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How does exploitation of prey fish affect population growth rate in changing seas?

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Population growth, hence the population's persistence, is affected by several factors such as climate, species interaction, and harvesting pressure the last having been shown to make the marine populations more sensitive to climate forcing. The age truncated or juvenescent populations are a worldwide consequence of the protracted size-selective mortality of commercial fishing on the older and larger individuals. This process also increases a populations' ability to directly respond to environmental fluctuations, emphasizing the importance of the interaction between fisheries, environment and internal dynamics that produces complex synergic effects on the population dynamics of marine species. We used a comparative approach investigating commercially fished species on different systems: the Norwegian sea-Barents Sea (Northeast Arctic cod), the Atlantic Ocean (European hake), the Mediterranean Sea (European hake), and the Bering Sea (Pollock). Our objective was to address in a comparative way the ecological consequences of fisheries effect on population properties (e.g., intrinsic growth rate) in relation to different external conditions (fishing intensity or climate). For this, we have applied techniques based upon age-structured population matrices to analyze estimated stock sizes. By combining all sources of information, we investigated differences in the coupling between life history traits and population dynamics for all stocks that display different level of juvenescence. This study will advance our understanding of the underlying mechanisms behind the transitory relationships between climate and fish populations.

Keywords: Barents Sea, Mediterranean Sea, Bering Sea, Northeast Arctic cod (*Gadus morhua*), European hake (*Merluccius merluccius*), Pollock (*Theragra chalcogramma*), Leslie matrix, fisheries.

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INTRODUCTION

The Code of Conduct for Responsible Fisheries of 1995 (FAO 1995) and the Reykjavik declaration on Responsible Fisheries of 2001 (FAO, 2002) – which was reinforced at the World Summit of Sustainable Development in Johannesburg in 2002 (UN 2002) – require nations to base their policies related to the exploitation of marine resource on an ecosystem approach. Adopting such an approach is, however, rather difficult as it requires much data and insight pertaining to the dynamic interactions within the ecosystem (Stenseth et al., 2002). A solution is to use the population growth rate as an information integrator; which has been demonstrated to reflect the population persistence (Hastings and Botsford, 2006).

The strength of the effect of climate and seasonality on marine ecosystems is different with latitude, e.g. becoming increasingly pronounced as one moves towards the poles. The life cycles of organisms in high latitude seas have adapted to a strong pulse of primary productivity in spring, short summers, and ice cover in parts of the year. Also, food resources and suitable habitat for young are often spatially clustered. There is a continuous evolutionary pressure towards developing adaptive strategies such as optimizing the timing of life cycle events (e.g., reproduction), timing and length of spawning and feeding migrations, and using environmental cues (e.g., photoperiod and temperature). Oligotrophic systems, such as the Mediterranean Sea, may display similar patterns because the coupling between the phenology of the biological processes and favourable environmental conditions can be highly relevant for the recruitment success (Hidalgo et al., 2009b).

Population growth, hence the population's persistence, is affected by several factors such as climate, species interaction, and harvesting pressure the last having been shown to make the marine populations more sensitive to climate forcing. The age truncated or juvenescent populations are a worldwide consequence of the protracted size-selective mortality of commercial fishing on the older and larger individuals. This process also increases a population's ability to directly respond to environmental fluctuations, emphasizing the importance of the interaction between fisheries, environment and internal dynamics that produces complex synergic effects on the population dynamics of marine species (Planque et al., 2010).

In this study we used a comparative approach investigating commercially fished species the North East Arctic cod (*Gadus morhua*) in the Norwegian sea-Barents Sea, the European hake (*Merluccius merluccius* L.) in the Northeast Atlantic Ocean and the Mediterranean Sea, and the pollock (*Theragra chalcogramma*) in the Bering Sea. All three species are harvested. We investigated how the synergies between climate, fishing effects and internal population properties operate across heterogeneous environments and fishing exploitation patterns. Here, we aim to investigate how the interaction between external drivers (climate and fishing) and internal population properties modulates the population dynamics of fish at different areas. To do so, we use the realized population growth calculated on yearly transitory Leslie matrices. We hypothesise the density-dependent regulations of the recruitment dynamics depends on the capability of a population to grow independently of such incoming recruitment. We investigated spatial differences in the interacting processes between external and internal drivers that contribute to the population growth rate variability.

MATERIAL AND METHODS

The North East Arctic cod (*Gadus morhua*) of the Lofoten-Barents Sea system

The North East Arctic (NEA) cod population is assessed on a combination of catch data and survey data, and takes cannibalism into account (ICES, 2010). NEA cod currently mature at 6–7 years of age (Nakken, 1994) and migrate out of the Barents Sea to spawn along the Norwegian coast around the Lofoten from March to May (Bergstad et al., 1987). Eggs and larvae are carried by currents into the southern Barents Sea and south and west of Svalbard, and the larvae settle towards the bottom at the age of approximately 5 months. The immature cod make seasonal migrations, the extent of which increases with age.

The study is based on age-specific estimates of abundance derived from annual bottom trawl sampling in the winter feeding area of NEA cod in 1981–2010 (Fig. 2). Survey data were collected from (ICES, 2010). For more detailed information about the survey see et al.

(Hjermann et al., 2004). For the age classes with no mature individuals (age less than or equal to 4 years), we assumed that the number of cod of that age ($N_{\text{age, year}}$) was equal to the survey estimate $N'_{\text{age, year}}$. For age-classes with some mature individuals (age more than 4 years), we took into account that mature cod is outside the survey area at the time of sampling, since they start their annual migration to the spawning grounds in December-January and return to the Barents Sea in May (Bergstad et al., 1987). We therefore estimated the total abundance of each age from the relationship $N_{\text{age, year}} = N'_{\text{age, year}} \cdot (1 - P_{\text{age, year}})^{-1}$, where $P_{\text{age, year}}$ is the proportion of mature individuals (Hjermann et al., 2004). Estimates of $P_{\text{age, year}}$, based on a combination of Norwegian and Russian survey data, were also taken from (ICES, 2010). Trawl survey data are influenced by catchability (the proportion of fish inside the area swept by the trawl that are caught), which is low and variable for age 1 and 2 cod. We therefore disregarded the estimates of these age groups. Fishing mortality, based on Virtual Population Analysis, was also taken from (ICES, 2010).

The walleye pollock (*Theragra chalcogramma*) of the Bering Sea system

Walleye pollock currently constitutes the second largest single species fishery in the world (FAO, 2002). Information on Bering Sea pollock (BS pollock) year-class strength is available as number back to 1964 (Ianelli et al., 2009). Year-class strength is estimated from an age-structured stock assessment model tuned statistically to the commercial harvests and acoustic and bottom trawl surveys (Ianelli et al., 2009).

Data available for the BS pollock are similar to the ones for the NEA Cod and we applied the same techniques to calculate the effective population growth rates. The difference is that the mature fish are not outside the survey area and no correction was required. We didn't have a proportion of mature per age and per year but only an average per age.

European hake (*Merluccius merluccius* L.)

The European hake, from now on referred to simply as hake, is an overharvested groundfish species inhabiting the North Atlantic European coast (latitudinally from north of Norway to the Mauritanian waters) and the whole Mediterranean Sea. Three areas with available age-structured information on hake are considered in this study, two in the Atlantic Ocean always referred (for management purposes) as North Atlantic stock (NA) and South Atlantic stock (SA), and one in the Mediterranean Sea, Balearic Islands (BI). This study is based on age-specific estimates of abundances and maturing information available from five age-structured stock assessment groups for hake from the Atlantic Ocean (International Council for the Exploration of the Sea, (ICES, 2009) and the Mediterranean Sea (General Fisheries Commission for the Mediterranean (FAO-GFCM, 2009)). A mean over the more harvested age classes was calculated for each stock based on the F_a profile at age for area (FAO-GFCM, 2009, ICES, 2009): F_{2-6} for NA, F_{2-5} for SA and F_{2-4} for BI.

Environmental data

We have used global climate indices that have been demonstrated to considerably influence ecological processes (Stenseth et al., 2003). The application of climate indices by definition reduces complex space and time variability into simple measures, 'packages of weather'. For the Northeast Atlantic system and Barents Sea, we used the North Atlantic Oscillation (NAO) index (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) which is the dominant climate pattern in the North Atlantic region (Stenseth et al. 2003). NAO described as an out-of-phase behaviour between the climatological low pressure centre near Iceland and the high-pressure centre near the Azores (Hurrell, 1995), was used as a proxy for the North Atlantic climate. We

used the winter average (December-March) of the NAO index because its influence in the Atlantic is higher during winter when the coupled ocean-atmosphere system is more active (Hurrell, 1995). Gulf Stream (GULF) index was also used a proxy of influence on the Northeast Atlantic stocks, and is calculated as the first Principal Component of the position of the North Wall of the Gulf Stream 1966-2008 (Taylor, 1995). Month to month variability in the data is high because of Gulf Stream meandering and, therefore, we used annual mean values or averages over several months (<http://web.pml.ac.uk/gulfstream/data.htm>). For the Barents Sea we also used the Arctic Oscillation (AO) and the Atlantic multidecadal oscillation (AMO). For the Bering Sea system we used the Pacific Decadal Oscillation (PDO) and the AO. For the Mediterranean Sea we used the IDEA index. Seasonal averages were calculated for each stock in winter (from December to February) and spring (from March to May) over each study area. IDEA is a mesoscale (regional) hydro-climatic index based on the air-sea heat fluxes in the Gulf of Lions during winter months and is a proxy of the strength of the current and vertical mixing activity in the NW Mediterranean (Monserrat et al., 2008). Lower values of IDEA index indicate a larger formation of Western Mediterranean Intermediate Waters (WIW) in winter at intermediate layers (100-300 m) in the Gulf of Lions; this implies a larger presence of these water masses in the NW Mediterranean platform during spring increasing the productivity (Massuti et al., 2008).

We have also used Sea Temperature (ST) as local climate index. For the Barents Sea we used yearly average sea temperature measured monthly at 0-200 m depth on the Russian Kola meridian transect (33° 30' E, 70° 30' N to 72° 30' N) (see refs in Hjermann et al., 2004a). ST for the Hake obtained from the Climate Diagnostics Center (NCEP/NCAR) reanalysis fields (Kalney et al., 1996) on a 1x1-degree grid and averaged over the area of each studied stock. Seasonal averages were calculated for each stock in winter (from December to February) and spring (from March to May) over each study area; those selected will cover critical periods: spawning, early life stages survival, post-settlement period or recruitment feeding. For the Bering Sea we used the bottom trawl average temperature (1982-), the May SST (1964-) and the Ice cover index (ICI) downloaded from <http://www.beringclimate.noaa.gov/>.

The model

One way to reduce the complexity of age-structured population dynamics is to approach the question of population persistence through the use of matrix models (Hastings and Botsford, 2006, Caswell, 2001). Leslie matrix models are age- or stage-structured population models that use estimates of demographic rates for different age or size classes to project population dynamics (Caswell, 2001). Vital rates are summarized in an annual transition matrix \mathbf{A} , which define the population sizes in the following year (n_{t+1}) as the product of the matrix \mathbf{A} and the current year's population size (n_t), where the n_t 's are vectors defining the number of individuals within each age class. The long-term population growth rate, λ , is given by the logarithm of the dominant eigenvalue of \mathbf{A} (Caswell, 2001). Population persistence is reduced to whether the matrix model has a dominant eigenvalue greater than one or not.

We used this technique by constructing annual Leslie matrices for each species studied. For the NEA Cod, since we did not have satisfactory data for age-1 and 2, we replaced age-1 numbers for year $t+1$ with the estimates of age-3 at year $t+4$, and then set survivals between age-1 to 2 and between age 2 to 3 equal to 1. This correction was made for the hake stocks between age-0 and age-1, setting survival at age-1 equal to the arbitrary value of 1 (the dominant eigenvalue of the matrix is not affected by setting an arbitrary value). The recruitment elements (the first row of the matrix) were based on estimates of the proportion of matures ($P_{\text{age, year}}$, see above) assuming that each mature individual contributed equally to

recruitment (i.e., age-3 cods 3 years later, age-0 hakes 1 year later). The eigenvalues of matrices for these 22 years were calculated to examine the differences between years.

We related the change in different species instantaneous population growth (natural logarithm of dominant eigenvalue) with selected covariates (see below) using Generalized Additive Model (GAM) formulations, as implemented in the *mgcv* library of R 2.11.1 (Wood and Augustin, 2002). We applied a backward selection strategy GAM regressions based on the minimization of the Generalized Cross Validation (GCV), and a measure of the model predictive squared error R^2 (Green and Silverman, 1994). A covariate was retained if it caused a decrease of the model GCV. Specifically, let λ_t be the instantaneous population growth time t . Let X_t^i be a vector of the explanatory variables at time t where the superscript i identifies the single components. Let f_i (g_i for non-fished population) be nonparametric, smoothing functions, specifying the effect of the covariate X^i on the demographic variable λ_t . The formulation is:

$$\lambda_t = \alpha + \sum_i f_i(X_t^i) + \varepsilon_t \quad (1)$$

where α is an intercept and ε is a stochastic noise term. Initially, we included all interacting terms; however, in the final formulation we only retained those that minimized the model GCV and increased the R^2 .

The covariates tested in the models where fishing mortality and mean age of the spawning stock and abiotic factors such as winter NAO index, sea surface temperature, GULF index, IDEA index, AMO index, PDO index, ICI index or AO index.

We found no auto-correlation (using ACF function) in the residuals of the selected models. No correlation was found between covariates.

RESULTS and DISCUSSION

$\ln(\lambda)$	intercept	x_1	x_2	x_3	Dev
NEA cod	i ** -0.12 ± 0.04	outlier. 0.35 ± 0.19	MA _{ssb} * s(MA _{ssb} , edf=1.75)	AMO* -0.71 ± 0.26	43
NA Hake	i *** 0.016 ± 0.001	MA _{ssb} *** S(MA _{ssb} , edf=1.42)	GULF index* 0.003 ± 0.001	F ₂₋₆ *** S(F ₂₋₆ , edf=1.82)	93.3
SA Hake	i ** -0.08 ± 0.009	MA _{ssb} *** -0.08 ± 0.01	GULF index** S(GULF, edf=1.68)		68.9
BI Hake	i *** 2.57 ± 0.36	MA _{ssb} *** -0.68 ± 0.12		F ₂₋₆ * -0.31 ± 0.12	55.6
BS pollock	i *** -0.53 ± 0.09	PDO s(PDO, edf=1.71)	ICI s(ICI, edf=1.63)		23.6

Our results evidences the context dependency of the internal (biological) and external drivers (environment and fishery) shaping the population persistence at each area.

Three out of the five stocks here analyzed show evidence of truncation of the age structure within the study period, which were clearly related to their population persistence. However, for the BS pollock we did not find an effect of the age structure of the population on the realized population growth rate $\ln(\lambda)$. The mean age of spawners (MA_{SSB}) for the BS pollock however was showing a trend with a slight decrease before 1980 followed by a clear increase of the average age until 2006. For this species it was difficult to obtain a model explaining the realized population growth rate change observed. The best model was using two environmental variables that are PDO and ICI. While the effect of these variables was not significant, our model nevertheless indicates an effect of climate on the population growth of the BS pollock. The addition of fishing mortality to our models may improve them.

Mean age of spawners (MA_{SSB}) and AMO index modulate $\ln(\lambda)$ variability for the NEA cod stock in the Barents Sea. The relationship between MA_{SSB} and $\ln(\lambda)$ was generally positive, indicating the native effect of the demographic degradation on the population persistence. The effect on $\ln(\lambda)$ of AMO was negative. The AMO is a fluctuation in de-trended sea surface temperatures in the North Atlantic Ocean. In other words, the relationship between the $\ln(\lambda)$ of AMO showed the negative effect of the recent warming on the cod population.

Mean age of spawners (MA_{SSB}) and GULF index modulate $\ln(\lambda)$ variability for the two hake stocks in the Atlantic. However, the relationship between MA_{SSB} and $\ln(\lambda)$ were positive for NA, indicating the native effect of the demographic degradation on the population persistence, while this relationship was negative for the SA and BI stocks (i.e., the lower the MA_{SSB} is, the faster hake population grows). This indicates the SA stock is able to respond/regulate/react to the truncation of the demographic structure, probably through a higher variability of the recruitment and sensitivity (i.e., more strongly related with) to the environmental variability (Hidalgo et al., in prep). Mehault et al. (2010) show evidence of these changes in the maternal effects through a shift in the contribution of total egg production of the spawning stock at SA, shifted from older age classes to young spawners in the recent years. These authors showed these changes positively affected the recruitment dynamics of hake in SA.

In the case of the BI, recent studies show BI populations a truncated population was in the whole study period (Hidalgo et al., in review), which explains the high recruitment dependency demonstrated for this species in this area (Hidalgo et al., 2009a). The results obtained could suggest that a high unstructured population (which is the case for BI) with a low reproductive potential may turn demographic strategy to maximize survival rates for young age classes with the aim to achieve a diverse and stable reproductive stock (Hidalgo et al., in prep). This is a common strategy in long-lived unexploited vertebrates which exhibit stable adult survival (Tavecchia et al., 2001).

Fishing mortality showed negative additive effects on $\ln(\lambda)$ variability for some populations (NA and BI for hake). As expected, a low harvesting regime favours the population persistence. For the NEA cod we did not see any significant effect of fishing mortality on $\ln(\lambda)$. For the BS pollock we were lacking this variable.

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