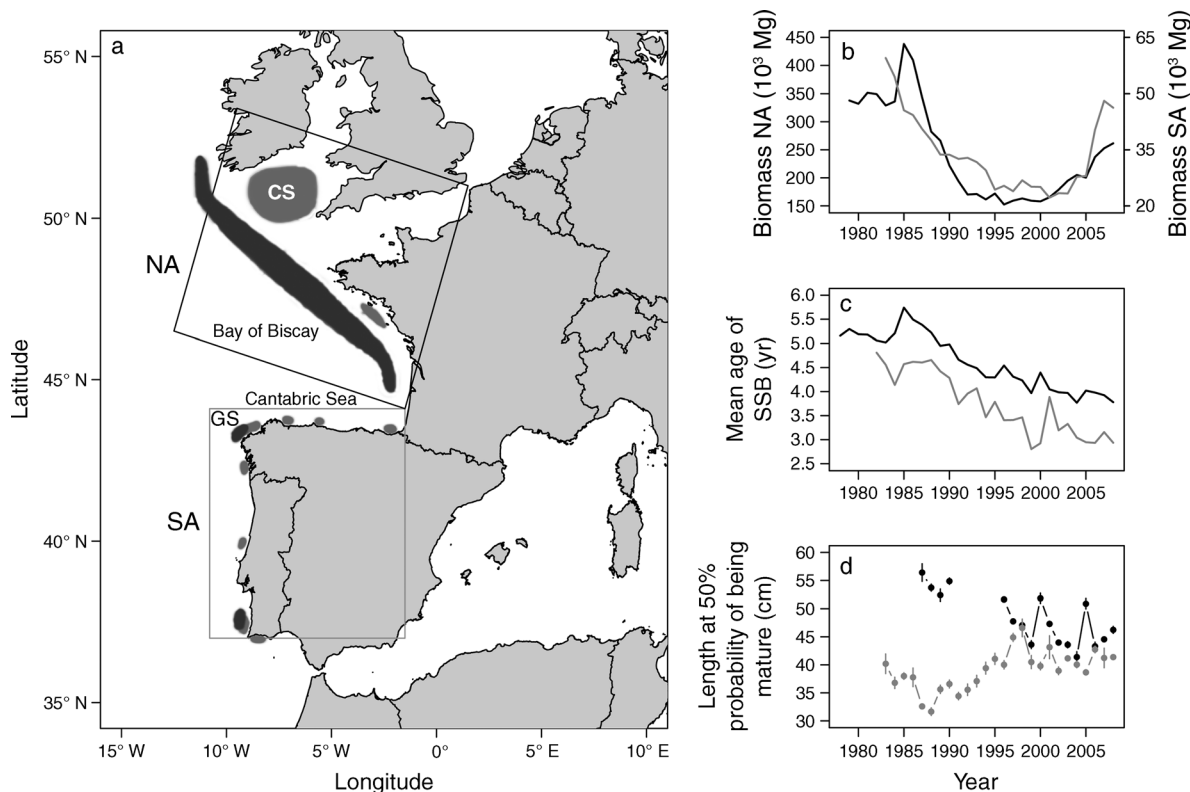


FIG. 1. (a) Area covered by the north (NA, black square) and south (SA, gray square) management units of hake investigated as independent demes (Pita et al. 2011). Light and dark gray areas of the ocean indicate the main nursery and spawning areas, respectively; GS and CS refer to Galician shelf and Celtic Sea (see *Materials and Methods* for study system description). Graphs show temporal variation of (b) deme biomass, (c) mean age of spawners (spawning stock biomass, SSB) and (d) lengths at 50% probability of being mature (error bars represent SE). Black and gray lines refer to the north and the south demes, respectively.

fishing also causes evolutionary changes in fitness-related traits like growth and maturation (Olsen et al. 2004, Swain et al. 2007). However, few studies have investigated how fishing-induced changes in life history and demography interact to shape population dynamics. This remains a serious challenge for fisheries ecology.

Evolutionary demography, or eco-evolutionary dynamics, aims to integrate ecological responses in evolutionary studies, as well as evolutionary responses in ecological studies, to comprehend the interplay between these processes (Pelletier et al. 2007, Ezard et al. 2009). Phenotypic plasticity (i.e., the ability of a genotype to produce different phenotypes across an environmental gradient) can modify this interplay due to its potential to reduce evolutionary change (Price et al. 2003, Reed et al. 2010, Ellner et al. 2011). This is of paramount importance in exploited marine populations because phenotypic plasticity may constrain the evolutionary impact of human-induced selection (Law 2000, Marshall and McAdam 2007). In addition, individuals inhabiting heterogeneous environments are more prone to display plastic changes in their life history traits (Reed et al. 2010). This is the case in spatially structured marine populations, in which subunits (i.e., demes) can be affected differently by environmental heterogeneity

(Kareiva 1990). In this case, evolutionary demography may differ for subpopulations colonizing environments of different complexity, provided that local selection pressures outweigh the homogenizing effect of gene flow. To investigate the influence of fishing in shaping evolutionary demography, a first step is to study populations or sub-populations of the same species.

We selected a long-term exploited species in the Eastern Atlantic (European hake, *Merluccius merluccius*; see Plate 1) that exhibits a complex spatial structure with two main demes consistent with two current management units (i.e., stocks). These demes are not genetically different (Pita et al. 2011) but display spatially independent and temporally stable spawning aggregations (Fig. 1a), and distinct recruitment dynamics (Hidalgo et al. 2012; see also *Material and Methods*). Thus, they were investigated as independent demes within a population. The two demes were historically affected by the same size-selective pattern of fishing mainly targeting the adult stock (ICES 2009, Murua 2010), displaying similar temporal trends in population biomass (Fig. 1b) and a progressive demographic erosion of age structure (Fig. 1c). By contrast, temporal trends in length at maturity differed considerably between the two demes (Fig. 1d; Domínguez-Petit et

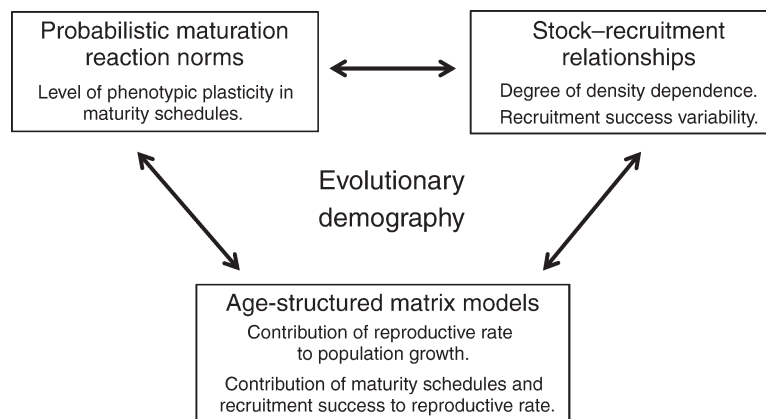


FIG. 2. Evolutionary demography framework applied combining information from three modeling techniques (probabilistic maturation reaction norms, stock–recruitment relationships, and age-structured matrix models) in a combined and integrative manner. Key information to be discussed and analyzed for each technique within an evolutionary demography framework is specified. Note that temporal variation of ecological and evolutionary properties are investigated in the present study applying time-varying analytical approaches, with the exception of the reaction norms due to data restrictions (see specific methodology in *Maturation reaction norms*).

al. 2008). These characteristics make hake a suitable case study to investigate interactions between ecological processes (i.e., recruitment) and life history dynamics (i.e., maturation) on population dynamics, and whether fishing alters this interaction.

The underlying hypothesis is that the level of phenotypic plasticity in length at maturation shapes the interaction between phenotypic changes and ecological processes. To understand how fishing modifies this interaction, we synthesize and combine results from three modeling techniques within an evolutionary demography framework (Fig. 2). First we investigate temporal changes in the phenotype, estimating maturation reaction norms for each deme to elucidate the relative contribution of adaptive changes vs. phenotypic plasticity in the maturation schedules. Second, we examine the temporal changes in the recruitment process by analyzing variation in recruitment success and how the density-dependent regulation in stock-recruitment models changes over time. Finally, we used age-structured matrix models to investigate the population dynamics consequences of the interaction between changes in the recruitment success and those in maturation schedules. Matrix models are well suited to investigate this interaction since one of the vital rates of the matrix structure is the reproductive rate, which explicitly results from the combination of maturation rates and recruitment success (see *Materials and Methods* and Fig. 2).

MATERIALS AND METHODS

Two contiguous contrasting systems

The two contiguous demes of the hake population in the Northeast Atlantic inhabit contrasting environments (e.g., hydrographical characteristics) that results in different degrees of environmental and population

heterogeneity (Fig. 1a). The north deme displays a large spawning area along the shelf break of the broad continental shelf of the Bay of Biscay, while the Celtic Sea being the main nursery area. The large-scale hydrography in the Bay of Biscay controls the zooplankton dynamics and the recruitment success of hake in the whole north deme (Goikoetxea and Irigoien 2013). By contrast, the south deme is distributed along the Atlantic Iberian coast and the Cantabric Sea, which are both characterized by a narrow continental shelf. This makes spatial distributions more patchy compared to the north deme. The spawning areas are mainly located in the Galician waters (Dominguez-Petit et al. 2008) while the nursery areas are often found around orographic structures such as big capes where primary and secondary production locally increases (Sánchez and Gil 2000). Thus, small hydrographical processes such as Iberian upwelling (Dominguez-Petit et al. 2008) or the strength of shelf-edge currents (Sánchez and Gil 2000) are the main environmental drivers influencing the recruitment dynamics at the south deme.

The window of data analyzed in the present study includes two periods of contrasting demography (mean age, Fig. 1c) of the spawning stock as well as different lengths at 50% probability of being mature (Fig. 1d). Both the north and the south deme experienced a similar progressive truncation of age structure that is maximized around the early nineties in both stocks (Hidalgo et al. 2012). The strategy of the present study is, therefore, to compare two periods that are contrasted in terms of age structure and lengths at 50% probability of being mature in both population subunits. For comparative analytical purposes (i.e., a balanced number of years between periods) and synthesis of the results between population subunits, two periods were selected: before 1995 and from 1996 onward. Note that the lack of maturity-at-length (see *Life history and demographic*

information section hereafter) in a critical period between 1991 and 1995 influences the selection of these two periods. Given the contrasting age structure between periods for the two subunits, we refer to the time period before 1995 as the “pre-truncated period” and to the period from 1996 onward as the “truncated period.”

Life history and demographic information

Maturity was macroscopically assessed using gonads sampled monthly in the main spawning areas from 1983 to 2008 for the south deme and for 1987–1990 and 1996–2008 for the north deme (details in Domínguez-Petit et al. 2008). Age-structured abundance and spawning stock biomass were extracted for the period 1978–2008 (north deme) and 1982–2008 (south deme) from the hake assessment of the International Council for the Exploration of the Sea (ICES 2009). These ICES groups used virtual population analyses with extended survivor analysis (VPA-XSA) to estimate abundance-at-age based on commercial catch data tuned to survey data. In these assessment procedures, no stock–recruitment relationship is assumed. Note that annual estimates of maturity-at-age for the north deme are not available for two periods: 1978–1986 and 1991–1995. For population dynamics purposes of this subunit, the maturity-at-age matrix of 1986 was extended backward, while a weighted estimation was applied to interpolate between 1991 and 1995. To do that, we considered a progressive contribution of the information of the two years on the edge (1990 and 1996), applying a weighting vector (0.16, 0.33, 0.5, 0.66, 0.83) to calculate the maturity-at-age of the five unavailable years.

Maturation reaction norms

We applied the probabilistic maturation reaction norms approach to compare the reaction norm midpoints (i.e., combinations of age and size for which the estimated probability of maturing is 50%) between the two contrasting periods. This methodology can help to disentangle phenotypically plastic and evolutionary changes in maturation schedules (Barot et al. 2004, Olsen et al. 2004). Probabilistic reaction norms for age and size at maturation are defined by the age- and size-specific probabilities at which individuals within a cohort mature during a given time interval (Heino et al. 2002), which overcomes the confounding effects of growth and mortality (often environment dependent). The probability of maturing at a given age and size ($m(a,s)$) was calculated from the probability of being mature at that age and size (i.e., the maturity ogive, $o(a,s)$) and the probability of being mature at the previous age and size ($o(a-1, s - \Delta s(a))$), which was inferred on the mean annual growth increment (Δs): $m(a,s) = [o(a,s) - o(a-1, s - \Delta s(a))]/[1 - o(a-1, s - \Delta s(a))]$. To compare periods with contrasting demographic structure (Fig. 1c) and different lengths at 50% probability of being mature (Fig. 1d), information of the

pre-truncated and of the truncated period was pooled for each of the two demes. For each deme and period we calculated the probabilistic reaction norm midpoints for age-2 and age-3, corresponding to the size classes at which most of the fish mature. We expect that large differences between reaction norms of each period could suggest a potentially higher contribution of evolutionary changes to the maturation schedules compared to phenotypically plastic variation.

Age estimations for hake have an inherent uncertainty due to the difficulty of interpretation of the annual rings of the otoliths (ICES 2009, Murua 2010). This would bias our reaction norm estimates due to the sensitivity of the probabilistic reaction norms to changes in somatic growth (Dieckmann and Heino 2007), and thus prevent of the calculation of probabilistic maturation reaction norms by cohort. To circumvent this limitation and to be able to evaluate a potential effect of changes in somatic growth on the reaction norms, we adopted the strategy of testing the sensitivity of the reaction norms estimated to simulated variation in hake aging using a range of somatic growth rate scenarios (Ohlberger et al. 2011). Particularly, we used simulations to identify the most likely somatic growth scenarios (higher, equal, or lower) in the pre-truncated period compared to the more recent period, which was used as known reference (see simulations in Appendix A). These growth scenarios illustrate the different contributions of plastic and adaptive mechanisms at each population subunit by allowing a comparison of the maturation reaction norm midpoints between periods. Once the most likely somatic growth scenario was identified for each population subunit, we averaged information for age-2 and age-3 to present the maturation reaction norm midpoints for each population subunit and for each of the selected periods.

Non-stationarity of population regulation

Growing evidence suggests that stock–recruitment relationships (SRs) of fish populations are not temporally static (Enberg et al. 2010, McClatchie et al. 2010, Olsen et al. 2011). Ecological characteristics such as environmental influences, density dependence or steepness can change with time at different time scales. We here investigate potential temporal changes in the density-dependent regulation of the recruitment success. We particularly examine changes in the density-dependent parameter of SRs that has been observed to temporally correlate with changes in life history characteristics (Goodwin et al. 2006). Several studies highlight the utility of stock–recruitment relationships to investigate density-dependent processes (e.g., survival; Minto et al. 2008) and their relationships with life history (Goodwin et al. 2006).

As preliminary analyses we compared the fit over the whole time series of the two most common SRs assuming density-dependent regulation in order to identify which model best explains SR: the Ricker

model (overcompensation regulation) and the Beverton-Holt model (saturation regulation; see Appendix B). The Ricker model displayed a better fit for the two demes over the whole period (Appendix B). We then applied a 12-year moving window fitting the linearized transformation of the model: $\log(R_t/SSB_{t-1}) = a_0 - b(SSB_{t-1}) + \varepsilon_t$, where R_t is the recruitment (age-0) at year t , SSB_{t-1} the spawning abundance at year $t - 1$, a_0 and b are the estimated parameters, and ε_t the error term at year t . To analyze the temporal variation of the density-dependent parameter (b), we applied the nls function provided in R 2.12.1 (R Development Core Team 2010), which uses the Gauss-Newton algorithm to minimize the nonlinear least-squares estimates of the model parameters. Note that the size of the window was arbitrarily fixed to 12 years, which represents a compromise between the limited length of the time series and the generation time of the species, 5.5 years (T. Rouyer, *personal communication*). We expect that a significant temporal drift in b would reflect a change in the density-dependent regulation of recruitment within population subunit.

Population dynamics consequences

We investigated the population dynamics implications of the interaction between maturation schedules and recruitment success by calculating the temporal variation in population growth (r), as well as the relative contribution (i.e., elasticity) of the reproductive rates to changes in r . We used an age-structured matrix model (Caswell 2001), which summarizes age-specific vital rates: survival (S) and the reproductive rate (RR). The fundamental relationship of age-structured matrix models is given by $N_{t+1} = A_t N_t$, where N_t is a vector representing the number of individuals for each age class at time t , and A_t is a transition (Leslie) matrix that summarizes the dynamics of the populations between time t and time $t + 1$ (Leslie 1945, Caswell 2001). A_t summarizes the vital rates and the logarithm of its dominant eigenvalue (λ) provides the population growth rate, r . For a given year, the transition matrix (A_t) is defined as follows:

$$A_t = \begin{pmatrix} RR_{0,t} & RR_{1,t} & RR_{2,t} & \dots & RR_{imax,t} \\ S_{1-0,t} & 0 & 0 & \dots & 0 \\ 0 & S_{2-1,t} & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & S_{imax-(imax-1),t} & 0 \end{pmatrix} \tag{1}$$

with $S_{i-(i-1),t}$ the survival between age-class i at year t and age-class $i - 1$ at year $t - 1$, and with $RR_{i,t}$ the reproductive rate of the year-class i at year t defined as follows:

$$RR_{i,t} = \frac{R_t \text{Mat}_{i,t-1}}{\sum_{i=1}^{imax} \text{Mat}_{i,t-1} N_{i,t-1}} = RS_t \times \text{Mat}_{i,t-1} \tag{2}$$

where $\text{Mat}_{i,t-1}$ is the maturation rate at age a and at time

$t - 1$, $N_{i,t-1}$ the abundance at age-class i and at time $t - 1$, and R_t the recruitment at time t . Therefore, $RR_{i,t}$ represents the key component of the present study because results from the interaction between Mat and the recruitment success (RS_t , recruitment/(total abundance of spawners), $R_t/N_{sp,t-1}$), which is an annual value independent of age. Though the two demes displayed a similar trend in density (Fig. 1a), we had preliminary evidence of a contrasting non-stationary pattern of density dependence between demes. Therefore, density dependence was not explicitly included in the matrix model to facilitate the inter-deme comparison.

We also computed the elasticity (E) of population growth rate to changes in reproductive rate following methodology provided in Caswell (2001). E has been shown to provide direct information on the effect of size-selective fishing on the population performance by modifying the relative contribution of the reproductive rate to the annual variation of the population growth (Rouyer et al. 2011, Hidalgo et al. 2012). Since the reproductive rate results from the interaction of Mat and recruitment success, we specifically aim at disentangling the influence of the changes in Mat on the population dynamics from the ecological effects of the recruitment success. To do that, we applied two complementary approaches.

First, we compared the realized growth rate (r) with the capability of a population to grow independent of the recruitment success variability. To do that, recruitment-independent growth rate (r^{RI}) was calculated using a ‘‘partial life cycles analyses’’ (i.e., demographic models in which part of the age-specific estimates are lacking, e.g., Oli and Zinner [2001]). In these analyses, the reproductive rate was replaced by Mat in the Leslie matrix with recruitment success remaining at a constant value of 1 for the whole study period. The parameter r^{RI} can easily track the influence of changes in Mat (Hidalgo et al. 2012), and contributes to identify the absolute contribution of the recruitment success to r depicted by the difference between r and r^{RI} . We also computed elasticity of r^{RI} to Mat variation to be compared with elasticity of r to reproductive rate variation. To investigate whether an increasing or decreasing pattern of elasticity led to an overall influence on the population growth rate trajectories at short-term scale, we applied the 12-year moving window previously described to calculate Pearson correlations between each type of growth rate and their respective elasticity to reproductive-related rates. The relationship between elasticity values and population growth rate has been previously used to demonstrate that population growth is not uniformly sensitive to demographic rates across different environmental conditions and demographic states (Ezard et al. 2008). We ask, in the present study, whether this causative relationship changes over time according to a change in the demographic state of the sub-populations. We expect a change in the sign of the correlation between elasticity and r (or r^{RI}) from the pre-

truncated period to the truncated period that would indicate a switch in the control of the population dynamics from a survival-dependent to a reproductive-rate (or Mat, in the case of r^{RI})-dependent population dynamics. The number of degrees of freedom was adjusted to account for autocorrelation in all the correlations performed (Pyper and Peterman 1998).

Second, we focus on the dynamics of the reproductive rate by evaluating the relative importance of changes in heritable phenotypic traits (i.e., Mat) and ecological processes (i.e., recruitment success) affected by fishing in influencing the population dynamics. To do that, we applied Hairston et al.'s framework (Hairston et al. 2005), which aimed at comparing "ecological and evolutionary dynamics." The rationale behind this framework is that temporal changes in some attributes of the population dynamics are the consequence of temporal changes in ecological and evolutionary processes (Hairston et al. 2005, Ezard et al. 2009, Ellner et al. 2011). The simplified mathematical expression in discrete time to one ecological and one evolutionary effect is

$$X(t+h) - X(t) = \frac{\partial X}{\partial k} \Delta k + \frac{\partial X}{\partial z} \Delta z + \dots \quad (3)$$

where X is an attribute of the population dynamics, k is an ecological variable, z is an evolutionary variable, h is the interval between samples and " \dots " are higher-order terms including interactions between the changes in the driving variables. In our study, we focus on the two population dynamics attributes (X) that will contribute to understand the evolutionary demography of harvested fish populations because they are shaped by the interaction of ecological and evolutionary variables possibly influenced by fishing. These attributes were the reproductive rate and the elasticity of r to changes in the reproductive rate (i.e., contribution of reproductive rate to r).

Hairston et al. (2005) was the seminal work providing a framework to investigate the consequences of temporal changes in ecological and evolutionary processes on population dynamics attributes. However, Ellner et al. (2011) have recently updated Hairston et al.'s approach to disentangle ecological impacts of evolutionary change vs. non-heritable trait change to avoid misestimating the contribution of the ecological (k) and the evolutionary variable (z). However, since heritability information related to hake traits was not available and because our aim was to compare the two demes, we do not attempt to quantify the specific contributions and we adhere to Hairston et al.'s approach. Thus, z is hereafter referred to as a phenotypic variable in our study. In addition, note that we do not aim at investigating the effect of the environment in the present study, so we retain the global ecological effect (k), which includes demographic and environmental effects. We used age at 50% probability of being mature as z , a heritable phenotypic trait that summarizes the maturation schedules, and the recruit-

ment success as ecological variable (k). To quantify the relative contributions of k and z on X , we apply a general linear model for each deme in which k and z are treated as additive or interactive covariates (Hairston et al. 2005). The Akaike information criterion (AIC) was used to select between the additive and the interactive model. We applied this modeling framework to the complete period, to the pre-truncated (before 1995) and the truncated period (after 1996). We expect different effects of z and k on X for each deme at each period that would indicate a contrasting evolutionary demography within the population (Ezard et al. 2009). For every model, residuals were checked for homogeneity of variance, absence of temporal autocorrelation and violation of normality assumptions.

RESULTS

Maturation reaction norms

For the north deme, the most likely growth scenario was similar between periods (Appendix A), suggesting low phenotypic plasticity in somatic growth. Based on this growth pattern, maturation reaction norms had a negative slope and thus older individuals are more likely to mature than younger ones at a given size (Fig. 3a). Further, maturation reaction norms differed between periods, with midpoints for the truncated period considerably shifted toward young age and small size compared to the pre-truncated period (Fig. 3a). This suggests an evolutionary change in the maturity schedules of the north deme.

In contrast, the south deme displayed a high dependency on somatic growth with a lower growth rate in the pre-truncated than in the more recent truncated period (see Appendix A). This suggests a higher phenotypic plasticity in somatic growth in the south compared to the north deme. This also explains the uncertainty of the reaction norm estimate at later ages during the truncated period, because fish grew faster and matured at age-2 thereby reducing the number of first maturing individuals at age-3 (Fig. 3b). The resulting averaged maturation reaction norms (Fig. 3b) did not vary significantly between periods indicating no influence of evolutionary processes on maturity schedules, which were instead likely shaped by plastic responses in growth. In addition, the low variation between periods for age-2 and the overlapping standard deviation for age-3 suggest a maturation reaction norm less variable in terms of size and more independent of age compared to the north deme.

Non-stationary density dependence in stock-recruitment relationships

The Ricker model applied over the whole time series indicated a similar general pattern for the two demes with significant density dependence ($b = 4.55 \times 10^{-6} \pm 5.86 \times 10^{-7}$ [mean \pm SE], $P \ll 0.001$, Fig. 4a for the north deme; $b = 3.59 \times 10^{-5} \pm 9.55 \times 10^{-6}$, $P < 0.001$, Fig. 4b for the south deme). However, clear differences

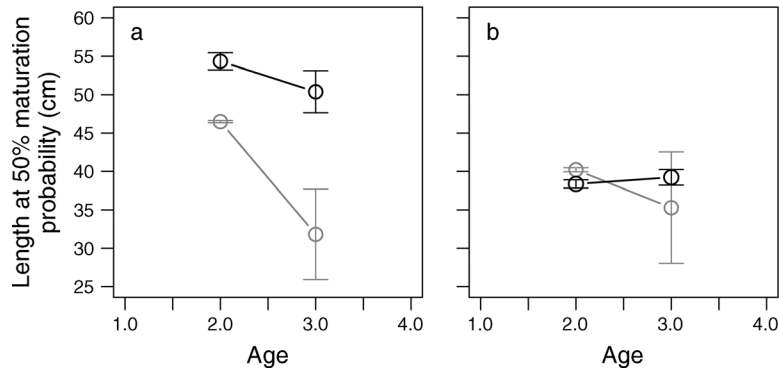


FIG. 3. Midpoints of the probabilistic maturation reaction norm for age-2 and age-3 estimated for the pre-truncated period (black lines) and truncated period (gray lines), and for (a) north deme and (b) south deme. Error bars indicate SD. Note that, for the pre-truncated period (black lines), midpoints are calculated based on the most likely growth scenarios obtained from simulations (Appendix A): similar somatic growth between periods for the north deme while lower somatic growth in the pre-truncated than in the truncated period for the south deme.

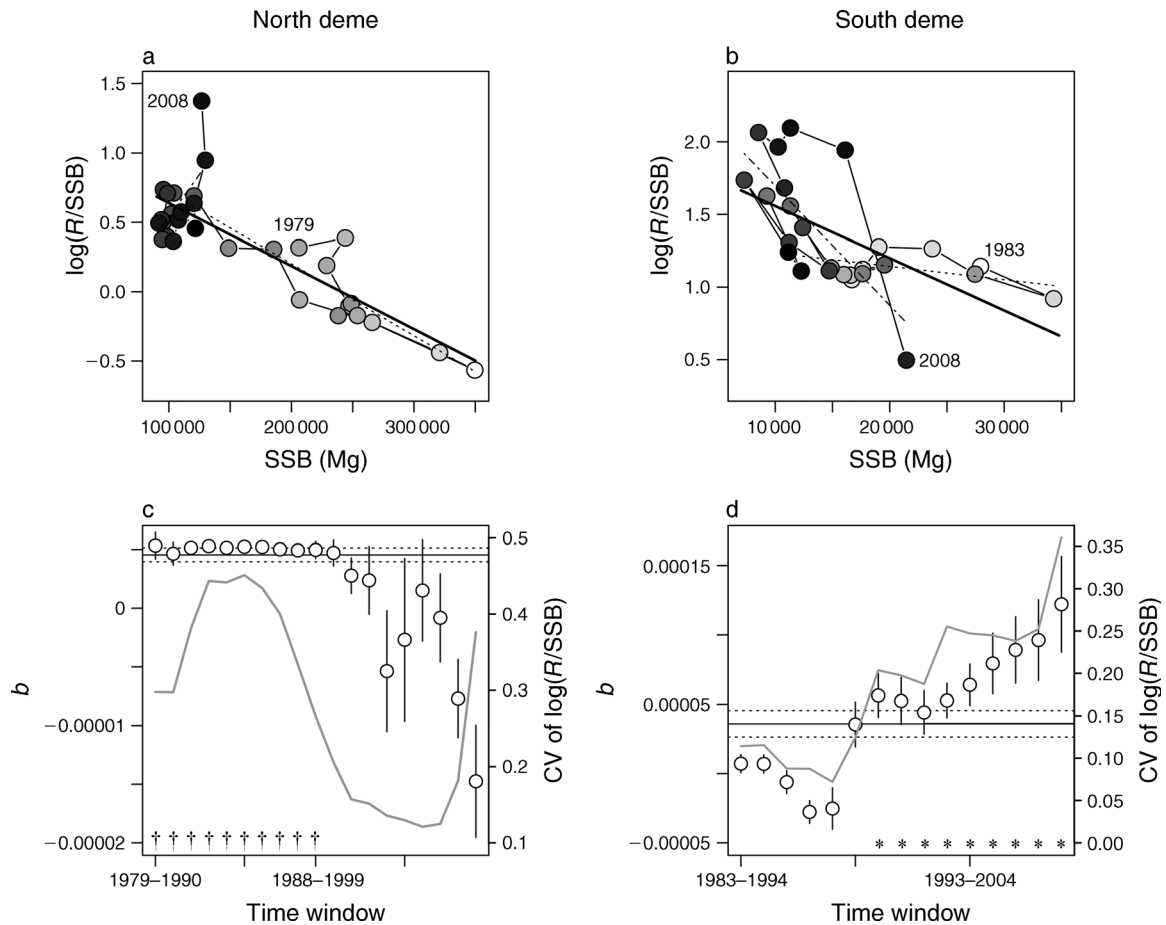


FIG. 4. (a, b) Relationships between spawning stock biomass (SSB) and recruitment at age-0 (R) for the (a) north and (b) south deme. Solid lines represent the predicted Ricker model for the whole time series, while the color of the circles represents the mean age of spawners (lighter is lower, darker is higher). Dashed-dotted and dotted lines represent the predicted Ricker model for the pre-truncated (before 1995) and post-truncated (after 1996) period respectively. (c, d) Density-dependent parameter (b ; open black circles) and coefficient of variation of log recruitment success (R/SSB ; gray lines) estimated applying a 12-year moving-window. Vertical lines indicate SD and the symbols indicate the significance of b ($\dagger P < 0.005$ in c and $* P < 0.05$ in d). Horizontal lines (solid line, mean; broken lines, SD) indicate estimated b values for the whole period from Fig. 4a and 4b.



PLATE 1. European hake (*Merluccius merluccius*) at the Galician (northwestern Spain) waters. European hake is a long-term exploited demersal species at both the North East Atlantic and Mediterranean waters. Photo credit: Jorge Hernández Ucera.

appeared when the model was fit for each period with different demographic structure (Fig. 4a, b). Density dependence calculated using a 12-year moving window displayed a strong and stable effect on the recruitment dynamics of north deme until the early 1990s, consistent with the b value of the complete time series. After that, density dependence rapidly disappeared, presumably due to the fishing-induced demographic erosion (Fig. 4c), though the low range of spawning abundance in the truncated period of the north deme does not allow to properly defining a stock–recruitment relationship. Nonsignificant values of b were generally consistent with low values of the coefficient of variation (calculated with the same moving window) of the recruitment success (Fig. 4c). By contrast, density dependence does not seem to influence the recruitment dynamics at the south deme during the first part of the study period when the age structure was older (Fig. 4d). Density dependence increased (i.e., b became significant) as the demographic truncation progressed toward the recent years concomitant with an increase of the coefficient of variation of the recruitment success (Fig. 4d). This indicates that the b parameter of the whole time series for the south deme represents an average value of the transition from

absence of density-dependent regulation in the pre-truncated period to that recovered in the recent period (Fig. 4d).

Population growth rates and contribution of reproductive-related vital rates

Realized growth rate (r) and the relative contribution (i.e., elasticity) of the reproductive rate to changes in r were estimated from transition matrices to investigate the population dynamic implications of changes in the maturation schedules and in the recruitment success. Time series of r displayed, in general, negative values for the two demes, which indicate the simultaneous tendency in these subpopulations to decrease until early 2000s (Fig. 5a). By contrast, recruitment-independent growth rate (r^{RI} , capability of a population to grow independent of the recruitment success variability) was always lower compared to r for the south deme (Fig. 5b), while r^{RI} and r were quite similar for the north deme (Fig. 5a). In addition, the variability of the absolute contribution of the recruitment success (i.e., offspring survival, $r - r^{\text{RI}}$) increased through the last decades for the south while that for north deme was cyclic and relatively stable around zero (Fig. 5a). The parameter r^{RI} was thus used

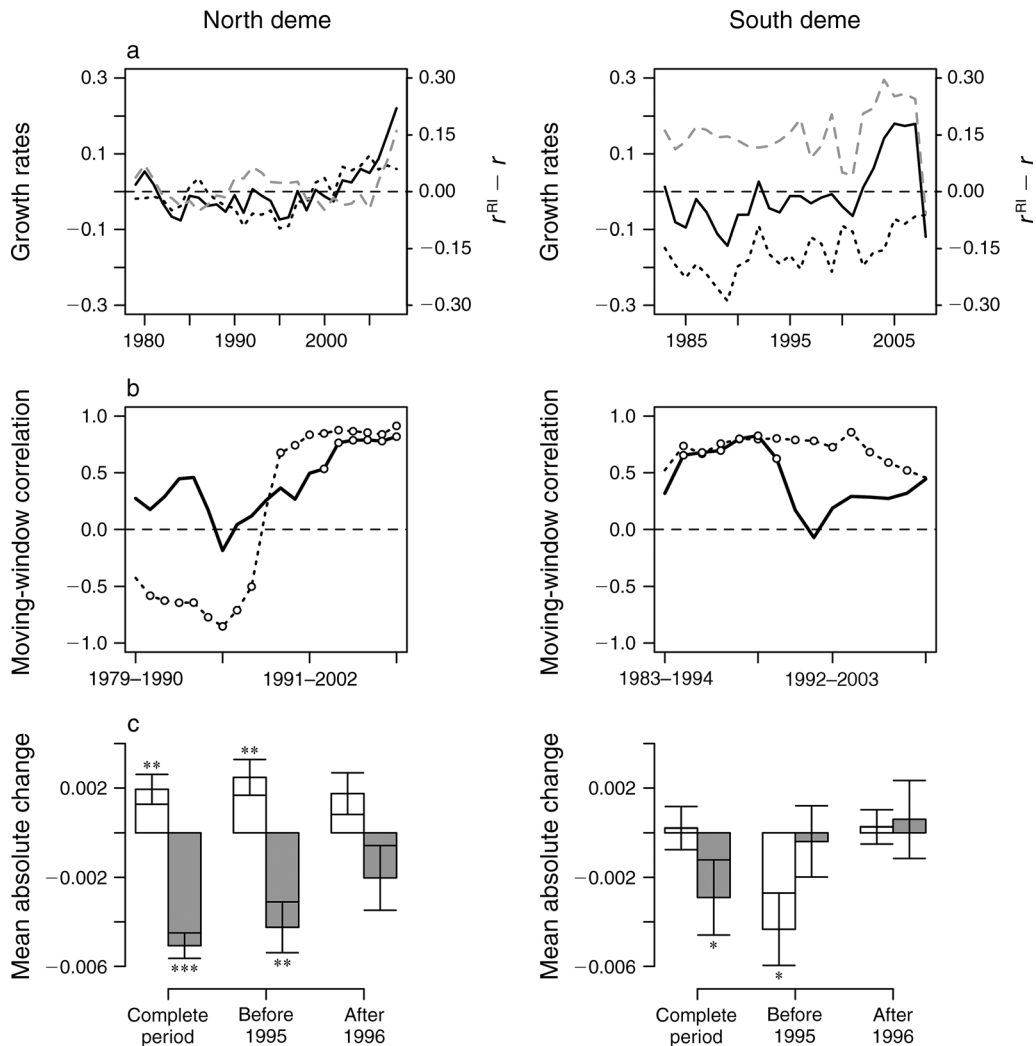


FIG. 5. (a) Temporal variation of realized growth rate (r , solid black line), recruitment-independent growth rate (r^{RI} , dotted black line) and the global recruitment success contribution ($r - r^{RI}$, dashed gray line) calculated for the north (left-hand column) and the south (right-hand column) deme. (b) The 12-year moving-window correlation coefficients between growth rates (r in solid line and r^{RI} in dotted line) and their elasticity values to reproduction-related rates (see Appendix C). Circles represent significant correlation coefficients ($P < 0.05$ accounting for autocorrelation). (c) Absolute change (mean \pm SE) of elasticity of r to reproductive rate (population dynamics attribute) due to recruitment success (ecological variable, white) and length at 50% probability of being mature (phenotypic variable, gray) for the entire period, before 1995 and after 1996. Asterisks represent statistical significance.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

to disentangle the influence of the changes in maturity rates from the ecological effects of the recruitment success. These results suggest a high influence of the annual offspring survival on the population performance of the south deme compared to the north deme.

In both population subunits, r^{RI} and r became more elastic to (i.e., relatively more dependent on) the respective reproductive-related vital rates (i.e., maturity [Mat] and reproductive rate) with increasing age truncation (see Appendix C). However, moving-window correlations between growth rates and the elasticity values showed that the overall contribution of changes in the vital rates to changes in the growth rate was non-

stationary, displaying a different temporal pattern for each subpopulation (Fig. 5b). For the north deme, the correlation between r^{RI} and its elasticity to changes in Mat shifted from negative and significant in the first part of the study period to positive and significant in the second part, a similar pattern observed in the correlation between r and its elasticity to the reproductive rate (Fig. 5b). This indicated that the switch in the control of the population growth from survival to reproductive rate was primary mediated by the change in the maturity rates. By contrast, while r^{RI} at the south deme displayed a high dependency on changes of Mat for the entire period (Fig. 5b), the correlation between r and the

elasticity to the reproductive rate shifted from positive and significant in the first part of the study to nonsignificant in the more recent years (Fig. 5b); an opposed pattern to that observed for the north deme. Thus, changes in heritable maturation traits had high influence on the population performance in the south deme independently of the demographic state, while a change in the recruitment success could trigger the change in the correlation between r and the elasticity to the reproductive rate.

Significant moving-window correlation coefficients between r and its elasticity to the reproductive rate (Fig. 5b) were negatively correlated to significant density-dependent parameters (b) estimated from the non-stationary stock–recruitment relationships for the two demes (binomial correlation, $\text{cor} = -0.71$, $P \ll 0.001$ for the north deme; $\text{cor} = -0.72$, $P < 0.05$ for the south deme). This suggests that density dependence is significantly regulating the population (at stock–recruitment level) when the reproductive rate does not drive the population growth. This trade-off between density dependence and reproductive rate influence was observed in the two demes suggesting that it occurs irrespective of the fishing effect on the demographic structure.

Finally, Hairston et al.'s framework was used to investigate the effect of recruitment success (ecological variable) and maturation schedules (phenotypic variable) on reproductive rate and the elasticity of r to reproductive rate—two population dynamics attributes affected by ecological and evolutionary processes. The additive form for all models showed lower AIC values compared to the interactive form (see Appendix D). Models fitted for the reproductive rate were mainly affected by the recruitment success variability (see Appendix D), while those fitted for the elasticity of r indicated a different pattern for each deme (Fig. 4c). Both recruitment success and maturation schedules showed a significant effect on the elasticity at the north deme for both the whole and the truncated period. By contrast, maturation schedules variability was the unique significant effect on the elasticity at the south deme attending to the entire period, while an effect of the recruitment success was observed for the truncated period (Fig. 4c). This suggests that the effect of fishing on a low plastic phenotype and ecological processes may additively affect population growth in the north deme through the contribution (i.e., elasticity) of the reproductive rate. By contrast, changes in the phenotype may reduce the demographic effect of fishing in the south deme due to the influence of phenotypic variation on the recruitment success.

DISCUSSION

Here we have demonstrated that the level of adaptive phenotypic plasticity may influence how maturation schedules respond to size-selective removal of fish biomass. Our study adds to the understanding of how phenotypic plasticity influences population dynamics

and the ability of populations to respond to natural and anthropogenic drivers (Hutchings et al. 2007, Reed et al. 2010, 2011). We argue that populations with less plastic but more adaptive phenotypes may display fishing-induced additive effects of the phenotype and the demographic change on the population dynamics. This is supported by the results obtained for the north deme, in which the detrimental effects of fishing on both maturation schedules and recruitment success negatively influenced reproductive rate with direct consequences for the population growth. By contrast, populations with more plastic phenotypes such as the south deme may dampen the detrimental effects of the demographic erosion due to the influence of phenotypically plastic changes in the maturation schedules on the recruitment success (see discussion hereafter).

As a general rule, heterogeneous environments favor the evolution of phenotypic plasticity (Reed et al. 2011). Thus, optimal phenotypes in complex environments differ from optimal phenotypes in homogenous environments (Tuljapurkar et al. 2009). Although our results on the probabilistic maturation reaction norms support that phenotypic variation of exploited species result from the combination of harvest selection and natural selection (Olsen and Moland 2011), the relative contribution of each driver depends on the degree of environmental heterogeneity (Marshall et al. 2010). Phenotypes adapted to more homogeneous environments should be more prone to fishing-induced adaptive modifications through earlier maturation. This is likely the scenario in the north deme, which is affected by the large scale hydrography in the Bay of Biscay and displays a large spawning area in which the selective effect of fishing may favor early–maturing relative to late–maturing genotypes (e.g., Barot et al. 2004, Olsen et al. 2004). By contrast, the changes in the maturation schedules of the south deme were likely the result of a plastic response in somatic growth. Reduced intraspecific competition triggered by the removal of biomass due to fishing (i.e., density-dependent somatic growth; e.g., Trippel 1995, Helsen and Almeida 1997) may be one of the plausible underlying mechanisms, while a potential influence of environmental variability cannot be disregarded (Dominguez-Petit et al. 2008, Devine and Heino 2011). The shape of the maturation reaction norm of this subunit suggests that growth variability maintains maturing probability independent of age. Since spawners of different age can occupy space and time for reproduction differently (Hutchings and Myers 1993), life history traits in the south deme are likely adapted to maintain age spawners diversity to colonize the high spatial and temporal environmental heterogeneity that maximizes offspring survival.

We acknowledge, however, that maturation reaction norms can fail in identifying growth-independent effects of environmental variation (e.g., Morita et al. 2009, Uusi-Heikkilä et al. 2011). It is worth noticing that the two demes analyzed here were affected by a similar

increasing pattern of mean temperature during the whole study period (Hidalgo et al. 2012), while the maturation schedules progressed in the opposed direction. We recognize that the sharp difference in the maturation reaction norms in the north deme could be partially influenced by the growth-independent effects of increasing temperature. However, we consider its effect to be marginal compared to that induced by the size-selective removal due to fishing. In fact, recent studies on cod in the North Sea (a neighboring area to the Bay of Biscay) concluded that fishing-induced selection toward earlier maturation is the most parsimonious explanation for the maturation trends observed once the temperature effect is accounted for (Wright et al. 2011, Neuheimer and Grønkvær 2012).

The relative contribution of human and natural drivers to the phenotypic response is inherently linked to the relative importance of maturation schedules and recruitment success on the reproductive rate (Marshall et al. 2010), and this is supported by our results. Thus, if variation in maturation schedules is more relevant, then the fecundity–age relationship has a strong effect on the reproductive success increasing the maturing-age dependence. Under this situation fishing-induced phenotypic and demographic changes may have additive effects on the population dynamics, which is supported by our results for the north deme. By contrast, in populations (or subunits) in which life histories are more variable (allowing the population to cope with the fluctuating environment), recruitment success may be more important for the population dynamics. In this case, life history variation is better adapted to maximize recruitment success and can dampen demographic effects of fishing, which remains consistent with our results for the south deme. This could also partially explain the non-stationary pattern of population regulation depicted by the stock recruitment models.

Density-dependent regulation (i.e., overcompensation or saturation) requires food competition or/and predation affecting the survival of early life and pre-recruit stages (Rose et al. 2001). Cannibalism on young age classes is a known regulatory mechanism in the north deme due to the spatial coexistence of different cohorts on the broad continental shelf of the Bay of Biscay (Mahe et al. 2007). This regulation was clearly removed by the demographic erosion (Hidalgo et al. 2012), yet a synergistic effect of increasing temperature in the North Atlantic in recent decades could contribute to the survival of early life stages in the north deme (Goikoetxea and Irigoien 2013). In addition to this ecological effect, the natural selection resulting from cannibalism on small fish historically acted in opposite direction to the long-term harvesting selection on large fish. Together, this could promote stabilizing selection for maturation in the north deme (Carlson et al. 2007). Contemporary removal of adults cannibalizing on young fish could disrupt this stabilizing pattern and magnify the directional selection toward earlier matu-

ration. By contrast, the phenotypic change in somatic growth in the south deme caused individuals to mature at younger age that could influence the population regulation mechanisms. An increased contribution of younger spawners may favor to colonize a higher diversity of spatial and temporal environmental opportunities for reproduction proposes (Hutchings and Myers 1993). This would stabilize density dependence and increase the recruitment success variability, which represents a key vital rate contributing to the absolute population growth rate in the south compared to the north deme. In addition, it is worth noticing that density-dependent regulation could be also favored due to a potential contraction of the spawning areas at lower densities, which could strengthen competition for resources (Rose et al. 2001).

Fishing-induced demographic erosion decreases the overall dependence of population growth rate upon the adult survival while it increases the dependence on the reproductive rate (Rouyer et al. 2011, Hidalgo et al. 2012, Durant et al. 2013). However, within this scenario, inter-annual variation of reproductive rate dependence does not necessary lead to a correlated variation in the growth rate. Since annual variation in reproductive rate results from the interaction of changes in the phenotype (i.e., maturity schedules) with variation in the recruitment success, the resulting interplay may range from additive to buffering effects on the population growth rate. Here, we illustrate that the combination of demographic truncation (i.e., reduction of the adult component of a population) and adaptive juvenescence (i.e., evolutionary change to mature at younger age) of the spawning stock of the north deme triggered an additive effect on the increasing dependence of the inter-annual variability of population growth upon reproductive rate. However, the plastic response of the maturation schedules of the south deme dampened such reproductive rate dependence. Recent studies based on long-term simulations suggest that fishing induced evolution may have a low influence on population growth rate at longer time scales (Kuparinen and Hutchings 2012). Our study focuses on a shorter time scale but the results remain consistent with the study by Kuparinen and Hutchings (2012). Our findings further show how the interaction of evolutionary and ecological processes through the reproductive rate may contribute to reduce the variation in population growth and stabilizing it in the long term.

It is worth emphasizing that our study shows two contrasting scenarios within the same population. This highlights the importance of embracing ecological processes and phenotypic variation in spatially complex populations, especially for those ecosystems shaped by spatial fragmentation of the environment or those receiving individuals from different geographical origin. Heterogeneous populations, characterized by complex population structure and life history diversity, produce more temporal stability because of the independent but

complementary dynamics among conspecific subpopulations, so called biocomplexity (Hilborn et al. 2003, Schindler et al. 2010). Demes within complex populations such as hake in the Atlantic do not differ in the neutral genetic variation. However, differences in the adaptive phenotypic traits suggest that adaptive evolution may be faster than neutral evolution and can act at a smaller spatial scale (Conover et al. 2006). Thus, divergence of local adaptations on a finer scale can be found even if no clear difference in genetic structure can be detected by microsatellites (Conover et al. 2006, Hutchings et al. 2007), which is supported by our results.

Concluding remarks, study limitations, and future challenges

Knowledge about mechanisms leading to spatial variation in the degree of phenotypic plasticity within populations is critical for understanding the interplay of evolutionary and ecological dynamics (Reed et al. 2011). The nascent field of evolutionary demography represents an emerging approach to investigate the consequences of phenotypic variation on population dynamics/growth (e.g., Kinnison et al. 2008, Ezard et al. 2009), communities (e.g., Post et al. 2008, Carlson et al. 2011), ecosystems (Harmon et al. 2009, Palkovacs et al. 2009) and the potential reciprocal feedbacks between ecology and evolution. Here, we demonstrate the necessity of expanding this approach to the case of harvested species, especially to those displaying complex spatial structures. Our study also highlights the importance of the reproductive rate for shaping the evolutionary demography of exploited fish populations, because fishing can affect both its phenotypic (i.e., maturity rate) and its ecological (i.e., recruitment success) component.

It is worth noticing some limitations of our study as well as future challenges. First, we acknowledge that applying a time-varying approach to the maturation information would have improved our study (i.e., calculating maturation reaction norms by cohort). Due to our data restrictions, we simulated somatic growth scenarios for the two contrasting periods, which was used to illustrate the different contributions of plastic and adaptive changes for each deme. Second, though we demonstrate that density-dependent regulation changes with time, future studies will benefit from including density dependence explicitly in matrix models in a non-stationary manner. This implies several methodological modifications, not only applying a different density-dependent structure to each year but also investigating whether a different density-dependent structure might be applied at different age classes within each year. Third, further research will need to investigate the temporal scale at which evolutionary demography processes operate. Kuparinen and Hutchings (2012) showed that a long-term population growth tends to stabilize around zero growth independently of fishing-induced evolution-

ary change. However, our results demonstrate that at a short temporal scale (i.e., management scale), the relative contribution of evolutionary and ecological mechanisms that stabilize population growth are highly diverse, even within two genetically indistinguishable subpopulations of the same species.

To conclude, the mounting evidence that fishing may cause contemporary evolution calls for the implementation of a Darwinian fisheries management (Jørgensen et al. 2007). Our study moves forward on this view and underscores the necessity to understand how fishing affects the trait-mediated interactions with ecological processes. This remains a keystone for the functioning of harvested marine ecosystems and for preserving their services to the society. Thus, our study calls for a more comprehensive management approach, in which species are not only numerically assessed, but where ecological, evolutionary, and environmental processes are also integratively accounted for.

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LITERATURE CITED

- Anderson, C. N., C. H. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835–839.
- Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Reaction norms for age and size at maturation: study of the long-term trend (1970–1998) for Georges Bank and Gulf of Maine cod stocks. *Ecological Applications* 14:1257–1271.
- Carlson, S. M., E. Edeline, L. A. Vøllestad, T. O. Haugen, I. J. Winfield, J. M. Fletcher, J. B. James, and N. C. Stenseth. 2007. Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecology Letters* 10:512–521.
- Carlson, S. M., T. P. Quinn, and A. P. Hendry. 2011. Eco-evolutionary dynamics in Pacific salmon. *Heredity* 106:438–447.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Conover, D. O., L. M. Clarke, S. B. Munch, and G. N. Wagner. 2006. Spatial and temporal scales of adaptive divergence in marine fishes and implications for conservation. *Journal of Fish Biology* 69:21–47.
- Devine, J. A., and M. Heino. 2011. Investigating the drivers of maturation dynamics in Barents Sea haddock (*Melanogrammus aeglefinus*). *Fisheries Research* 110:441–449.
- Dieckmann, U., and M. Heino. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series* 335:253–269.
- Dominguez-Petit, R., M. Korta, F. Saborido-Rey, H. Murua, M. Sainza, and C. Piñeiro. 2008. Changes in size at maturity of European hake Atlantic populations in relation with stock

- structure and environmental regimes. *Journal of Marine Systems* 71:260–278.
- Durant, J. M., M. Hidalgo, T. Rouyer, D. Ø. Hjermann, L. Ciannelli, A. M. Eikeset, N. Yaragina, and N. C. Stenseth. 2013. Population growth across heterogeneous environments: effects of harvesting and age structure. *Marine Ecology Progress Series* 480:277–287.
- Ellner, S. P., M. A. Geber, and N. G. Hairston, Jr. 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters* 14:603–614.
- Enberg, K., C. Jørgensen, and M. Mangel. 2010. Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. *Canadian Journal of Fisheries and Aquatic Science* 67:1708–1719.
- Ezard, T. H. G., S. D. Côté, and F. Pelletier. 2009. Ecoevolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philosophical Transactions of the Royal Society B* 364:1491–1498.
- Ezard, T. H. G., J.-M. Gaillard, M. J. Crawley, and T. Coulson. 2008. Habitat dependence and correlations between elasticities of long-term growth rates. *American Naturalist* 172:424–430.
- Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. *Marine Ecology Progress Series* 405:1–13.
- Goikoetxea, N., and X. Irigoien. 2013. Links between the recruitment success of northern European hake (*Merluccius merluccius* L.) and a regime shift on the NE Atlantic continental shelf. *Fisheries Oceanography* 22:459–456.
- Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Science* 63:494–509.
- Hairston, N. G., Jr., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* 8:1114–1127.
- Harmon, L. J., B. Matthews, S. DesRoches, J. Chase, J. Shurin, and D. Schluter. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458:1167–1170.
- Heino, M., U. Dieckmann, and O. R. Godø. 2002. Measuring probabilistic reaction norms for age and size at maturity. *Evolution* 56:669–678.
- Helser, T. E., and F. P. Almeida. 1997. Density-dependent growth and sexual maturity of silver hake in the north-west Atlantic. *Journal of Fish Biology* 51:607–623.
- Hidalgo, M., et al. 2012. Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. *Ecography* 35:637–649.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences USA* 100:6564–6568.
- Hsieh, C. H., A. Yamauchi, T. Nakazawa, and W. F. Wang. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Science* 72:165–178.
- Hutchings, J. A., and R. A. Myers. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Science* 50:2468–2474.
- Hutchings, J. A., D. P. Swain, S. Rowe, J. D. Eddington, V. Puvanendran, and J. A. Brown. 2007. Genetic variation in life-history reaction norms in a marine fish. *Proceedings of the Royal Society B* 274:1693–1699.
- ICES. 2009. Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk, and Megrim [WGHMM]. 5–11 May 2009. ICES CM 2009/ACOM:08. International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Jørgensen, C., et al. 2007. Managing evolving fish stocks. *Science* 318:1247–1248.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society B* 330:175–190.
- Kinnison, M. T., M. J. Unwin, and T. P. Quinn. 2008. Eco-evolutionary vs habitat contributions to invasion in salmon: experimental evaluation in the wild. *Molecular Ecology* 17:405–414.
- Kuparinen, A., and J. A. Hutchings. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. *Proceedings of the Royal Society B* 279:2571–2579.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57:659–668.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183–222.
- Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society B* 269:49–54.
- Mahe, K., R. Amara, T. Bryckaert, M. Kacher, and J. M. Brylinski. 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES Journal of Marine Science* 64:1210–1219.
- Marshall, C. T., and B. J. McAdam. 2007. Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. *Marine Ecology Progress Series* 335:301–310.
- Marshall, D. J., S. S. Hepell, S. B. Munch, and R. R. Warner. 2010. The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology* 91:2862–2873.
- McClatchie, S., R. Goericke, G. Auad, and K. Hill. 2010. Re-assessment of the stock–recruit and temperature–recruit relationships for Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Science* 67:1782–1790.
- Minto, C., R. A. Myers, and W. Blanchard. 2008. Survival variability and population density in fish populations. *Nature* 452:344–348.
- Morita, K., J. Tsuboi, and T. Nagasawa. 2009. Plasticity in probabilistic reaction norms for maturation in a salmonid fish. *Biology Letters* 5:628–631.
- Murua, H. 2010. The biology and fisheries of European hake, *Merluccius merluccius*, in the north-east Atlantic. *Advances in Marine Biology* 58:97–154.
- Neuheimer, A. B., and P. Grønkvær. 2012. Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. *Global Change Biology* 18:1812–1822.
- Ohlberger, J., Ø. Langangen, E. Edeline, E. M. Olsen, I. J. Winfield, J. B. James, J. Fletcher, N. C. Stenseth, and L. A. Vøllestad. 2011. Pathogen-induced rapid evolution in a vertebrate life-history trait. *Proceedings of the Royal Society B* 278:35–41.
- Oli, M. K., and B. Zinner. 2001. Partial life cycle analysis: a model for birth-pulse populations. *Ecology* 82:1180–1190.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- Olsen, E. M., and E. Moland. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evolutionary Ecology* 25:695–710.
- Olsen, E. M., G. Ottersen, M. Llope, K.-S. Chan, G. Beaugran, and N. C. Stenseth. 2011. Spawning stock and recruitment in north sea cod shaped by food and climate. *Proceedings of the Royal Society B* 278:504–510.

- Ottersen, G. 2008. Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod and possible consequences for recruitment. *Canadian Journal of Fisheries and Aquatic Science* 65:523–534.
- Palkovacs, E. P., et al. 2009. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. *Philosophical Transactions of the Royal Society B* 364:1617–1628.
- Pelletier, F., T. Clutton-Brock, J. Pemberton, S. Tuljapurkar, and T. Coulson. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* 315:1571–1574.
- Pita, A., M. Pérez, S. Cerviño, and P. Presa. 2011. What can gene flow and recruitment dynamics tell us about connectivity between European hake stocks in the Eastern North Atlantic? *Continental and Shelf Research* 31:376–387.
- Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific phenotypic variation in a predator affects community structure and cascading trophic interactions. *Ecology* 89:2019–2032.
- Price, T. D., A. Qvarnström, and D. E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B* 270:1433–1440.
- Pyper, B., and B. Peterman. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Science* 55:2127–2140.
- R Development Core Team. 2010. R 2.12.1. R Project for Statistical Computing, Vienna, Austria. www.r-project.org
- Reed, T. E., D. E. Schindler, and R. S. Waples. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology* 25:56–63.
- Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society B* 277:3391–3400.
- Rose, K. A., J. H. Cowan, K. O. Winemiller, R. M. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2:293–327.
- Rouyer, T., G. Ottersen, J. M. Durant, M. Hidalgo, D. Ø. Hjernmann, J. Persson, L. C. Stige, and N. C. Stenseth. 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology* 17:3046–3057.
- Sánchez, F., and J. Gil. 2000. Hydrographic mesoscale structures and poleward current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. *ICES Journal of Marine Science* 57:152–170.
- Schindler, D., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–613.
- Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B* 274:1015–1022.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* 45:759–771.
- Tuljapurkar, S., J. M. Gaillard, and T. Coulson. 2009. From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B* 364:1499–1509.
- Uusi-Heikkilä, S., A. Kuparinen, C. Wolter, T. Meinelt, A. C. O'Toole, and R. Arlinghaus. 2011. Experimental assessment of the probabilistic maturation reaction norm: condition matters. *Proceedings of the Royal Society B* 278:709–717.
- Venturelli, P. A., C. A. Murphy, B. J. Shuter, T. A. Johnston, P. J. de Groot, P. T. Boag, J. M. Casselman, R. Montgomerie, M. D. Wiegand, and W. C. Leggett. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. *Ecology* 91:2003–2012.
- Wright, P. J., C. P. Millar, and F. M. Gibb. 2011. Intra-stock differences in maturation schedules of Atlantic cod *Gadus morhua*. *ICES Journal of Marine Science* 68:1918–1927.

SUPPLEMENTAL MATERIAL

Appendix A

Sensitivity analysis of maturation reaction norms to a range of somatic growth rates scenarios ([Ecological Archives A024-063-A1](#)).

Appendix B

Description, a figure, and a table presenting the stock–recruitment model selection ([Ecological Archives A024-063-A2](#)).

Appendix C

A figure presenting the elasticity of growth rate to survival and reproductive-related vital rates ([Ecological Archives A024-063-A3](#)).

Appendix D

A table presenting the model selection for the contribution of ecological and evolutionary processes ([Ecological Archives A024-063-A4](#)).