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Temperature-Driven Growth Variation in a Deep-Sea Fish: The Case of *Pagellus bogaraveo* (Brünnich, 1768) in the Azores Archipelago

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The deep ocean ecosystem hosts high biodiversity and plays a critical role for humans through the ecosystem services it provides, such as fisheries and climate regulation. However, high longevity, late reproduction, and low fecundity of many organisms living in the deep ocean make them particularly vulnerable to fishing and climate change. A better understanding of how exploitation and changing environmental conditions affect life-history parameters (e.g., growth) of commercially important fish species is crucial for their long-term sustainable management. To this end, we used otolith increment widths and a mixed-effects modeling approach to develop a 42-year growth chronology (1975–2016) of the commercially important deep-sea fish species blackspot seabream (*Pagellus bogaraveo*) among the three island groups of the Azores archipelago (Northeast Atlantic). Growth was related to intrinsic (age and age-at-capture) and extrinsic factors (capture location, temperature-at-depth, North Atlantic Oscillation (NAO), Eastern Atlantic Pattern (EAP), and proxy for exploitation (landings)). Over the four decades analyzed, annual growth patterns varied among the three island groups. Overall, temperature-at-depth was the best predictor of growth, with warmer water associated with slower growth, likely reflecting physiological conditions and food availability. Average population growth response to temperature was separated into among-individual variation and within-individual variation. The significant among-individual growth response to temperature was likely related to different individual-specific past experiences. Our results suggested that rising ocean temperature may have important repercussions on growth, and consequently on blackspot seabream fishery production. Identifying drivers of blackspot seabream growth variation can improve our understanding of past and present condition of the populations toward the sustainable management of the fishery.

Keywords: environmental change, mixed-effects modeling, otolith, blackspot seabream, reaction norms, sclerochronology

INTRODUCTION

The deep ocean, below 200 m depth, hosts ecosystems of high biodiversity and plays a critical role for humans through the services it provides, such as fisheries (Van den Hove and Moreau, 2007; Thurber et al., 2014). Currently, seafood from the deep ocean is estimated to fall by as much as half in the next 100 years, mainly due to resource exploitation and impacts of climate change (Sweetman et al., 2017). Global environmental change and exploitation can have major consequences on marine ecosystems, including demographic and evolutionary changes in exploited populations, distribution range shifts, altered phenology, and marine productivity (e.g., Edwards et al., 2004; Cheung et al., 2010; Perry et al., 2014; Audzijonyte et al., 2016; Tu et al., 2018). The effects of these changes on ecosystems depend on species sensitivities, ecological functions and processes, and spatial scales that in turn make it difficult to detect and identify the species' biological responses (Brown et al., 2010; Poloczanska et al., 2016).

For a better understanding of the fundamental mechanisms responsible for biological responses to environmental change, long-term biological data (continuous information, collected and archived over time) with the appropriate spatial-temporal resolution are needed. Such data can provide valuable and robust information on marine ecosystem changes and allow exploring species growth responses to environmental changes and exploitation, concerning their habitat, life history, and potential of adaptation (Thresher et al., 2007; Shelton et al., 2013; Coulson et al., 2014; Martino et al., 2019). Unfortunately, especially for deep-sea species, long-term data sets are scarce, however, samples containing valuable long-term information on growth variation are readily available from fish otoliths (Campana and Thorrold, 2001). These structures contain growth information, that allows the development of chronologies based on the variation in their growth increment widths and thus are a useful tool for understanding the effects of different extrinsic drivers on growth (Morrongiello et al., 2012, 2019; Matta et al., 2018). Since environmental variables generally play a key role in driving growth variation and population dynamics in aquatic organisms (Morrongiello et al., 2012), this biochronological approach also allows the prediction of species' responses to future climate change (Rountrey et al., 2014; Barrow et al., 2018).

Otolith increment-based growth chronologies have been successfully developed using linear mixed-effects models that allow analyzing intrinsic effects, such as age and age-at-capture, simultaneously with potential extrinsic sources of variation, including environmental drivers (e.g., temperature, SST, ENSO) (Weisberg et al., 2010; Helser et al., 2012; Rountrey et al., 2014; Morrongiello and Thresher, 2015). Furthermore, mixed-effect models allow the decomposition of population-level variation into its within- and among-individual components, and the inclusion of individual reaction norms allows exploring phenotypic plasticity that can provide valuable information about the adaptive potential of populations to deal with future environmental and exploitation changes (van de Pol and Wright, 2009; Morrongiello and Thresher, 2015; Fox et al., 2019). A better understanding of population resilience, adaptive potential, and individual phenotypic plasticity is key for deep-sea fish species as they are known to be vulnerable to changing environment and exploitation due to their high longevity, late reproduction, and low fecundity (Cheung, 2007; Thresher et al., 2007).

In this context, this work investigates long-term growth patterns of a deep-sea fish in the Azores archipelago (Northeast Atlantic), the blackspot seabream (*Pagellus bogaraveo*), a commercially highly valuable species with a complex life history (Pinho and Menezes, 2006; Higgins et al., 2015). Blackspot seabream is a protandrous hermaphrodite (Krug, 1990) that presents ontogenetic migrations, moving from island coastal waters to deeper island slopes or offshore seamounts (Menezes et al., 2006; Afonso et al., 2012) and exhibiting complex individual spatial behavior (Afonso et al., 2012, 2014). The complex life history characteristics of this species (i.e., protandrous hermaphroditism and late maturity of females) make it highly sensitive to overfishing and climatic changes (Lorance, 2011; Gutiérrez-Estrada et al., 2017; Sanz-Fernández and Gutiérrez-Estrada, 2021).

Using archived otoliths of adult blackspot seabream collected in the three island groups of the Azores archipelago, this study aimed to evaluate how growth is affected by intrinsic (age-related variables) and extrinsic factors (environmental and fisheries-related variables) and to detect possible growth differences between island groups. The extrinsic factors driving growth variation were further investigated to estimate their importance in individual growth responses.

MATERIALS AND METHODS

Area and Study Species

Azores archipelago has been selected as study area (**Figure 1** and **Table 1**), which is part of the Macaronesian biogeographical region, located in the Northeast Atlantic Ocean (Friedlander et al., 2017). The Azores marine ecosystem has been defined as oceanic (Pinho and Menezes, 2009) characterized by an abundant abyssal area, narrow or absent coastal platform, pronounced slopes, and the existence of banks and seamounts (Menezes et al., 2013). The selected species, *P. bogaraveo* (Brünnich, 1768; blackspot seabream), is a deep-water sparid commonly found at depths of 100–600 m, both around coastal areas of the islands and offshore seamounts (Menezes et al., 2006; Pinho et al., 2014). Small individuals (<13 cm furcal length (FL)) live preferentially in coastal areas and shallow waters (nursery areas), pre-adults (<30 cm FL) in intermediate zones and larger individuals live at island slopes or offshore banks and deeper waters (Stockley et al., 2005; Pinho et al., 2014; Higgins et al., 2015).

This species is a protandric hermaphrodite with primary females (females at birth, not changing sex during the life cycle), and males who can change sex during their life cycle, before maturity (*c.* 5 and 8 years of age, at around 28.2 and 33.9 cm FL, for males and females, respectively (Krug, 1998)). The

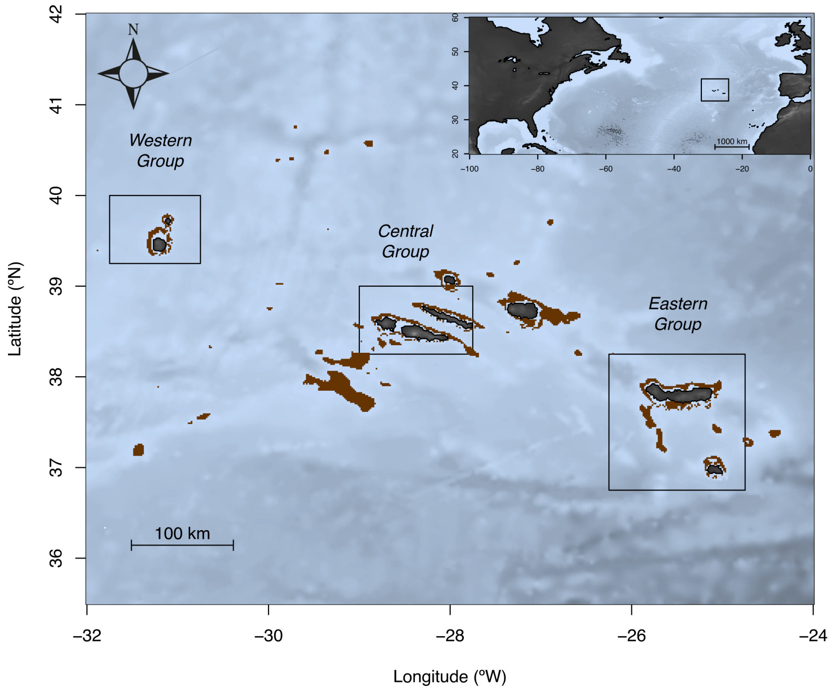

FIGURE 1 | Sampling locations map of *Pagellus bogaraveo* in the Azores. Boxes in each sampling location indicate areas for which temperature-at-depth was obtained. Brown areas represent the depth range where the species generally occurs.

maximum documented age and length are 15 years and 65 cm FL, respectively (Krug, 1989; Menezes et al., 2001).

Fish and Otolith Sampling

The otoliths of *P. bogaraveo* used in this study, archived at the Department of Oceanography and Fisheries (DOP) of the University of the Azores, located in Horta, Faial island, were collected during the annual monitoring surveys of demersal and deep-water fish abundance -ARQDAÇO surveys (e.g., Melo et al., 2003, 2004; Rosa et al., 2017), conducted between 1995 and 2017, aboard the R/V Arquipélago. These surveys follow a stratified random sampling and use long-line gear, similar to those used by the local demersal fishing fleet, to sample island slopes and seamounts in the Azores (for methodological details see Menezes et al., 2006). Data on fishing effort and catches by species, and samples (length, sex, gonadal maturation stage, otoliths) are regularly collected.

TABLE 1 | Summary of *Pagellus bogaraveo* samples used in the study.

Island group	N fish	N increments	Furcal length range (cm)	Fish age range (year)
East	90	1170	30–52	6–21
Central	196	2547	30–53	6–21
West	240	3699	30–51	7–28
Total	526	7416		

N fish = number of individuals, N increments = number of otolith increments measured.

For this study, adult female individuals sampled at island slopes were used. Selected individuals were aggregated by island groups (Eastern - São Miguel and Santa Maria islands; Central – Faial, Pico, and São Jorge islands; Western - Flores and Corvo islands) (**Figure 1**). Whenever possible, depending on sample availability, a similar number of individuals per capture year covering similar range of furcal length was selected (**Supplementary Table 1**).

Otolith Reading and Annual Growth Estimation/Increment Measurement

A total of 526 sagittal otolith pairs from fish ranging from 30 to 53 cm FL were selected (**Supplementary Table 1**). Otoliths were immersed in ethanol 72%, preferentially the left otolith was used, and immediately viewed through a Leica MZ16FA stereoscope to guarantee high quality increment visualization, and pictures were taken using a Leica MC190HD camera under reflected light against a dark background, and magnification between 7.11 and 24×. Annual growth increments or annuli were defined as consisting of one opaque and one translucent growth zone (Matta et al., 2018). Annuli were counted and measured using ImageJ software (version 1.52) with ObjectJ plugin (version 1.04) along an axis from the nucleus to the post-rostrum edge (Tanner et al., 2020). Increment measurements were marked at the border of each fully formed opaque growth zone. All otoliths were read twice by the same reader and only estimates with equal readings were included for further analysis.

The birth date of this species was assumed to be the 1st of January (Krug, 1989; Chilari et al., 2006). Due to the uncertainty that the first year of growth corresponds to a full year, measurements of the first increment were not included in the analysis (Morrongiello and Thresher, 2015; Tanner et al., 2020). Additionally, only increments up to age 20 were included in the data analysis to standardize the maximum age among island groups. 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 island group, this assumption was tested and confirmed in a subset of individuals ($N = 75$ individuals/location; Eastern: adjusted $R^2 = 0.692$, slope = 7.21; Central: adjusted $R^2 = 0.681$, slope = 6.38; Western: adjusted $R^2 = 0.639$, slope = 5.94, all $p < 0.0001$) (**Supplementary Figure 1**).

Data Analysis

Inter-annual variation in the width of otolith growth increments was used as a proxy of somatic growth of blackspot seabream, and linear mixed-effects models were used to partition variance in otolith growth increment widths among intrinsic (age-related) and extrinsic (environmental-related and fishery-related) sources of growth variation using a statistical framework based on Morrongiello and Thresher (2015). Fixed effects (e.g., Age, Age at capture, Year, Temperature, and Abundance) describe the entire population and random effects (e.g., FishID, Cohort, and Area) are associated with randomly selected experimental units within the population (Morrongiello and Thresher, 2015; Lee and Punt, 2018). This approach explicitly quantifies age-related growth patterns and allows the exploration of environmental responses, thus making it the best approach for analyzing these hierarchical time series (otolith growth data). Increments were log-transformed to meet assumptions of normality and homoscedasticity, and both intrinsic and extrinsic predictor variables were mean-centered to facilitate model convergence and interpretation of interaction terms (Morrongiello et al., 2014).

Intrinsic Effects on Growth

A series of linear mixed-effect models with increased complexity, which included fixed intrinsic covariates and a series of random effects structures, were developed, and compared to determine the best baseline model describing fish otolith growth (**Supplementary Table 2**). First, the best random-effects model with a complete fixed-effect structure was determined for the data set. The random effect structures applied included random intercepts for individual fish ("FishID"), year of otolith increment formation ("Year"), and birth year ("Cohort"), to allow for correlations among growth increments within individual fish, calendar year and year class. Random "Age" slopes were also investigated for these covariates thus allowing individuals to have age-related growth trajectories. The capture location of the specimen ("IslandGroup") was always included in combination with "Year" and "Cohort," allowing for island group-specific year or cohort growth responses. The best random-effects model was then used to select the appropriate fixed-effect structure. Optimized fixed effects included the intrinsic (i.e., internal to the individual) terms "Age" and "Age at capture" (**Supplementary Table 3**) in interaction with the island group (**Supplementary Table 2**) which accounted for age-specific effects on growth that can vary between capture locations and location-specific differences in potential sampling bias 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, 2002). Variance in otolith growth explained by the combined fixed and random effects were calculated by the conditional R2 metric (Nakagawa and Schielzeth, 2013). 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). The selected model with the best structure of intrinsic fixed effects was then extended in a stepwise procedure to determine if the addition of extrinsic fixed factors could further improve the model fit.

Extrinsic Variables Effects on Growth

Blackspot seabream growth variation was related to a series of extrinsic variables (i.e., environmental and exploitation) that potentially explain inter-annual variation in otolith growth (**Supplementary Table 3**). Monthly data of water temperature-at-depth in the approximate areas of fish sampling were obtained from Simple Ocean Data Assimilation (SODA3) reanalysis, version 3.4.2 (Carton et al., 2018). Based on the species' preferential depth distribution (100–600 m depth) (Menezes et al., 2006), depth levels between 98 and 618 m were selected. Both climatic indices, North Atlantic Oscillation (NAO) and Eastern Atlantic Pattern (EAP) were obtained from the NOAA Climate Prediction Center[1] since these large-scale phenomena can affect the local climate and flow of regional sea currents in the Azores and consequently the species dynamics (e.g., spatial distribution, reproduction, behavior, and feeding) (Pinho et al., 2011). Moreover, and specifically for *P. bogaraveo*, a lower abundance in the period 2010–2011 was associated with the negative phase of NAO during this period (Pinho et al., 2011). To explore potential fishery-dependent influences on growth variation, fish landings (tonnes) were used as a proxy for exploitation. Official data on landings were obtained from the public company managing Azores fish auction houses (Lotaçor S.A.). Data on temperature, NAO, EAP, and fishery proxy were available over the entire period of the chronologies (1975–2016) and so these four extrinsic variables were included in the optimized intrinsic model, using seasonal averages, and their influence was evaluated. Pairwise correlations among extrinsic variables were calculated (Pearson coefficient) and only variables with correlations <0.5 were simultaneously included as fixed effects into the models.

Average Thermal Reaction Norms

Within-subject centering was used to determine if the average population growth-temperature relationship and variation were driven by within-individual (representing evolutionary-fixed

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[1] http://www.cpc.ncep.noaa.gov

phenotypically plastic responses) or among-individual effects (representing individual differences in temperature response) (van de Pol and Wright, 2009; Morrongiello and Thresher, 2015; Martino et al., 2019; Morrongiello et al., 2019). This approach provides an estimate of the average growth phenotypic plasticity present within an individual (within-individual) and an estimate of how growth systematically varies across average lifetime conditions (among-individual) (Martino et al., 2019). For this purpose, two new variables were calculated, the average temperature experienced by each individual over its lifetime and the deviation of annual temperatures from this mean. The original temperature variable was replaced with the two new variables and resulting models were compared with the optimal extrinsic model using AICc (**Supplementary Table 4**). Differences in within-individual and among-individual effects were derived by replacing the within-individual term with the original temperature effect. The selected model also included a random within-individual reaction norm slope on FishID, representing the individual-specific differences in within-individual temperature slopes (Morrongiello and Thresher, 2015; **Supplementary Table 4**).

All analyses were conducted in R 3.6.1 (R Core Team, 2018) using the packages lme4 (Bates et al., 2014) for the linear mixed models.

RESULTS

Blackspot seabream otolith growth chronologies spanned 42 years, from 1975 to 2016 (**Supplementary Figure 2** and **Supplementary Table 1**). The individuals used in this study were aged between 6 and 28 years, and on average, the age at capture was 14.1 years (**Supplementary Table 1**). For a similar length range, the Western island group presented the oldest individuals (**Table 1**).

Intrinsic Effects

The optimal intrinsic random effect model contained a random intercept for FishID and IslandGroup:Year, and a random Age slope for FishID. For the fixed effects, the inclusion of Age and Age-at-capture as fixed effect terms was supported, both with IslandGroup interaction (**Table 2**). The otolith-derived growth chronologies for all island groups showed considerable inter-annual variation, with below and above average years of growth. The inter-annual variation pattern varied between locations, without a clear trend in any of the locations (**Figure 2**). Average growth in all locations declined with age (**Figure 3A**). Slight differences in age-related growth patterns of *P. bogaraveo* were observed among the three locations. Individuals from the Western island group showed the highest growth rate at the youngest age, whilst the growth rate at an older age in these individuals was lower than in the remaining groups (**Figure 3A**). For the Eastern group, a negative relationship between annual growth and Age-at-capture was identified, with individuals captured at younger age presenting higher growth rates than individuals captured at an older age (**Figure 3B**). On the other hand, no relationship between growth and Age-at-capture was found for the other islands' groups (**Figure 3B**).

Extrinsic Variables Effects

Seasonal means of temperature-at-depth, NAO, EAP, and annual landings were added to the optimized intrinsic model. All these environmental variables were included simultaneously in the model, except for seasonal temperature estimates which were included separately due to the high correlation among means. Average winter temperature-at-depth was the only variable included in the final extrinsic model (**Table 2**). Overall, winter temperature had a negative effect on blackspot seabream growth (**Figure 3C**). Average winter temperature-at-depth was higher in the Western island group compared to the Central and Eastern groups (**Supplementary Figure 3**), however, these differences did not affect the overall response of growth in the different island groups.

Within Versus Among Individual Growth Variation

Average population growth response to winter temperature was separated into among-individual variation (representing facultative environmental responses) and within-individual variation (representing evolutionary-fixed, phenotypically plastic responses). We found significant among-individual growth response to temperature while the within-individual variation was weakly negative (**Figure 4**). The inclusion of within-individual temperature random slopes improved the model. Still, the effect was minimal, with high variation in individual response.

DISCUSSION

Otolith chronologies from this study reconstructed fish growth over 40 years based on individuals ranging from 6 to 28 years of age. We documented differences in inter-annual growth variation of blackspot seabream populations among the Azores island groups. These differences in growth patterns may be partly related to regional differences in habitat, oceanographic conditions, and exploitation patterns, which are known to induce fluctuations in populations dynamics (e.g., Cheal et al., 2007; Powney et al., 2010; Frank et al., 2016). Environmental seabed characteristics in the Azores archipelago show a clear dissimilarity between the Western island and the other two island groups (Amorim et al., 2017), likely related to the topographic discontinuity caused by the Mid-Atlantic Ridge and the associated oceanographic transition zone. This discontinuity may act as an ecological barrier potentially isolating western island fish populations relative to the central-eastern groups' populations (e.g., Fontes et al., 2009) and may contribute to the distinct blackspot seabream growth patterns observed. On the other hand, regional-scale fishing pressure has varied among island groups over the last decades, with the Eastern island group subject to greater fishing pressure during the 1980s (Diogo et al., 2015), potentially adding further to the inter-island group growth variation documented.

TABLE 2 | Final *Pagellus bogaraveo* otolith growth model, with selected extrinsic fixed effects in bold.

	Intrinsic model			Extrinsic model		
Random effects	**Variance**	**SD**	**Correlation**	**Variance**	**SD**	**Correlation**
FishID	0.0237	0.1541		0.0236	0.1537	
Age| FishID	0.0257	0.1602	0.86	0.0257	0.1602	0.86
IslandGroup:Year	0.0004	0.0209		0.0004	0.0215	
Residuals	0.0495	0.2225		0.0495	0.2224	
Fixed effects	**Estimate**	**(95% CI)**		**Estimate**	**(95% CI)**	
Intercept	−1.3991	(−1.427, −1.372)		−1.4051	(−1.433, −1.377)	
Age	−0.8539	(−0.882, −0.826)		−0.8511	(−0.880, −0.823)	
IslandGroup_east	0.0078	(−0.039, 0.055)		0.0033	(−0.044, 0.051)	
IslandGroup_west	−0.0514	(−0.087, −0.016)		−0.0385	(−0.077, −0.001)	
Age-at-capture	−0.0011	(−0.007, 0.005)		−0.0017	(−0.008, 0.004)	
Age:IslandGroup_east	−0.0067	(−0.058, 0.044)		−0.0083	(−0.059, 0.043)	
Age:IslandGroup_west	−0.0718	(−0.109, −0.034)		−0.0731	(−0.111, −0.035)	
Age-at-capture:IslandGroup_east	−0.0104	(−0.020, −0.001)		−0.0100	(−0.019, −0.001)	
Age-at-capture:IslandGroup_west	0.0026	(−0.005, 0.010)		0.0028	(−0.005, 0.010)	
Temp_winter	–	–		**−0.0236**	**(−0.047, −0.0004)**	
				Reaction Norm		
				Estimate	**(95% CI)**	
Within-individual “Temp_winter” effect				−0.0164	(−0.042, 0.009)	
Among-individual “Temp_winter” effect				−0.0867	(−0.162, −0.012)	

Variance components and estimates of random and fixed effects of the optimal intrinsic and extrinsic models, and reaction norms, describing otolith growth in the three sampling locations.
Definitions of random and fixed effects are available in ***Supplementary Table 3****.*
Among-individual = coefficient for individuals’ average lifetime “Temp_winter” experienced; quantifies systematic among- individual differences in temperature response.
Within-individual = coefficient for individual-specific annual deviations from Among-individual; quantifies the average within-individual phenotypic plasticity in thermal reaction norms.
SD = standard deviation, CI = Confidence interval, Temp_winter = average temperature of winter (January–March) at 98–618 m depth.

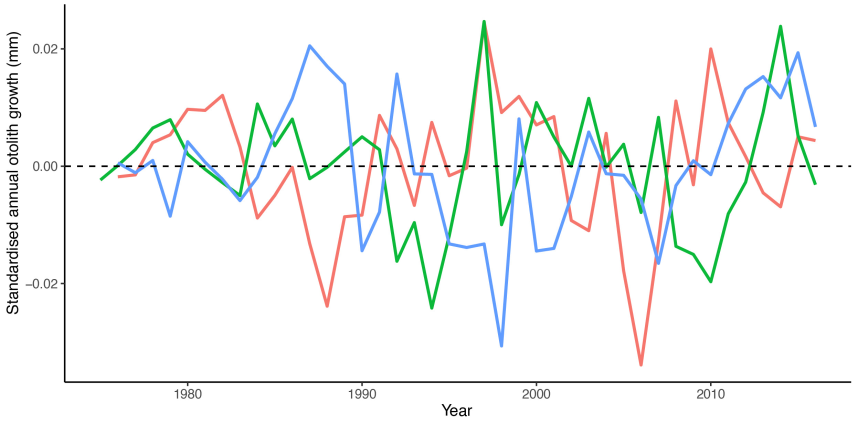

FIGURE 2 | *Pagellus bogaraveo* predicted variations in annual otolith growth collected in Western (blue), Central (red), and Eastern (green) island groups.

Age was the best predictor of growth, with growth decreasing with age. Otolith growth was considered a proxy for somatic growth, a widely accepted assumption (Matta et al., 2018; Martino et al., 2019; Tanner et al., 2019, 2020). This relationship and the age-at-length relationship have previously been validated for blackspot seabream (Krug, 1989, 1998; Chilari et al., 2006; Higgins et al., 2015). In our study, this relationship is less robust in older specimens, which contributed with the oldest individuals to this study. Length-at-age and maximum age determined in this study differed from those previously documented for the region (Krug, 1989; Menezes et al., 2001). These differences may be attributed to the fact that the previous works were elaborated

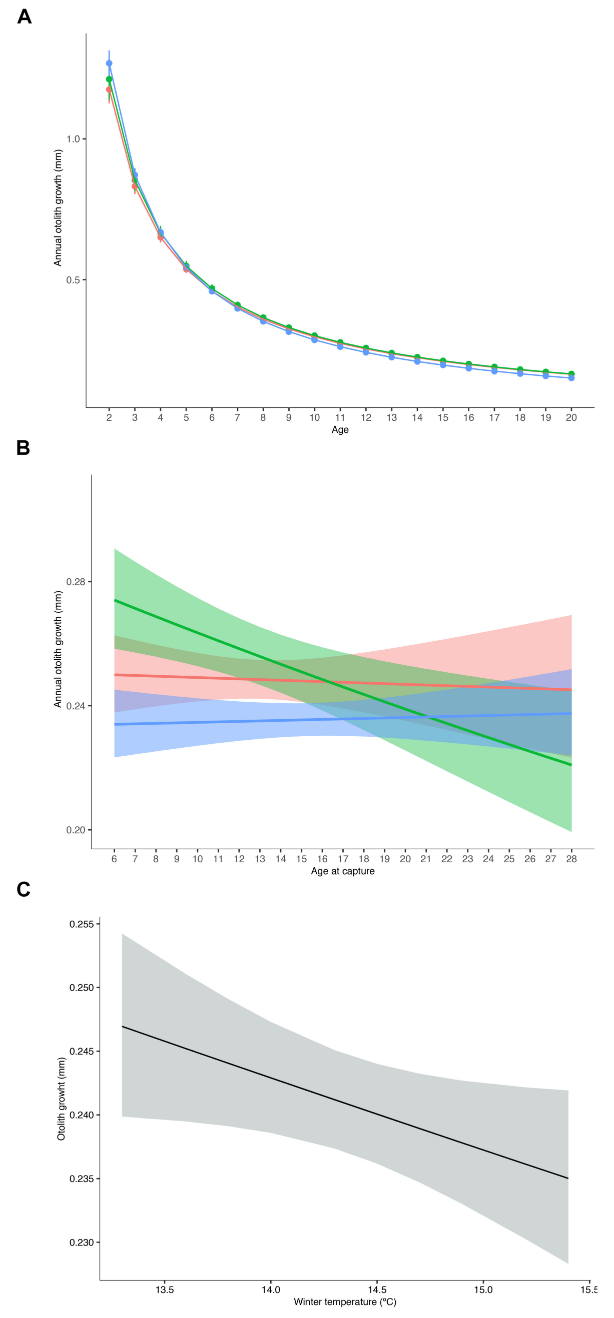

FIGURE 3 | Annual mean otolith increments from Western (blue), Central (red), and Eastern (green) island groups by **(A)** age and **(B)** Age-at-capture; and **(C)** overall effect of average winter temperature (January–March) at depth (98–618 m) on *Pagellus bogaraveo* otolith growth. Vertical lines in **(A)** and shaded areas in **(B,C)** denote ±95% CI.

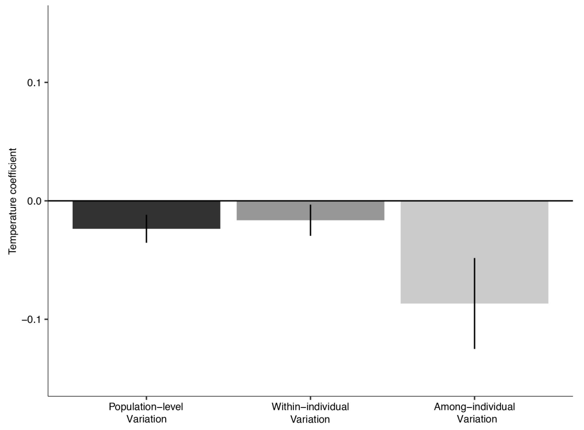

FIGURE 4 | Winter temperature-related population-level variation, compared with within-individual (representing evolutionary-fixed phenotypically plastic responses), and among-individual (representing facultative environmental responses) variations.

more than 20 years ago using different techniques and resolutions which likely led to distinct age determinations.

Regarding the Age-at-capture and annual growth relationship, significant differences were evident among the capture locations (island groups). Unequivocally in the Eastern group, a negative relationship between annual growth and Age-at-capture was identified, differentiating this group from the others. Individuals captured at a younger age presented higher growth rates than individuals captured at an older age. There are several possible explanations for the negative relationship between Age-at-capture and growth, such as life history trade-offs between growth rate, sexual maturity, and longevity; or higher vulnerability of fast growers to fishery activities (see e.g., Morrongiello and Thresher, 2015). For blackspot seabream from the Eastern island group, a fisheries-related mechanism appears to be the most plausible explanation since this group was subject to the highest exploitation rates in the archipelago resulting in local depletion of fish stocks (Diogo et al., 2015). Fast growers may be more vulnerable as they recruit to the fisheries earlier, or even showing a bolder behavior and consequently making them more vulnerable to fishing (Morrongiello and Thresher, 2015). Also, in fish populations under high fishing pressure, smaller fish tend to mature earlier, as a response to long-term, size-selective harvesting that removes the larger and faster-growing fish (Browman et al., 2000; Ernande et al., 2004; Olsen et al., 2009; Martino et al., 2019). Krug (1998) observed that female blackspot seabream matured at earlier ages and smaller size over a 10-year period which may have been a first indication of the effects of fishing pressure, environmental change, or an interaction of these factors on this species' growth in the Azores. The presence of slow-growing individuals and the occurrence of the oldest individuals for the same length range in the Western island group may be the result of differential fishing pressure among island groups (Diogo et al., 2015). The relationship between growth and fishing pressure was formally explored in our model using as a proxy for exploitation, landings of blackspot seabream, the only exploitation-related variable available for the entire range of the chronology. However, this variable was not significant and consequently not included in the final model, which may be an indication of the lack of suitability of this proxy.

We identified temperature-at-depth during winter as the best predictor of growth across all locations, with higher values influencing the annual growth negatively. Water temperature may affect fish growth directly by influencing metabolism within the species-specific thermal optimum or indirectly by modulating other environmental variables such as dissolved oxygen concentration or food availability (Dutta, 1994; Pörtner and Farrell, 2008; Massie et al., 2020). Warmer winters in deep waters may lead to decreased dissolved oxygen concentration and higher metabolic rates, which require more energy (food) and oxygen (Pauly and Cheung, 2018). Physiological capacity disturbance, related to temperature and oxygen variations, can alter not only the growth but also affect other vital functions such as maturation or reproduction (Pörtner and Knust, 2007; Pauly, 2021). In the Azores archipelago, the reproduction of blackspot seabream occurs during the winter months (Krug, 1998; Estácio et al., 2001), coinciding with the temperature-at-depth used in our model, that negatively influenced somatic growth. The negative effect of warmer water on fish growth is expected in the context of Gill-oxygen limitation theory that states that lower relative oxygen supply induces sexual maturation and promotes a slowing of growth (Pauly, 2019a,b, 2021). Following this theory, blackspot seabream may invest more energy in reproduction and spawning, depriving the somatic growth, during winter periods with warmer water temperatures and potentially reduced oxygen availability, leading to the observed negative effect on growth. Temperature can also influence food availability which has been shown to play a considerable role in fish growth rates (Jones, 1986; Dutta, 1994; Anderson and Sabado, 1995; Cominassi et al., 2020). In the Azores archipelago, seasonal maximums of sea surface temperature (SST) have been shown to coincide with seasonal lows of chlorophyll (Caldeira and Reis, 2017), and winter temperature-at-depth during the study period were positively correlated with winter SST ($r_{(df = 109)} = 0.38$, $p < 0.001$). Thus, warmer winters may result in lower primary productivity with potential effects on higher levels in the food chain. It has been previously recognized that the energy transfer rate from phytoplankton to mesopelagic fishes in oligotrophic regions (such as the Azores) is high, linking fishes' biomass and primary production (Irigoien et al., 2014). Since mesopelagic fish (myctophids) and invertebrates are the main components in the diet of blackspot seabream (Morato et al., 2001) warmer winter resulting in lower primary production may lead to less food availability and energy intake, impacting growth negatively.

In addition to environmental and oceanographic factors, the genotype and physiological condition of the individual may also regulate growth (Dutta, 1994), and can promote different growth rates at the individual level. Exploring among-individual variation and individual thermal responses is particularly interesting in species with complex life histories, such as *P. bogaraveo* (Higgins et al., 2015), since these components differ in their evolutionary and ecological implications and thus may allow a better understanding of the species' ability to respond to global change (Brommer et al., 2008). In this study, we found a negative among-individual variation in thermal response. Among-individual variation may result from genetic differences and individual-specific past experiences or a combination of both (Morrongiello and Thresher, 2015; Martino et al., 2019). For blackspot seabream, possible individual past experiences giving rise to among-individual variations in thermal response may be related to complex individual spatial feeding behavior, that includes vertical and horizontal migrations (Afonso et al., 2012, 2014). As a consequence of genetic differences, it has been proposed that slower-growing individuals will be favored through long-term adaptation to higher temperatures (Martino et al., 2019). For blackspot seabream, such a genetic adaptation may also be possible although among-individual thermal responses were consistent for the three island groups. Furthermore, genetic differentiation in blackspot seabream in the Azores archipelago is low although a restriction of gene flow between the Western island group and the rest of the archipelago has been suggested (Stockley et al., 2005).

Our results showed differing growth patterns among Azorean island groups, with an overall negative temperature-at-depth effect on blackspot seabream growth which likely acted as an indirect factor affecting physiological condition, reproduction, and food availability. Also, the partitioning of the thermal population-level response into among-individual and within-individual variation is likely related to different individual-specific past experiences of blackspot seabream. Identifying drivers of blackspot seabream growth variation can promote an improved understanding of the present condition of the populations which represents essential information for the sustainable management of the fishery considering the future environmental change. In fact, the observed negative impact of warmer water on the growth of blackspot seabream may have important implications in the future as ocean temperature is forecasted to increase (Lyman et al., 2010) with potential repercussions for blackspot seabream fishery production. Thus, vulnerable species, such as blackspot seabream, may require more careful considerations in terms of management, and a better understanding of the factors involved in key life-history events. The long-term annually resolved growth information that can be derived from otoliths present significant potential to be used for this species from different locations, studying intra-regional differences in growth or even for other slow-growing species to obtain precise information on responses to biological and environmental effects. Considering the importance of age determination in fisheries assessment, long-term chronologies, such as developed in this study, can provide relevant contributions for the sustainable management of deep-sea resources.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

ST and EG conceived and designed the study and secured funding. JN contributed to the design of the study. JN, EG, and GM collected sample information and organized the database. JN performed the laboratory processing and sample preparation, collected, and analyzed the otolith images. JN and ST performed the statistical analysis. JN wrote the first draft of the manuscript. All authors revised the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.703820/full#supplementary-material

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