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Title:
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Date:
2020-12

Citation:
Tanner, S. E., Giacomello, E., Menezes, G. M., Mirasole, A., Neves, J., Sequeira, V., Vasconcelos, R. P., Vieira, A. R. & Morrongiello, J. R. (2020). Marine regime shifts impact synchrony of deep-sea fish growth in the northeast Atlantic. OIKOS, 129 (12), pp.1781-1794. https://doi.org/10.1111/oik.07332.

Persistent Link:
https://hdl.handle.net/11343/276133

Marine regime shifts impact synchrony of deep-sea fish growth in the Northeast Atlantic

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Decision date: 01-Aug-2020

Abstract

The complexity and spatio-temporal scale of populations' dynamics influence how populations respond to large-scale ecological pressures. Detecting and attributing synchrony (i.e. temporally coincident fluctuations in populations' parameters) is key as synchronous populations can become more vulnerable to stochastic events that can affect the viability of harvest and have profound consequences to community structure. Here, we aimed to estimate the level of synchrony in fish growth within and among species across 1 million km^2 and identify the environmental drivers contributing to synchronous population fluctuations. We developed otolith increment-based growth chronologies for two deep-sea scorpaenid fishes (*Helicolenus dactylopterus* and *Pontinus kuhlii*) from geographically and bathymetrically disjunct populations in the Northeast Atlantic (one species in three locations; two species with different depth preferences). We used hierarchical models to partition variation in growth within and between populations attributing it to intrinsic (age, species, population) and extrinsic (environmental variables) drivers. We assessed synchrony in growth variation within and among species and identified common change points in population specific growth patterns. We documented time-variant synchrony in growth variation of geographically and bathymetrically segregated deep-sea fish populations, lasting 25 and 18 years, respectively. The observed synchrony was likely driven by shared environmental forcing (Moran effect) as large-scale climate indices (East Atlantic pattern and North Atlantic Oscillation) were important environmental drivers of overall growth variation while the onset of synchrony in growth variation was likely related to marine regime shifts occurring in a wide area of the Northeast Atlantic that affected the entire ecosystem. However, our capacity to extrapolate growth information across species and locations was dependent on the timing and magnitude of environmental change. Developing a better understanding of the mechanisms driving growth synchrony is key to ensure sustainable management of populations in habitats that are fragile and highly sensible to environmental change, such as the deep-sea.

Keywords: East Atlantic pattern (EAP), Moran effect, North Atlantic Oscillation (NAO), Otolith, Regime shift, Spatial scaling

Introduction

Understanding mechanisms driving population dynamics has been the central motivation for numerous ecology studies for over a century (Koenig and Liebhold 2016). This continues to be a key issue in modern ecology as the complexity and spatio-temporal scale of population dynamics greatly influences population responses to large-scale ecological pressures, such as climate change, overharvesting or habitat fragmentation (Marquez et al. 2019).

Among the more intriguing of ecological phenomena is spatial synchrony, where, for example, temporal patterns of abundance, growth or survival show coincident fluctuation across populations (reviewed in Liebhold et al. 2004). Whilst many studies on synchrony have focused on geographically disjunct populations of the same species, synchronous fluctuations in biological parameters can also occur across species (interspecific synchrony) (Hansen et al. 2013, Koenig and Liebhold 2016). Three main processes are known to enforce spatially synchronous fluctuations across populations and species (Liebhold et al. 2004): 1) regional-scale fluctuations in environmental variables, such as climate (known as the 'Moran Effect' - Moran, 1953; Koenig 2002, Sæther et al. 2007); 2) large-scale trophic interactions such as predator-prey or parasite-host regulation (Huitu et al. 2005, Ims and Andreassen 2000) or widespread harvesting of species (Frank et al. 2016, Gamelon et al. 2019); and 3) individual dispersal (Koenig 2001, Ranta et al. 1997). These processes often act simultaneously on populations (Cheal et al. 2007) and are further affected by other factors, such as geographical patterns or habitat (Powney et al. 2010).

Detecting the presence, and understanding the drivers, of synchrony is essential for natural resource management (Gamelon et al. 2019, Schindler et al. 2010). In synchronously fluctuating populations, parameters such as density, growth or survival rate are more likely to covary, which can make them more vulnerable to stochastic events and to local or global extinction (Liebhold et al. 2004), can affect commercial viability of harvest (Frank et al. 2016, Schindler et al. 2010), and can have far-reaching consequences to community structure (Hansen et al. 2013, Post and Forchhammer 2002). Consequently, it is key to assess how the magnitude and direction of spatial synchrony changes over time, and whether these changes can be attributed to specific drivers. Increasing synchrony in local environmental factors (e.g. air temperature) over wide geographical range, likely related to climate change, can be involved in increasing spatial synchrony of biological processes as was shown for North American wintering birds' abundances over the past 50 years (Koenig and Liebhold 2016). Large-scale climate indices, such as the North Atlantic Oscillation (NAO) or the El Niño Southern Oscillation (ENSO), can also induce synchrony in a wide range of taxa and over large geographical scale (Black et al. 2018, Post and Forchhammer 2002). Abrupt changes in large-scale climate indices (shifting phases) can have synchronizing effects by causing regime shifts that affect whole ecosystems. For example, in the late 1980s a NAO phase shift led to water temperature increase and synchronous regime changes in multiple European aquatic systems which involved several trophic levels (Alheit and Bakun 2010).

Studies on spatial synchrony have a long tradition in terrestrial ecosystems where spatio-temporally replicated data is readily available (reviewed in Liebhold et al. 2004). In the marine environment, data at the appropriate spatio-temporal resolution is sometimes more difficult to obtain (but see Cheal et al. 2007, Marquez et al. 2019, Myers 1995). Otolith-based growth biochronologies provide unique long-term data of past biological variation, making them a powerful yet under-utilized tool to assess synchrony in marine fish populations' growth patterns and identify potential drivers of change. Individual growth integrates the effects of physical and biological processes representing an ideal parameter to measure organisms' responses to environmental changes and fishing pressure which allows insight of the effects of these processes on the productivity of fish populations (Morrongiello et al. 2012). Moreover, coupled atmosphere-ocean forcing, commonly represented by large-scale climate indices is considered a primary driver in large-scale synchronous variations in marine population dynamics (Lehodey et al. 2006). More recent studies have also shown synchronizing effects of exploitation (Frank et al. 2016). Otolith-increment based time-series have successfully identified regime shifts in higher trophic levels (Smoliński and Mirny 2017, Tanner et al. 2019), synchrony of growth patterns across multiple species over a large spatial scale (3000 km) (Ong et al. 2018), and drivers of growth pattern variation of different taxa (trees, fish, bivalves and corals) (Black 2009, Black et al. 2014, Ong et al. 2016).

Here, we focused on fish inhabiting the deep-sea, commonly defined as ocean environments beyond 200 m depth, which represent the largest and still least explored biome of the Earth. Deep-sea organisms are generally characterized by high longevity, late reproduction and low fecundity, which make them highly sensitive to multiple human pressures (e.g. fisheries) and environmental change (Danovaro et al. 2017). Information on population dynamics of deep-sea organisms is often scarce, hampering our understanding on how these populations will respond to future environmental conditions. Thus, it is key to assess synchrony (and its inducing factors) in deep-sea species and to determine whether changes in one site or species can be used to draw inference at other locations or species, which could be critical for long-term deep-sea monitoring. We used individual-based, annually resolved growth estimates of two deep-sea fish species in disjunct populations - geographically (one species in three locations) or bathymetrically (two species with different depth preferences in one location). The aim was to assess synchrony in interannual variation of populations growth rates within and among species, identify common change points in population specific growth patterns and identify environmental drivers that contribute to the spatial scaling in synchronous populations dynamics fluctuations.

Material & Methods

Study area and species

Samples were obtained from fish captured at three different locations in the Portuguese exclusive economic zone: off the mainland continental shelf in central Portugal (Portugal hereafter), off the central islands of Azores and the island of Madeira (Fig. 1). The Portuguese continental shelf is part of the northern limb of the Canary Current Upwelling System and is characterized by persistent upwelling-type circulations during late spring and summer (Peliz et al. 2002), promoting high primary productivity in the area. The archipelagos of Azores and Madeira are part of the Macaronesian biogeographical region located in the Northeast Atlantic Ocean off the coast of Europe and Africa (Friedlander et al. 2017). Both archipelagos are surrounded by seamounts and are connected via oceanic currents.

Our study focused on two bathydemersal fish species: the blackbelly rosefish, *Helicolenus dactylopterus* (Delaroche, 1809) (rosefish hereafter) sampled in all three locations, and the offshore rockfish, *Pontinus kuhlii* (Bowdich, 1825) (rockfish hereafter) sampled in the Azores only (Fig. 1). Both species are commercially valuable deep-water scorpaenids, commonly found at depths of 200-1000 m and 100-450 m, respectively. The rosefish is widely distributed in the eastern Atlantic Ocean (Sequeira et al. 2009) whereas the rockfish has a more southern distribution ranging from Portugal to Angola including the Macaronesian region (Barros Paiva et al. 2013). Maximum age reported is 43 years for rosefish (Sequeira et al. 2009) and 30 years for rockfish (Barros Paiva et al. 2013).

Sample collection, age and increment measurements

Otoliths for populations of the two species from the Azores were obtained from archived samples at the Department of Oceanography and Fisheries (DOP) of the University of the Azores. Fish were collected during fisheries-independent research cruises carried out in Azorean waters from 1996 – 2017. Rosefish otoliths from continental Portugal and Madeira were obtained from archived samples (Sequeira et al. 2009) which were then complemented with more recent samples obtained from commercial fisheries (Table 1, Fig. S1). Procedures for otolith image acquisition and increment measurements were identical for both species. Otoliths were immersed in water with the concave side down and images were acquired using a digital camera (Leica DFC 290) coupled to a stereomicroscope (Nikon SMZ 745T). Otolith increment widths were measured along the growth axis from the nucleus to the posterior edge using ObjectJ (ImageJ plugin). Measurements of the first increment were not included in the analyses, as they did not necessarily represent a complete growth year.

The use of otolith increments as a proxy of fish growth relies on the premise of an allometric relationship between otolith and somatic growth. For each species, this assumption was tested and confirmed in a subset of individuals for which length data was available (rosefish: adjusted R^2=0.88, n=173; rockfish: adjusted R^2=0.79, n=182, Fig. S2).

Growth predictors

Variation in deep-sea fish growth was explored as a function of a series of intrinsic and extrinsic variables. Intrinsic variables included fish age (in years, based on the formation of otolith increments), age-at-capture, sex, and species (rosefish or rockfish). Extrinsic variables included sampling location (Azores, Madeira or Portugal), monthly mean ocean temperature at the species median depth of distribution (weighted by species abundance: rosefish ~500m; rockfish ~220m; Menezes et al. 2006), monthly North Atlantic Oscillation index (NAO) and monthly East Atlantic pattern index (EAP). The less well-known EAP is the second mode of inter-annual variability of the tropospheric circulation in the study area and is at least as important as the NAO in determining the region's air temperature, SST, precipitation and wind (Iglesias et al. 2014).

Temperature-at-depth estimates were obtained from the Simple Ocean Data Assimilation (SODA3) reanalysis, version 3.4.2 (Carton et al. 2018). SODA3 temperature estimates have a monthly resolution ranging from 1980 to 2016 and a spatial resolution of 0.5º x 0.5º horizontally with 50 vertical levels. Temperature-at-depth data was obtained from the areas where fish were collected (Fig. 1), growth estimates prior to 1980 (earliest available temperature data) were excluded from extrinsic covariate models. Both climatic indices (NAO and EAP) were obtained from NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov). Landings data of both species contained many missing values and could therefore not be included in the analyses.

Data analysis

A series of mixed effects models were developed following the statistical framework of Morrongiello and Thresher (2015) to partition intrinsic and extrinsic variation of annual growth: within- and across-locations (rosefish) - i.e. hereafter referred to as ‘rosefish location model’, and within- and across-species (rosefish and rockfish) - i.e. hereafter referred to as ‘Azores species model’. Otolith increment width and the corresponding fish age data were log transformed to meet assumptions of normality and homoscedasticity, and all predictor variables were scaled (mean=0, standard deviation=1) to facilitate model convergence and interpretation of interaction terms.

In a first step, models with increasingly complex random effects structures and the maximal fixed effects structure (see below) were developed and compared to determine the optimal random effects model describing otolith growth. The random structures included random intercepts for individual fish (FishID), year of otolith increment formation and cohort (birth year) both within each location or species, and random age slopes for these covariates thus allowing for individual age-dependent growth trajectories.

In a second step, the optimal random effects model was used to select the appropriate fixed effect structure. For the rosefish location model, the maximal fixed effect structure included a three-way interaction between location, age and sex, and an interaction between location and age-at-capture. For the Azores species model, the maximal fixed effect structure contained an interaction of species with age, age-at-capture and sex. Interaction terms in both models accounted for age-specific effects on growth that can vary between locations, species and sex as well as location- and species-specific differences in potential sampling bias (Biro 2013) or growth selectivity associated to certain phenotypes (Morrongiello and Thresher 2015). Model selection was based on the comparison of the Akaike Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2016). Variance in otolith growth explained by the combined fixed and random effects was calculated by the conditional R^2 metric (Nakagawa et al. 2017). Model parameters were estimated using restricted maximum likelihood (REML). For fixed effects optimization, models were fitted using maximum likelihood and the best model was subsequently refitted using REML to provide unbiased estimates (Zuur et al. 2009).

Best linear unbiased predictors (BLUPs) for the year and cohort random effects for each location and species were extracted to visualize temporal variation in otolith growth. Synchrony in otolith growth among locations and species was assessed by 15-year running correlations among BLUPs extracted for the random year terms of the otolith growth models. The critical p-value of running correlations was determined using Monte Carlo simulations to calculate maximum correlation. Furthermore, a Bayesian change point analysis was used to identify rapid shifts in the different location- and species-specific growth chronologies.

The influence of the extrinsic environmental conditions on deep-sea fish growth was evaluated using an exploratory sliding window analysis technique (Bailey and van de Pol 2016, van de Pol et al. 2016). This stepwise approach is data driven, with no *a priori* assumptions made on the time windows of environmental variables. It allows testing the effect of different environmental variables over varying temporal windows (e.g. two months in winter or six months covering spring and summer) on the response variable (deep-sea fish growth) and comparing the different time windows to identify the best environmental predictor (Smoliński 2019, Smoliński and Mirny 2017). First, a baseline model without the environmental variables was produced to act as the null. Second, a set of models with competing combinations of environmental variables was created by identifying all the potentially relevant environmental variables, varying their time windows and then allowing for no interactions, age interactions, and age and species or location interactions with environmental variables. These interaction terms allowed exploring age-specific responses of growth to environmental variables as well as to account for species- and location-specific effects of the environmental factors. Finally, all models were compared to identify the best environmental predictor and time window.

For both the rosefish dataset and the Azores dataset, we used mean aggregate statistics of the environmental variables, an absolute time window (allows using calendar dates to define windows (e.g. mean March temperature)) and linear relationship between response (growth) and environmental variables. The environmental variables included for both datasets were temperature-at-depth, NAO and EAP, and their time windows were explored within the12 months corresponding to the growth year. After identifying the best environmental predictor and associated interactions, the analyses were rerun to consider additional environmental predictors until the increasing model complexity did not further improve the model fit. The exploratory sliding window approach tests a high number of temporal windows and thus misclassification of environmental predictors (false positives) can occur by chance. This issue was addressed by performing 1000 randomizations and comparing the ΔAICc of the best model fitted to the observed data to the distribution of ΔAICc in a dataset where no relationship existed between environmental and response variable. During randomization tests the date variable in the original response dataset is reordered (i.e. removing the relationship between response and environmental variables) while maintaining any relationship between the response variable and other covariates and keeping auto-correlation within the environmental data (Bailey and van de Pol 2016, van de Pol et al. 2016). All analyses were conducted in R 3.5.1 using the packages lme4, bcp and climwin.

Results

Intrinsic effects on growth

The best supported random effects structure for the rosefish location model contained a random age slope and intercept for FishID and random intercepts for each location by year and location by cohort combination. Fixed effects included age, age-at-capture and sex all interacting with location (Table 2, Table S1). The optimized rosefish location model explained 81.2% of variance in rosefish growth in the three locations. For the Azores species model, the best supported random effects structure included a random age slope and intercept for FishID and random intercepts for each species by year combination. Fixed effects included interactions between species and age and species and sex (Table 3, Table S2). The optimal intrinsic effects model for the Azores explained 82.3 % of variance in deep-sea fish growth.

Average growth in both models declined with age (Fig. S3). Slight differences in age-related growth patterns of rosefish were observed among the three locations: younger rosefish presented higher growth rates in Madeira and lower growth rates in Azores; and this pattern was inverted at older age – older rosefish grew relatively faster in Azores and slower in Madeira. Absolute, species-specific differences in age-related growth patterns between the two species used in the Azores species model were removed by scaling (subtract mean, divide by SD) increments within each species. Rockfish grew relatively faster at younger ages whilst rosefish grew relatively faster at older ages (Fig. S4). The inclusion of the age-at-capture term was only supported in the rosefish location model (Fig. S3). Fish collected in Azores and Madeira showed a negative relationship with age-at-capture, suggesting that fish caught at a younger age are faster juvenile growers than those caught at older ages. For the Portuguese rosefish the relationship between growth and age-at-capture was positive, possibly indicating that fish caught at an older age have higher growth. Sex was included in all models to account for sex-specific differences in growth (Table 2 and 3). For rosefish, there were location-specific differences in how sex affected growth rate. Azores males grew faster than Azores females, whereas the opposite pattern was observed for rosefish collected in Madeira while Portugal individuals showed little effect of sex (Table 2). Rockfish females grew slightly faster than males (Table 3).

Rosefish and rockfish chronologies from the Azores spanned 46 and 45 years, respectively (1971/1972 – 2016), while rosefish chronologies from Madeira and Portugal each ranged from 1981 to 2016, covering 36 years (Fig. 2 and 3). All chronologies showed considerable interannual variation with below and above average years of growth that lasted for about 5 to 15 years. Abrupt change points in growth patterns were identified in all chronologies (Fig. 2a and 3a). Growth of Azores rosefish showed abrupt changes in growth in 1977, 1997 and 2014 whilst rosefish collected in Madeira and Portugal presented shifts in 1999 and 2009; and in 2015, respectively (Fig. 2a). For the Azores rockfish, four sudden shifts in growth pattern were observed occurring in 1978, 2000, 2007 and 2015 (Fig. 3a). Further, we found that rosefish growth in specimens collected in Azores and Madeira was negatively correlated for the first 20 years of our data, before switching to a significant positive correlation, indicative of spatial synchrony lasting for 25 years (1990-2014) (Fig. 2b). We detected little, or marginally negative correlations in growth among other location combinations (Azores-Portugal and Madeira-Portugal) (Fig. 2c and 2d). For the two species collected in Azores, we detected an increasing trend in interspecific synchrony over the study period, with significant positive correlations lasting for 18 years (1997-2014) (Fig. 3b).

Extrinsic effects on growth

For the rosefish location model, the sliding window approach firstly identified the mean EAP from May to October as the best environmental signal (Fig. 4, S5, Table S3). Secondly, the inclusion of temperature-at-depth from January to March in interaction with age and location was best supported by the lowest AICc. Randomization tests showed that the strong environmental signals obtained by the two temporal windows identified was unlikely to be achieved by chance (p-value<0.05 for both windows, Fig. 4). Correlation between the two environmental predictors was low (r=0.12) and thus both variables were included in the final model. The final extrinsic rosefish location model showed that rosefish growth was negatively affected by the EAP and location- and age-dependent effects of temperature-at-depth (Fig. 5). Younger rosefish collected in Azores and Portugal grew faster as waters warmed while older fish were little affected. In contrast, younger rosefish from Madeira grew slower as waters warmed with the opposite pattern evident for older fish (Fig. 5).

For the Azores species model, the sliding window approach identified the mean EAP from May to September in interaction with age and species as the best environmental signal which was also strongly supported by the randomization test (Fig. 6, S6, Table S4). In a second step, NAO from May to August also in interaction with age and species was identified as the second-best environmental predictor; however, for this second predictor the signal randomization test showed that the window could occur by chance ($p>0.05$). The inclusion of the next best predictor based on ΔAICc, NAO from May to August in interaction with age was supported by the randomization test (Fig. 6, S6, Table S4). The final extrinsic Azores species model showed that deep-sea fish growth was significantly related to the climatic indices EAP and NAO (Table 3, Fig. 7). These relationships differed depending on age, and for EAP a species-specific effect was also detected. Growth of both species at younger ages decreased with positive EAP (Fig. 7). In rosefish this relationship was maintained for older age whereas growth of older rockfish slightly increased with positive EAP. The climatic index NAO positively impacted growth of both species only at young ages whereas the effect was negligible at older ages (Fig. 7).

Discussion

We documented significant synchrony in growth variation of geographically and bathymetrically segregated populations of deep-sea fishes in the Northeast Atlantic Ocean. The strength and direction of these synchronous fluctuations varied over time with populations out of phase in the early 1980s becoming entrained in the early 1990s and finally drifting out of phase in recent years. Two populations of rosefish (Azores and Madeira), separated by more than 1000 km showed clearly synchronous growth patterns over 25 years (1990-2014), while synchrony in the two species occupying different depth strata in the Azores spanned over 18 years (1997-2014). The large-scale climate pattern EAP was the most important environmental driver of growth variation in deep-sea fish independent of location or species, while NAO only impacted Azores fish growth. Temperature-at-depth had a more population-specific effect on rosefish growth with the response direction varying with location.

Drivers of growth synchrony

Shared environmental forcing (Moran effect), movement (dispersal) and spatial patterns of species' interactions (predation or exploitation) are generally viewed as the main drivers of synchrony in population dynamics (Liebhold et al. 2004). The fish growth synchrony patterns observed here were most likely driven by environmental forcing (Moran effect) since both species have constrained home ranges leading to low dispersal rates (Higgins et al. 2013). Further, there are location-specific differences in the commercial importance and harvest technique of each species that lead to location-specific fishing pressures (Sequeira et al. 2009). Temporal changes in spatial population synchrony have been documented both linked and independent from environmental synchrony (Koenig and Liebhold 2016). Moreover, rising climate variability due to climate change has been observed (Black et al. 2018, Sydeman et al. 2013) which can increase synchronous fluctuations in population dynamics (Koenig and Liebhold 2016, Post and Forchhammer 2004). Regime shifts, characterized by abrupt, substantial and persistent changes in the state of ecosystems, can profoundly alter population dynamics in terrestrial and marine species (Rocha et al. 2015) and have also been found to induce changes in spatial synchrony patterns of populations (Defriez et al. 2016, Saitoh et al. 2006). We postulate that the sudden onsets of synchrony in our deep-sea fish growth chronologies are in part linked to regime shifts that occurred in the Northeast Atlantic over the last three decades. Growth variation from spatially segregated rosefish populations from Azores and Madeira synchronized in 1990. This onset of synchrony coincided with a large marine regime shift observed in the entire Northern Hemisphere spanning both the Atlantic and the Pacific (Beaugrand et al. 2014, Reid et al. 2016). Conversely, the growth of two Azores species (rosefish and rockfish) became synchronous in 1997 and appeared to be linked to an abrupt decline in the rosefish somatic growth trajectory, and record-low rosefish abundance (considering abundance data from 1996-2010; Giacomello pers. comm.). Similar abrupt changes in rosefish and rockfish growth observed in the late 1970's did not result in synchronization of growth patterns. We can only speculate on the underlying causes of this pronounced decrease in growth of the two deep-sea fish species. One possible explanation could be related to the "great salinity anomaly" of the North Atlantic that occurred in the 1970s. These anomalies arose from outpourings of low-salinity surface water and ice from the Arctic that was tracked entering the Atlantic and had an influence as far south as northeast of the Azores (Dickson et al. 1988, Pollard and Pu 1985). The freshening of the upper 500-800m of the ocean led to food web changes and negatively affected deep-sea fish populations (Mertz and Myers 1994). Growth variation patterns of our two fishes drifted out of phase again in 2015. A large-scale abrupt biological shift, unprecedented in magnitude and extent, has been predicted to have occurred after 2014 in response to a strong El Niño event and major changes in the Northern hemisphere climate (Beaugrand et al. 2019). We suspect that these large-scale climate phenomena had differing impacts on rosefish and rockfish growth and caused them to desynchronize. Notwithstanding that regime shifts were likely the main drivers of synchronization and desynchronization of deep-sea fish growth, other factors were likely involved. The rosefish population from the Portuguese continental shelf did not synchronize with any other studied population. This lack of synchrony from one site could be driven by localized habitat differences among locations as habitat similarity can positively affect population synchrony (Powney et al. 2010). The Azores and Madeira rosefish populations are found on seamounts close to oceanic islands. Conversely, Portuguese rosefish live on the continental shelf. Furthermore, local-scale environmental processes in the coastal area may supersede regional oceanographic signals explaining the uncorrelated variation of growth among these populations.

Drivers of population growth variation

Large-scale climate variability has been suggested as a main driver of regime shifts in Northern hemisphere marine ecosystems. These climate phenomena also have the potential to interact with other drivers that affect food web structure and alter the resilience of biological systems (Möllmann and Diekmann 2012). The NAO index has been implicated as a major synchronizing agent across all trophic levels in European marine and freshwater ecosystems (Alheit and Bakun 2010). Our results identified the EAP as the ubiquitous driver of deep-sea fish growth variation, with more positive values of EAP impacting growth negatively. Recent works have highlighted the key role of the EAP and its interactions with the NAO in European Atlantic climate variability where it modulates the multidecadal variability of the position and strength of the NAO (Mellado-Cano et al.

2019, Moore et al. 2013). Summer EAP is positively related to Sea Surface Temperature (SST) over the North Atlantic at mid-latitude, including our study locations (Iglesias et al. 2014). Higher summer SST might exacerbate the seasonal cycle of sea surface productivity in temperate regions which is characterized by spring phytoplankton blooms, followed by the prevalence of thermal stratification which leads to exhaustion of nutrients and subsequent demise of phytoplankton during summer-autumn (Amorim et al. 2017, Vidal et al. 2017). Additionally, ocean warming has been related to past and future marine phytoplankton declines (Lewandowska et al. 2014). Changes in surface productivity can impact on life in the deep-sea as these ecosystems strongly depend on the external input of organic material produced in surface waters of the oceans (Danovaro et al. 2017). Furthermore, diel vertical feeding migrations of the preferential prey (squid) of a deep-sea fish (*Polyprion oxygeneios*) have been shown to contribute to the energy transfer from the surface to depth (Nguyen et al. 2015). Thus, the observed negative impact of EAP on deep-sea fish growth could be explained through this indirect mechanism where changes in summer SST affected the productivity transfer between surface and deep ocean.

The growth of younger Azores deep-sea fish was positively related to summer NAO. NAO is positively correlated with the eddy kinetic energy (EKE) of the Azores current (AzC) (Volkov and Fu 2011), one of the most prominent circulation features of the subtropical and mid-latitude North Atlantic, east of the Mid Atlantic Ridge. Stronger eastward flow of the AzC makes the current less stable and generates more eddies. These eddies have been found to intrude waters around the Azores Archipelago. Similarly, meanders and filaments originating from the Gulf Stream also enter the Azores area, creating dynamic processes that act to raise the nurticline to the euphotic zone and thus enhance primary productivity (Caldeira and Reis 2017). Contrary to the EAP, positive NAO phases can enhance surface primary productivity around the Azores. Higher surface productivity could positively impact the abundance of mysidacea, which are the main prey of immature rosefish (Neves et al. 2011) and thus may contribute to increased growth in younger individuals of deep-sea fish.

Temperature-at-depth was also identified as an important driver in rosefish growth variation, however the direction of growth response varied among locations. This more location-specific response was likely related to how winter temperature-at-depth increased over the analyzed period. Water temperature in Madeira showed the steepest increase and highest temporal correlation over the 36 years. Although temperature also increased in Azores and Portugal, there was a higher inter-annual variation around this trend. Owing to these differences in temperature increase and the fact that there is very low genetic differentiation among the three rosefish populations (Aboim et al. 2005), thermal adaptation in gene expression of rosefish, a species with a wide geographical distribution and thermal range, was likely population specific. Exposure to a wider range of temperatures can cause greater tolerance of subsequent thermal extremes, known as acclimation or preconditioning (Narum et al. 2013, Pörtner 2010). The larger temperature amplitudes experienced by Azores and Portuguese rosefish populations may have preconditioned them to cope with the temperature increase and even grow slightly faster at younger age. However, Madeira rosefish population was not able to benefit from the temperature increase and growth was affected negatively.

The age effect was the most important intrinsic factor driving growth variation, independent of species and location, accounting for the commonly observed pattern of growth decreasing as fish age. Plasticity in sexual dimorphism is a possible explanation for the location-specific differences we observed in rosefish, as studies have reported the existence and lack of sex-specific differences in growth of this species (Kelly 1999, Massutí et al. 2000, Sequeira et al. 2009). In rockfish, females grew slightly faster than males but the largest and oldest individuals were all male which is in line with the sexual dimorphism pattern commonly observed in rockfish (Barros Paiva et al. 2013, López Abellán et al. 2007).

Overall, our results documented time-variant synchrony in deep-sea fish growth patterns. Synchronization and desynchronization of growth fluctuations were likely related to marine regime shifts occurring in a wide area of the Northeast Atlantic that affected the entire ecosystem. The temporal variation of growth synchrony made extrapolating observed patterns from one system or species to others difficult. Nevertheless, large-scale climate indices, particularly EAP and NAO, were important drivers of region-wide intra- and inter-specific growth variation in the deep-sea. Temperature effects were more population specific. Synchronized populations can become more vulnerable to stochastic events, which increases their risk of local or global extinction and their vulnerability to human exploitation (Frank et al. 2016, Liebhold et al. 2004). Thus, better understanding spatio-temporal variation in growth synchrony and the mechanisms driving these fluctuations is key to ensure sustainable management of fish populations, especially in habitats that are fragile and highly sensible to environmental change, such as the deep-sea.

Acknowledgements

We would also like to thank all researchers that kindly provided access to archived otoliths. This study had financial support of Fundação para a Ciência e a Tecnologia (FCT) through

UIDB/04292/2020 and PTDC/AAG-GLO/5849/2014. SET, ARV and VS were supported by FCT, DL57/2016/CP1479/CT0022, CEECIND/01528/2017 and CEECIND/02705/2017, respectively. RPV was funded by "Programa Nacional de Amostragem Biológica" (EU Data Collection Framework). EG was supported by the Azores Regional Government, CONDOR /DEMERSAIS projects. JRM was partly supported by the Australian Research Council (DP190101627) and the Australian Academy of Science's Thomas Davies Research Grant.

Literature cited

Aboim, M. A. et al. 2005. Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. - Mol. Ecol. 14: 1343-1354.

Alheit, J. and Bakun, A. 2010. Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical–biological linkage mechanisms. - J. Mar. Syst. 79: 267-285.

Amorim, P. et al. 2017. Overview of the Ocean Climatology and Its Variability in the Azores Region of the North Atlantic Including Environmental Characteristics at the Seabed. - Front. Mar. Sci. 4.

Bailey, L. D. and van de Pol, M. 2016. climwin: An R Toolbox for Climate Window Analysis. - PloS one 11: e0167980.

Barros Paiva, R. et al. 2013. Age, growth and mortality of *Pontinus kuhlii* (Bowdich, 1825) (Scorpaeniformes: Scorpaenidae) in the Gorringe, Ampère, Unicorn and Lion seamounts. - Sci. Mar. 77: 95-104.

Beaugrand, G. et al. 2019. Prediction of unprecedented biological shifts in the global ocean. - Nat. Clim. Change 9: 237-243.

Beaugrand, G. et al. 2014. Synchronous marine pelagic regime shifts in the Northern Hemisphere. - Philos. Trans. R. Soc. Lond. B Biol. Sci. 370: 20130272-20130272.

Biro, P. A. 2013. Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. - Oecologia 171: 339-345.

Black, B. A. 2009. Climate-driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. - Mar. Ecol. Prog. Ser. 378: 37-46.

Black, B. A. et al. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. - Science 345: 1498-1502.

Black, B. A. et al. 2018. Rising synchrony controls western North American ecosystems. - Global Change Biol. 24: 2305-2314.

Burnham, K. P. and Anderson, D. R. 2016. Multimodel Inference. Understanding AIC and BIC in model selection. - Sociol. Methods Res. 33: 261-304.

Caldeira, R. M. A. and Reis, J. C. 2017. The Azores Confluence Zone. - Front. Mar. Sci. 4.

Carton, J. A. et al. 2018. SODA3: A New Ocean Climate Reanalysis. - J. Clim. 31: 6967-6983.

Cheal, A. J. et al. 2007. Spatial Synchrony in Coral Reef Fish Populations and the Influence of Climate. - Ecology 88: 158-169.

Danovaro, R. et al. 2017. The deep-sea under global change. - Curr. Biol. 27: R461-R465.

Defriez, E. J. et al. 2016. Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. - Global Change Biol. 22: 2069-2080.

Dickson, R. R. et al. 1988. The “great salinity anomaly” in the Northern North Atlantic 1968–1982. - Prog. Oceanogr. 20: 103-151.

Frank, K. T. et al. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. - Proc. Natl. Acad. Sci. U. S. A. 113: 8248-8253.

Friedlander, A. M. et al. 2017. Contrasts in the marine ecosystem of two Macaronesian islands: A comparison between the remote Selvagens Reserve and Madeira Island. - PloS one 12: e0187935.

Gamelon, M. et al. 2019. Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species? - J. Appl. Ecol. 56: 2186-2194.

Hansen, B. B. et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. - Science 339: 313-315.

Higgins, R. et al. 2013. Otolith elemental signatures indicate population separation in deep-sea rockfish, *Helicolenus dactylopterus* and *Pontinus kuhlii*, from the Azores. - J. Sea Res. 83: 202-208.

Huitu, O. et al. 2005. Spatial synchrony in vole population fluctuations - a field experiment. - Oikos 109: 583-593.

Iglesias, I. et al. 2014. Seasonal predictability of the East Atlantic pattern from sea surface temperatures. - PloS one 9: e86439.

Ims, R. A. and Andreassen, H. P. 2000. Spatial synchronization of vole population dynamics by predatory birds. - Nature 408: 194-196.

Kelly, C. 1999. Age estimation, growth, maturity, and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche 1809) from the Rockall Trough. - ICES J. Mar. Sci. 56: 61-74.

Koenig, W. D. 2001. Spatial Autocorrelation and Local Disappearances in Wintering North American Birds. - Ecology 82: 2636-2644.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. - Ecography 25: 283-288.

Koenig, W. D. and Liebhold, A. M. 2016. Temporally increasing spatial synchrony of North American temperature and bird populations. - Nat. Clim. Change 6: 614-617.

Lehodey, P. et al. 2006. Climate Variability, Fish, and Fisheries. - J. Clim. 19: 5009-5030.

Lewandowska, A. M. et al. 2014. Effects of sea surface warming on marine plankton. - Ecol. Lett. 17: 614-623.

Liebhold, A. et al. 2004. Spatial Synchrony in Population Dynamics. - Annual Review of Ecology, Evolution, and Systematics 35: 467-490.

López Abellán, L. J. et al. 2007. Age and growth of *Pontinus kuhlii* (Bowdich, 1825) in the Canary Islands. - Sci. Mar. 65: 259-267.

Marquez, J. F. et al. 2019. Spatial scaling of population synchrony in marine fish depends on their life history. - Ecol. Lett.

Massutí, E. et al. 2000. Age and growth of blue-mouth, *Helicolenus dactylopterus* (Osteichthyes: Scorpaenidae), in the western Mediterranean. - Fish Res 46: 165-176.

Mellado-Cano, J. et al. 2019. Examining the North Atlantic Oscillation, East Atlantic Pattern, and Jet Variability since 1685. - J. Clim. 32: 6285-6298.

Menezes, G. M. et al. 2006. Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). - Mar. Ecol. Prog. Ser. 324: 241-260.

Mertz, G. and Myers, R. A. 1994. The ecological impact of the Great Salinity Anomaly in the northern North-west Atlantic. - Fish. Oceanogr. 3: 1-14.

Möllmann, C. and Diekmann, R. 2012. Marine Ecosystem Regime Shifts Induced by Climate and Overfishing. - Adv. Ecol. Res. 47: 303-347.

Moore, G. W. K. et al. 2013. Multidecadal Mobility of the North Atlantic Oscillation. - J. Clim. 26: 2453-2466.

Moran, P. A. P. 1953. The Statistical Analsis of the Canadian Lynx cycle. 1. Structure and Prediction. - Aust. J. Zool. 1: 163.

Morrongiello, J. and Thresher, R. E. 2015. A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. - Ecol. Monogr. 85: 93-115.

Morrongiello, J. R. et al. 2012. Aquatic biochronologies and climate change. - Nat. Clim. Change 2: 849-857.

Myers, R. 1995. Synchrony of recruitment across the North Atlantic: an update. (Or, “now you see it, now you don't!”). - ICES J. Mar. Sci. 52: 103-110.

Nakagawa, S. et al. 2017. The coefficient of determination R(2) and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. - J. R. Soc. Interface 14.

Narum, S. R. et al. 2013. Thermal adaptation and acclimation of ectotherms from differing aquatic climates. - Mol. Ecol. 22: 3090-3097.

Neves, A. et al. 2011. Feeding habits of the bluemouth, Helicolenus dactylopterus dactylopterus (Delaroche, 1809) (Pisces: Sebastidae) in the Portuguese coast. - Helgoland Marine Research 66: 189-197.

Nguyen, H. M. et al. 2015. Growth of a deep-water, predatory fish is influenced by the productivity of a boundary current system. - Sci Rep 5: 9044.

Ong, J. J. et al. 2016. Evidence for climate-driven synchrony of marine and terrestrial ecosystems in northwest Australia. - Global Change Biol. 22: 2776-2786.

Ong, J. J. L. et al. 2018. A boundary current drives synchronous growth of marine fishes across tropical and temperate latitudes. - Global Change Biol. 24: 1894-1903.

Peliz, Á. et al. 2002. Fronts, jets, and counter-flows in the Western Iberian upwelling system. - J. Mar. Syst. 35: 61-77.

Pollard, R. T. and Pu, S. 1985. Structure and circulation of the Upper Atlantic Ocean northeast of the Azores. - Prog. Oceanogr. 14: 443-462.

Pörtner, H. O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. - J. Exp. Biol. 213: 881-893.

Post, E. and Forchhammer, M. C. 2002. Synchronization of animal population dynamics by large-scale climate. - Nature 420: 168-171.

Post, E. and Forchhammer, M. C. 2004. Spatial synchrony of local populations has increased in association with the recent Northern Hemisphere climate trend. - Proc. Natl. Acad. Sci. U. S. A. 101: 9286-9290.

Powney, G. D. et al. 2010. Synchrony of butterfly populations across species' geographic ranges. - Oikos 119: 1690-1696.

Ranta, E. et al. 1997. The spatial dimension in population fluctuations. - Science 278: 1621-1623.

Reid, P. C. et al. 2016. Global impacts of the 1980s regime shift. - Global Change Biol. 22: 682-703.

ocha, J. C. et al. 2015. Regime shifts in the anthropocene: drivers, risks, and resilience. - PloS one 10: e0134639.

Sæther, B. E. et al. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. - J. Anim. Ecol. 76: 315-325.

Saitoh, T. et al. 2006. Effects of regime shifts on the population dynamics of the grey-sided vole in Hokkaido, Japan. - Clim. Res. 32: 109-118.

Schindler, D. E. et al. 2010. Population diversity and the portfolio effect in an exploited species. - Nature 465: 609-612.

Sequeira, V. et al. 2009. Age and growth of bluemouth, *Helicolenus dactylopterus*, from the Portuguese continental slope. - ICES J. Mar. Sci. 66: 524-531.

Smoliński, S. 2019. Sclerochronological approach for the identification of herring growth drivers in the Baltic Sea. - Ecol. Indicators 101: 420-431.

Smoliński, S. and Mirny, Z. 2017. Otolith biochronology as an indicator of marine fish responses to hydroclimatic conditions and ecosystem regime shifts. - Ecol. Indicators 79: 286-294.

Sydeman, W. J. et al. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. - Global Change Biol. 19: 1662-1675.

Tanner, S. E. et al. 2019. Regional climate, primary productivity and fish biomass drive growth variation and population resilience in a small pelagic fish. - Ecol. Indicators 103: 530-541.

van de Pol, M. et al. 2016. Identifying the best climatic predictors in ecology and evolution. - Methods Ecol. Evol. 7: 1246-1257.

Vidal, T. et al. 2017. Phytoplankton dynamics in relation to seasonal variability and upwelling and relaxation patterns at the mouth of Ria de Aveiro (West Iberian Margin) over a four-year period. - PloS one 12: e0177237.

Volkov, D. L. and Fu, L.-L. 2011. Interannual variability of the Azores Current strength and eddy energy in relation to atmospheric forcing. - J. Geophys. Res. 116.

Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. - Springer.

Figure Legends

Figure 1. Map showing locations of sampling of rosefish (BRF) and rockfish (POI) in the Northeast Atlantic. Boxes in each sampling location indicate areas for which temperature-at-depth was obtained.

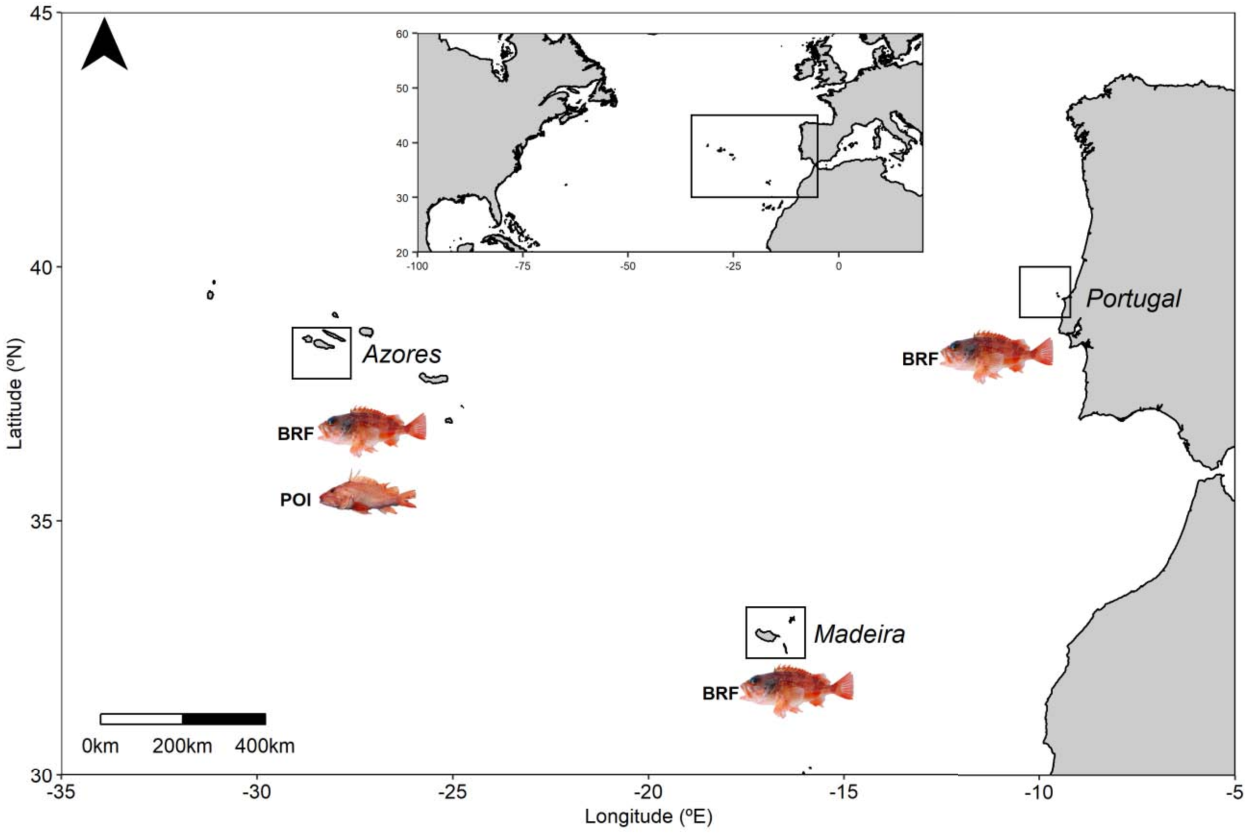

Figure 2. Rosefish location model showing a) predicted variations in annual otolith growth of rosefish (solid lines) collected in Azores (brown), Madeira (beige) and Portugal (aqua). Vertical dashed lines indicate identified abrupt changes in the growth chronologies (color code as solid lines). 15-year running correlations between growth chronologies from b) Azores and Madeira, c) Azores and Portugal, and d) Madeira and Portugal. In b)-d) each bar represents the endpoint of a 15-year running correlation and red dotted lines indicate significance at 95%.

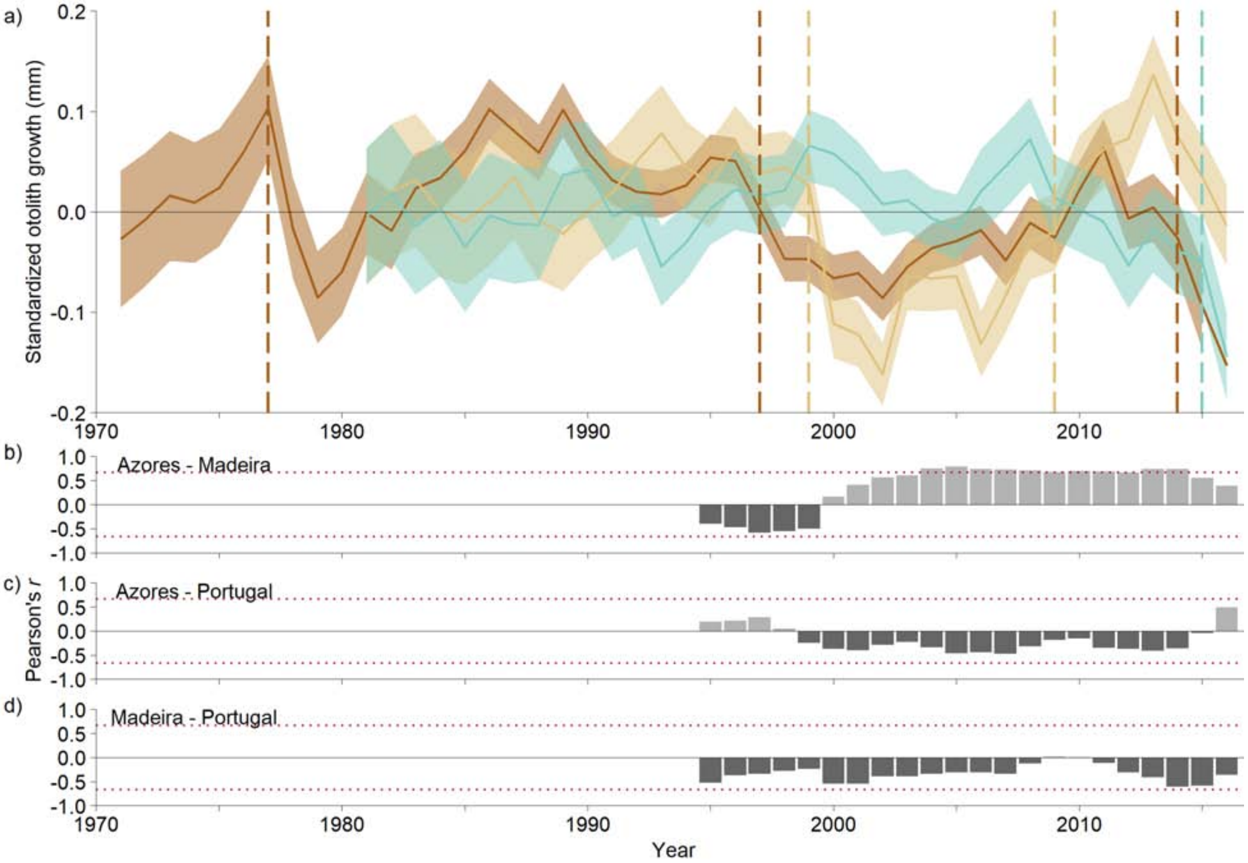

Figure 3. Azores species model showing a) predicted variations in annual otolith growth of rosefish (brown) and rockfish (turquoise) (solid lines). Vertical dotted lines indicate identified abrupt changes in the growth chronologies (color code as solid lines) and b) 15-year running correlations between growth chronologies of rosefish and rockfish. In b) each bar represents the endpoint of a 15-year running correlation and red dotted lines indicate significance at 95%.

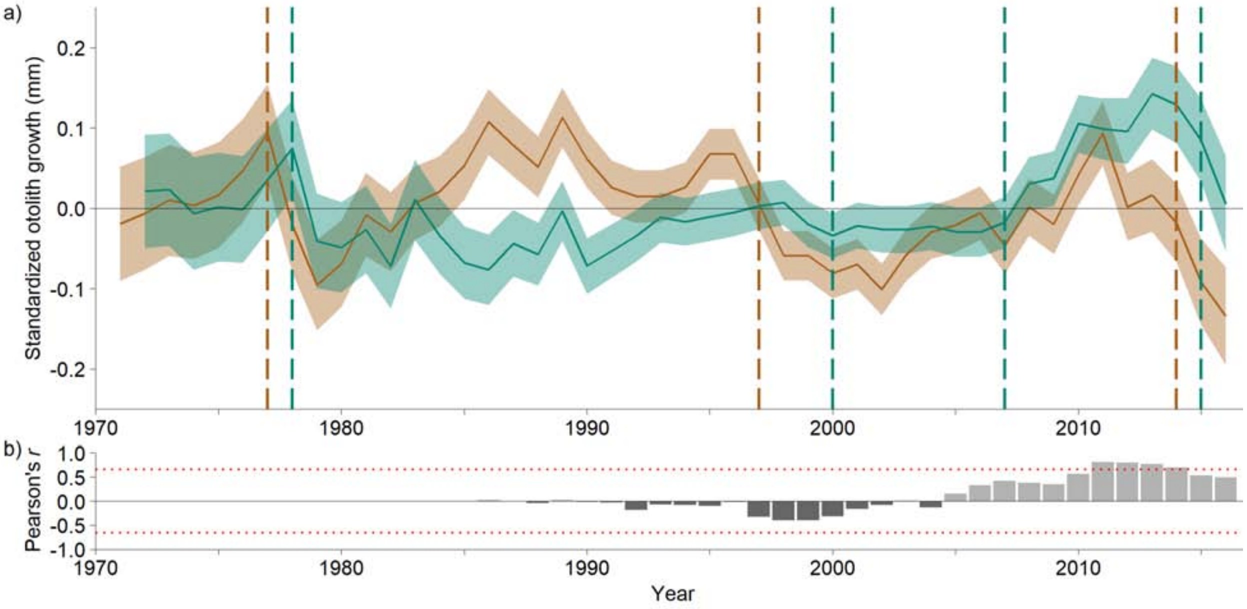

Figure 4. Identification of best environmental window models for the rosefish location dataset as determined by ΔAICc for a) East Atlantic pattern (EAP) and b) temperature-at-depth (Temp) interacting with age and location in rosefish growth in 3 locations compared to the baseline model with no environmental effects included. Squares and dotted lines indicate time windows best supported by the data (EAP: May-October; Temp: January-March). Distribution of ΔAICc of best supported model in 1000 randomizations for c) EAP and d) Temp. Dashed lines indicate best supported model of the rosefish location dataset. P-values are also shown.

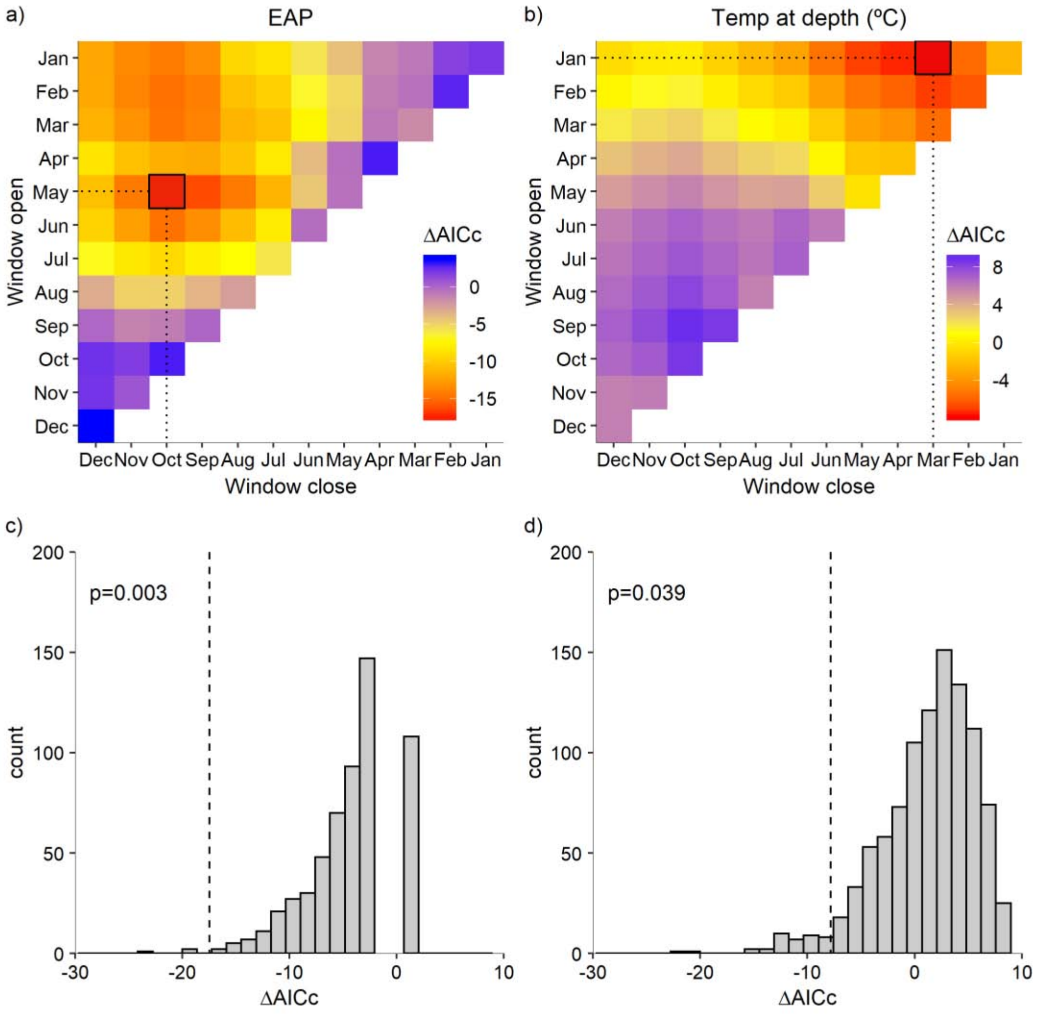

Figure 5. Overall effect of a) East Atlantic pattern (May-October) and age dependent effect of temperature at 500m (January-March) in b) Azores, c) Madeira and d) Portugal on rosefish growth. Environmental signals identified using sliding window analysis.

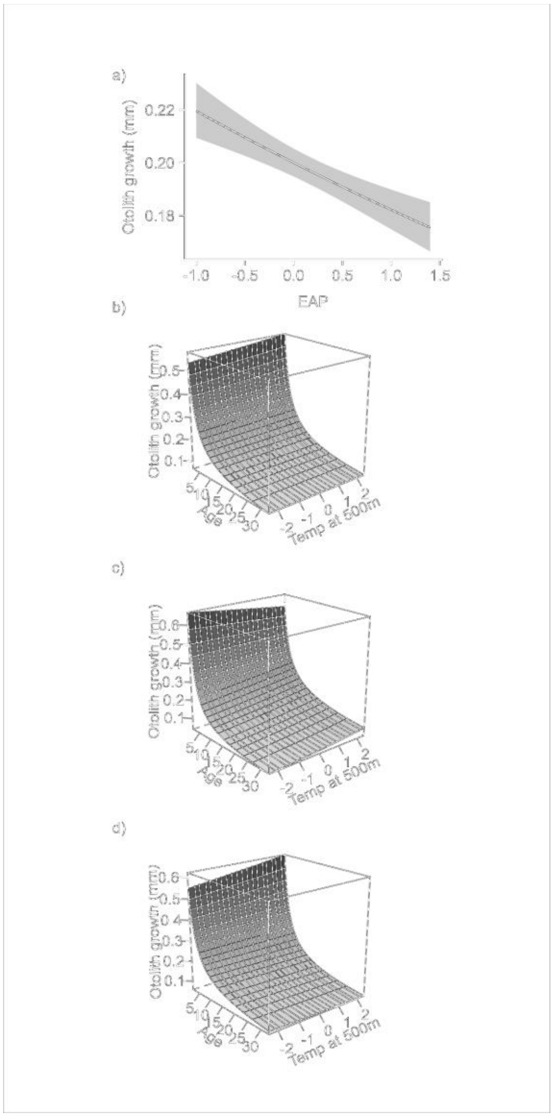

Figure 6. Identification of best environmental window models for the Azores species dataset as determined by ΔAIC for a) East Atlantic pattern (EAP) in interaction with Age and species, and b) North Atlantic Oscillation (NAO) with an Age interaction on rosefish and rockfish growth compared to the baseline model with no environmental effects included. Squares and dotted lines indicate the time windows best supported by the data (EAP: May-September; NAO: May- August). Distribution of ΔAICc of best supported model in 1000 randomizations for c) EAP and d) NAO. Dashed lines indicate best supported model of the Azores species dataset. P-values are also shown.

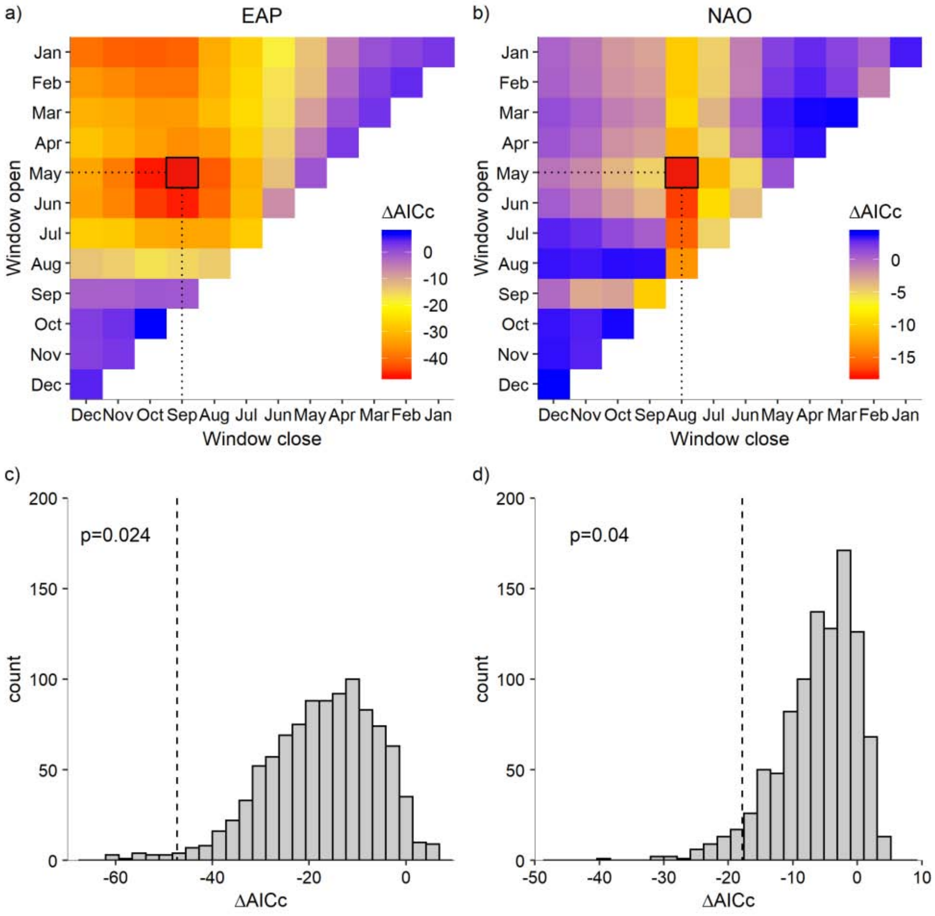

Figure 7. Age-dependent effect of East Atlantic pattern (May-September) in a) rosefish and b) rockfish, and c) North Atlantic Oscillation (May-August) on Azores deep-sea fish growth. Environmental signals identified using sliding window analysis.

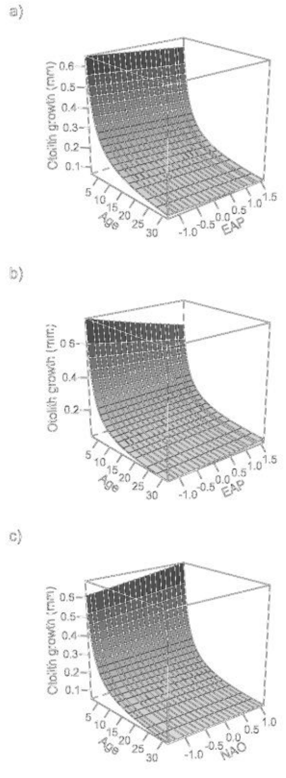

Table Legends

Table 1. Summary of samples used in this study

Species	FAO code	Area	Sampling years	Fish	Growth increments	Age range	Cohorts	Chronology length (yr)	Temporal range
Rosefish	BRF	Portugal	5	123	1434	2-26	23	36	1981-2016
Rosefish	BRF	Madeira	4	99	1434	6-27	22	36	1981-2016
Rosefish	BRF	Azores	21	337	4887	3-32	43	46	1971-2016
Rockfish	POI	Azores	21	472	5690	3-26	41	45	1972-2016

Table 2. Rosefish location model. Variance components and estimates of random and fixed effects of the optimal intrinsic and extrinsic location models describing rosefish otolith growth in the three sampling locations. SD = standard deviation, Corr. = Correlation, CI = confidence interval, EAP = East Atlantic pattern, Temp = Temperature at 500m.

	Intrinsic location model			Extrinsic location model		
Random effects						
	Variance	SD	Corr.	Variance	SD	Corr.
FishID	0.034	0.184		0.034	0.185	
Age|FishID	0.018	0.135	0.67	0.018	0.136	0.65
Location:Year	0.005	0.070		0.003	0.055	
Location:Cohort	0.003	0.055		0.003	0.051	
Residual	0.079	0.282		0.078	0.280	
Fixed effects						
	Estimate	(95% CI)		Estimate	(95% CI)	
Intercept	-1.641	(-1.68, -1.599)		-1.637	(-1.677, -1.597)	
Age	-0.512	(-0.532, -0.494)		-0.510	(-0.530, -0.49)	
Madeira	0.058	(-0.020, 0.141)		0.037	(-0.039, 0.116)	
Portugal	0.040	(-0.037, 0.128)		0.052	(-0.022, 0.128)	
Sex (male)	0.064	(0.026, 0.100)		0.067	(0.032, 0.105)	
AAC	-0.011	(-0.030, 0.011)		-0.014	(-0.037, 0.006)	
Age:Madeira	-0.065	(-0.108, -0.026)		-0.075	(-0.12, -0.031)	
Age:Portugal	-0.027	(-0.066, 0.015)		-0.020	(-0.062, 0.019)	
Madeira:Sex (male)	-0.104	(-0.189, -0.024)		-0.106	(-0.188, -0.025)	
Portugal:Sex (male)	-0.069	(-0.151, 0.006)		-0.072	(-0.147, 0.006)	
Madeira:AAC	-0.024	(-0.073, 0.023)		-0.022	(-0.075, 0.029)	
Portugal:AAC	0.056	(0.017, 0.093)		0.058	(0.020, 0.096)	
EAP	-	-		-0.093	(-0.129, -0.056)	
Temp	-	-		0.011	(-0.015, 0.036)	
Age:Temp	-	-		-0.003	(-0.014, 0.008)	
Madeira:Temp	-	-		0.053	(0.002, 0.106)	
Portugal:Temp	-	-		-0.018	(-0.055, 0.018)	
Age:Madeira:Temp	-	-		0.046	(0.008, 0.077)	
Age:Portugal:Temp	-	-		-0.013	(-0.037, 0.009)	

Table 3. Azores species model. Variance components and estimates of random and fixed effects of the optimal intrinsic and extrinsic species models describing rosefish and rockfish otolith growth in the Azores. SD = standard deviation, Corr. = Correlation, CI= confidence interval, EAP = East Atlantic pattern, NAO=North Atlantic Oscillation.

	Intrinsic species model			Extrinsic species model		
Random effects						
	Variance	SD	Corr.	Variance	SD	Corr.
FishID	0.079	0.281		0.082	0.286	
Age|FishID	0.033	0.182	0.65	0.036	0.191	0.64
Species:Year	0.005	0.072		0.002	0.048	
Residual	0.186	0.431		0.181	0.426	
Fixed effects						
	Estimate	(95% CI)		Estimate	(95% CI)	
Intercept	0.067	(0.016, 0.118)		0.069	(0.02, 0.123)	
Age	-0.772	(-0.799, -0.746)		-0.769	(-0.795, -0.741)	
Rockfish	-0.202	(-0.272, -0.132)		-0.225	(-0.3, -0.158)	
Sex (male)	0.101	(0.043, 0.159)		0.105	(0.041, 0.16)	
Age:Rockfish	-0.189	(-0.225, -0.152)		-0.2	(-0.237, -0.162)	
Rockfish:Sex (male)	-0.116	(-0.192, -0.04)		-0.126	(-0.195, -0.044)	
EAP	-	-	-	-0.098	(-0.149, -0.048)	
NAO	-	-	-	-0.004	(-0.034, 0.024)	
Age:EAP	-	-	-	-0.023	(-0.052, 0.006)	
Rockfish:EAP	-	-	-	0.161	(0.084, 0.24)	
Age:NAO	-	-	-	-0.038	(-0.055, -0.022)	
Age:Rockfish:EAP	-	-	-	0.111	(0.071, 0.151)	