



Contrasting ontogenetic shifts in habitat and metabolism of three sympatric key deep-sea fishes

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ABSTRACT: Many coastal fish species undergo ontogenetic shifts, but comparable knowledge for most exploited deep-sea fishes and their habitat use is lacking. We use otolith stable isotope analysis (SIA) to hindcast experienced temperature, depth, and field metabolic rate of 3 ecologically and commercially important deep-sea fishes from the Azores, mid-north Atlantic. Otoliths of bluemouth rockfish *Helicolenus dactylopterus*, Atlantic wreckfish *Polyprion americanus*, and black-spot seabream *Pagellus bogaraveo* were analysed to determine the stable isotope composition of carbon and oxygen in aragonite at core, mid and edge of otoliths. Oxygen SIA thermometry was used to infer water temperatures and depths, and carbon isotopes were used to derive individual field metabolic rate at each section. We identified sharp ontogenetic and interspecific differences in temperature, depth, and metabolism: juvenile rockfish inhabited intermediate depths before shifting to deeper waters as sub-adults; wreckfish occupied shallow waters before an abrupt ontogenetic shift to deep waters at maturity; juvenile seabream recorded the warmest temperatures, before gradually shifting to deeper waters as they grow. The mass-specific metabolic rates declined expectedly across all 3 species as individuals grew and occupied deeper and colder environments. Rockfish revealed the highest metabolic rates at low temperatures while in wreckfish, allometric scaling exponents for the whole organism field metabolic rate were comparatively low, potentially associated with changes in activity levels associated with ontogenetic depth changes. The thermal and metabolic differences throughout the ontogeny between the species illustrate the diversity of life cycles in deep-sea fishes and the relevance of integrating these into multispecies fisheries management.

KEY WORDS: Incremental tissue · Field metabolic rate · Retrospective environmental regimes · Demersal fish · Fish distribution

1. INTRODUCTION

In marine ecosystems, environmental conditions such as pressure, temperature, irradiance, and food availability vary drastically as depth increases. Consequently, physiological adaptations and life history characteristics of marine organisms change signifi-

cantly with depth (Mindel et al. 2016). For example, Drazen & Haedrich (2012) found a continuous decline in growth and fecundity with depth of occurrence of deep-sea fish. Additionally, many deep-sea teleosts rely on the dispersal of pelagic larval and juvenile stages prior to settling in deeper demersal habitats (Bradbury et al. 2008, Trueman et al. 2016). The tim-

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ing and extent of this shift from mesopelagic to benthic–demersal habitats can have reverberating consequences on the vulnerability of the species and trophic links between different ecosystems (see Trueman et al. 2014, Drazen & Sutton 2017). Thus, critical habitat-related life history characteristics such as depth distribution, habitat use, and metabolism are highly relevant.

Data-driven management and conservation measures are needed to ensure a sustainable future, as marine ecosystems face increasing anthropogenic pressures. Following the severe declines and collapse of coastal fish stocks as a result of overexploitation, industrial fisheries expanded to offshore and deeper environments (Watson & Morato 2013). To maintain profitable businesses and capitalize on increasing demand, fisheries relied progressively on subsidized exploitation of deep-sea and seamount stocks (Clark 2009, Norse et al. 2012). Concomitantly, mounting evidence of population declines has led scientists to question the sustainability of current deep-sea fisheries (Pitcher et al. 2010, Norse et al. 2012, Clark et al. 2016). To assure a more sustainable harvest of the marine resources, focus has been shifted to ecosystem-based management, in which scientific information on the respective ecosystems and species (such as habitat depth and growth, i.e. metabolism) is incorporated into the decision-making process. Large knowledge gaps remain in the life history characteristics and habitat use of most deep-sea fishes. As a result, links between different habitats through often contrasting ontogenetic shifts often remain oversimplified (Drazen & Haedrich 2012, Bergstad 2013), hampering sustainable management, especially in multispecies fisheries.

The Azores archipelago is located amidst the Mid-Atlantic ridge with an exclusive economic zone (EEZ) of over 1 million km², including over 450 seamount-like features. Here, open ocean, coastal, and deep-sea habitats and species exist in close proximity, offering a unique opportunity to study the ontogeny of deep-sea fishes. Rockfish *Helicolenus dactylopterus* Delaroche, 1809 (family Sebastidae), seabream *Pagellus bogaraveo* Brünnich, 1768 (family Sparidae) and wreckfish *Polyprion americanus* Bloch & Schneider, 1801 (family Polyprionidae) are the 3 main target species of the local demersal longline fisheries, representing over 20% of the commercial value of Azorean landings in the last 10 yr (LOTAÇOR - Serviço de Lotas dos Açores 2020). Adults of all 3 species are commonly caught close to the bottom at 300–600 m, yet studies indicate that the ecologies of earlier life stages and their ontogenetic shifts are highly divergent: Rockfish larvae develop in sub-surface pelagic

environments (Sobrinho-Gonçalves & Isidro 2001, Sequeira et al. 2011), whereafter juveniles grow in demersal habitats (although at shallower depths than adults) (Sequeira et al. 2012, Santos et al. 2020). Seabream larvae drift to the island coasts (Félix-Hackradt et al. 2013), where juveniles are expected to remain for approximately 1 yr before they recruit to demersal slope areas (Lorance 2011, Pinho et al. 2014). Wreckfish on the other hand, are presumed to spawn in the West Atlantic (Blake Plateau) (Sedberry et al. 1996, Ball et al. 2000), with larvae growing in the surface currents until they arrive in the Azores. Juveniles are then observed around floating objects in the epipelagic before shifting to demersal environments at an approximate size of 60 cm total length (TL) (Machias et al. 2003). The pronounced decline and even collapse of some of their fisheries in the Mediterranean and Atlantic (Lorance 2011) reiterates the necessity of a better understanding of the life cycles of these highly exploited yet very vulnerable deep-sea species. Ecosystem-based management requires information on life-long spatial ecology. For deep water species, the extent and timing of ontogenetic changes in depth distributions influence potential for catch and bycatch and may identify essential habitats, while data on metabolic rates can assist in parameterising bioenergetic models and predict physiological responses to future climates.

Stable isotope analysis (SIA) is a useful tool for aquatic ecology (Peterson & Fry 1987), in particular for the retroactive analysis of stable isotopes in incrementally grown tissues such as eye lenses or otoliths. These tissues are deposited in a time-resolved and metabolically inert manner and thus embody a detailed record of the organism's life. With declining costs of analysis with increased accuracy and precision, SIA has unlocked a variety of information encrypted in the otoliths. In otolith aragonite, oxygen stable isotopes primarily reveal the temperature experienced by the studied organism, while carbon isotopes can be used to infer the field metabolic rate expressed at that temperature (Campana 1999, Trueman et al. 2012a, 2016, Chung et al. 2019a). Using oxygen stable isotopes in inorganic carbonates as a proxy for temperature, allows hindcasting the depth inhabited by individuals as they migrate across vertical depth gradients (Shephard et al. 2007). The otolith oxygen isotope temperature proxy is based on well-studied thermal sensitivity of equilibrium fractionation of oxygen isotopes during precipitation of calcium carbonate polymorphs (Kalish 1991, Thorrold et al. 1997, Campana 1999, Trueman et al. 2012b). While seasonal and climate changes can lead to significant fluctuations in

stratification and water temperature in shallow waters, temperatures of deeper waters are comparatively stable below the thermocline. Otolith thermometry can therefore reveal information about the inhabited depth throughout the life cycle of deep-sea fish without tagging (see Trueman et al. 2013, Gerring et al. 2013).

An organism's metabolic rate is a measure of the expended energy per time unit and thus, in combination with other lines of evidence, provides information about energy partitioning, growth, and the species' role in an ecosystem. While laboratory tests can determine standard and maximum metabolic rates of captive fish, *in situ* measurement of the total energy expenditure of free-ranging animals — the field metabolic rate (FMR) — is more informative in an ecological context yet often difficult to obtain, especially for deep-sea species (Treberg et al. 2016). Deep-sea fishes present a particular challenge for experimental respirometry, and their estimates of metabolic rates are therefore commonly inferred from allometric relationships derived from experimental studies of shallow water species or even contrasting taxa. The isotopic composition of carbon in otolith aragonite can provide a measure of relative mass-specific metabolic rate. Carbon in otoliths is derived from 2 components: dissolved inorganic carbon (DIC) in the ambient seawater and carbon released from respiration of food (metabolic carbon) (Solomon et al. 2006, McConnaughey & Gillikin 2008). The proportion of metabolic carbon in the otolith increases as the rate of respiration of energy consumed increases, until respiration rates approach physiological limits (Sherwood & Rose 2003, Chung et al. 2019a). The isotopic composition of carbon in otolith aragonite therefore provides a measure of relative mass-specific metabolic rate. Until recently, the relationship between the relative otolith carbon and the absolute FMR remained unknown, but now experimental calibrations between otolith isotope-based FMR proxies and oxygen consumption rates determined from respirometry have been performed for cod (Chung et al. 2019b) and Australasian snapper (Martino et al. 2020). The otolith FMR proxy has since been applied to identify trends in metabolic rates in fish populations over time (Smoliński et al. 2021), to compare metabolic traits in sympatric populations (Chung et al. 2019b), to compare metabolic rates of myctophid fishes (Alewijns et al. 2021), and the thermal sensitivity of FMR has been used to predict future suitable habitats for tuna (Trueman et al. 2023).

Using oxygen stable isotopes as a proxy for temperature and metabolic rate, we aimed to investigate changes in depths and field metabolic rate along the ontogeny of 3 deep-sea fishes with contrasting eco-

logies (rockfish, seabream and wreckfish) and draw inferences about their divergent life-cycle adaptations.

This study provides new information about the timing and extent of the shift from pelagic to deeper demersal stages and quantifications of metabolism throughout these life stages, both having implications for spatial management and conservation strategies.

2. MATERIALS AND METHODS

2.1. Sample collection and preparation

Sampled individuals were caught during the annual demersal longline survey by the RV 'Arquipelago' in 1997 and 1999. All fish (rockfish $n = 12$, seabream $n = 10$ and wreckfish $n = 10$) were caught around Azorean seamounts at depths between 400 and 1100 m (see Fig. 1, Table 1). The sagittal otoliths were collected, cleaned mechanically to remove adhering tissue, and then stored in paper bags with the corresponding fish identification number. In the laboratory, the right otoliths were mounted in epoxy resin and sectioned longitudinally using a low-speed diamond precision cutter. Otolith sections were polished and age at capture determined assuming annual growth increments of the paired opaque and translucent annuli (*Helicolenus dactylopterus* [Abecasis et al. 2006]; *Pagellus bogaraveo* [Krug 1989]; *Polyprion americanus* [Peres & Haimovici 2004]).

2.2. Drilling and stable isotope analysis

Bulk stable isotope sample preparation and analysis was conducted in the Stable Isotope Mass Spectrometry Laboratory (SIRMS lab) of the University of Southampton following the methodology of Trueman et al. (2013). Otolith aragonite was sampled in 1 mm wide passes along growth rings using a Merchantek micromill (New Wave Research;) with a 1 mm diamond drill bit with a target mass of 30 μg . Where possible without overlapping of the drilling passes, 3 regions were sampled: around the nucleus, halfway to the edge, and at the edge. These otolith regions are hereafter referred to as core, middle, and edge regions, respectively. For the stable isotope analysis 100% phosphoric acid reacted with the aragonite powder at 70°C and, using CO_2 as a purification gas, was analysed by a GEO Instruments isotope ratio mass spectrometer (Sercon). The analytical errors were lower than 0.2 and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements, respectively, using repeated sampling of NBS-19 and in-

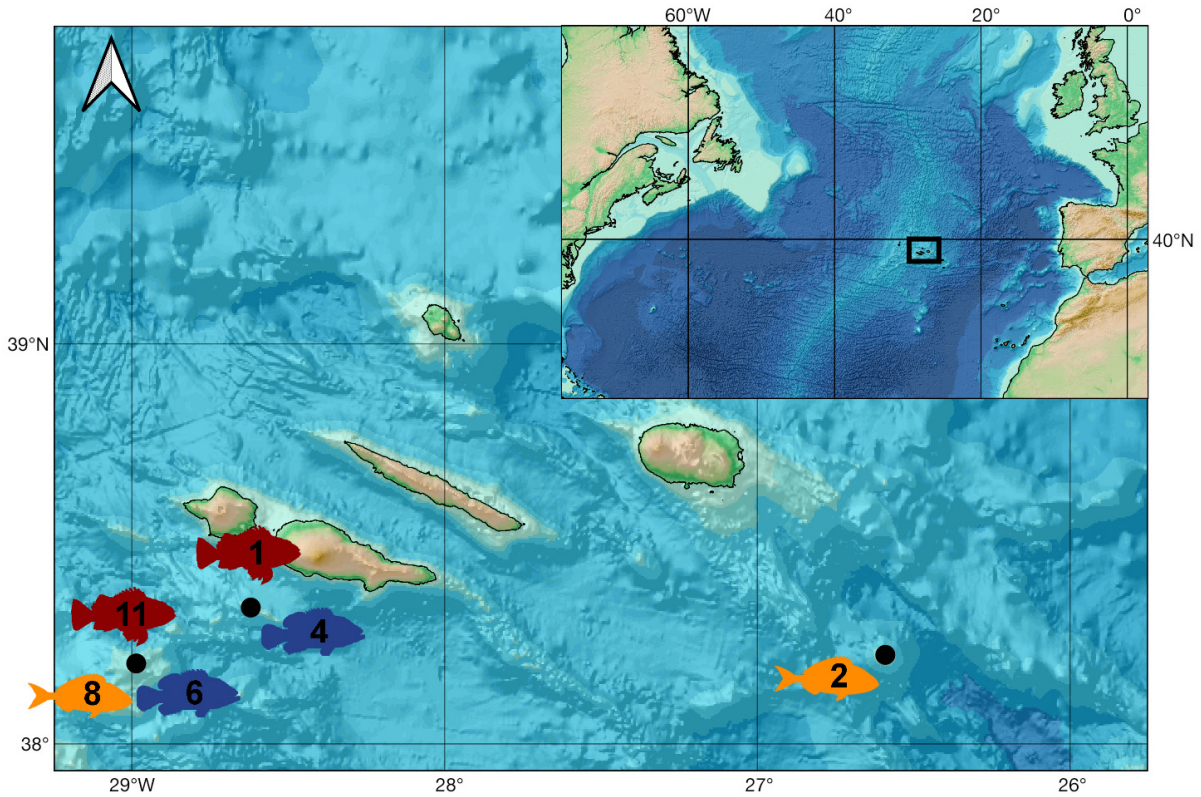


Fig. 1. Sampling locations (black points). Sample composition is denoted by numbers for each species (rockfish: red; wreckfish: blue; seabream: yellow) around the points. Map shades show General Bathymetric Chart of the Oceans (GEBCO) elevation data

Table 1. Sample count (M: male; F: female; HMF: hermaphrodite), with mean and range of size, age and capture depth of the study species individuals included in this study

	N (M:F:HMF)	Size mean (range) (cm)	Age mean (range) (yr)	Capture depth mean (range) (m)
Rockfish	12 (10:2:0)	34.6 (2341)	6.1 (38)	888 (8001 100)
Wreckfish	10 (6:4:0)	82.2 (73117)	13.4 (817)	441 (40 000)
Seabream	10 (1:6:3)	40.5 (3842)	9.8 (811)	705 (600 900)

house standards (Carrera marble). The resulting isotopic compositions of the samples are reported as δ values relative to international standards defined as:

$$\delta X (\text{‰}) = [(R_{\text{smp}} / R_{\text{std}}) - 1] \times 1000\text{‰} \quad (1)$$

where X stands for C or O and R represents the isotopic ratio of the sample (R_{smp}) and the standard (R_{std}).

2.3. Ecological context of otolith regions

To provide an ecological context for the sampled otolith regions, we back-calculated TL and age corresponding to the sampled regions of each fish (for

details about the applied equations see Table S1 in the Supplement; www.int-res.com/articles/suppl/m729p185_supp.pdf). Due to the absence of peer-reviewed back-calculation studies for wreckfish, the von Bertalanffy growth equation of Sedberry et al. (1999) was used to approximate the corresponding TL. As the otolith size at capture varied between specimen, the back-calculated sizes were then used to

identify outliers of each otolith region per species and thus assure comparable TLs within each region. Only 2 outliers were found for which the back-calculated TL from the edge region was the same as the TL from the middle regions of other specimens. The middle region isotope values were thus replaced with the edge region ones for these 2 individuals. Based on length at maturity values from the literature, the otolith regions of rockfish, wreckfish and seabream presented here represent young juveniles (core regions), premature juveniles and sub-adults (middle regions), and mature adults (edge regions) (Isidro 1987, Krug 1998, Peres & Klippel 2003).

2.4. Otolith thermometry and metabolism calculations

To calculate the temperature corresponding to the measured $\delta^{18}\text{O}$ of the otolith regions, the relationship established by Høie et al. (2004) was applied:

$$\delta^{18}\text{O}_{\text{Otolith(PBD)}} - \delta^{18}\text{O}_{\text{water(SMOW)}} = 3.90 (\pm 0.24) - 0.20 (\pm 0.019) \times T (\text{°C}) \quad (2)$$

where $\delta^{18}\text{O}_{\text{Otolith(PBD)}}$ is the measured otolith stable isotope ratio relative to the isotope standard Vienna PeeDee belemnite (VPDB); $\delta^{18}\text{O}_{\text{water(SMOW)}}$ the isotope ratio of sea water relative to standard mean ocean water (SMOW) and T is the temperature in °C. Due to the scarcity of water isotope studies in the study area, Eq. (3) (Craig & Gordon 1965) was used to estimate the $\delta^{18}\text{O}_{\text{water}}$ using local salinity (S) measurements.

$$\delta^{18}\text{O}_{\text{water}} = -21.2 + 0.61 \times S \quad (3)$$

To provide accurate thermometry calculations, section-dependent depth distribution data was used to derive environmental parameters for Eqs. (2) & (3). The back-calculated size ranges were used to compute the weighted mean depth distribution of each section for the 3 species using catch data from the annual Azorean bottom longline surveys between 1996 and 2019 following Pinho et al. (2020) (Table S1). Corresponding mean temperature and salinity values were calculated from 123 CTD casts in the Azores between 2010 and 2014.

As a proxy for metabolic activity, the ratio of metabolically derived carbon in the otolith aragonite (C_{resp}) was calculated using a 2-component mixing model (Schwarcz et al. 1998, Solomon et al. 2006):

$$\delta^{13}\text{C}_{\text{oto}} = C_{\text{resp}} \times \delta^{13}\text{C}_{\text{Diet}} + (1 - C_{\text{resp}}) \times \delta^{13}\text{C}_{\text{DIC}} + \varepsilon \quad (4)$$

where $\delta^{13}\text{C}_{\text{oto}}$ is the measured isotope ratio of the otolith, $\delta^{13}\text{C}_{\text{Diet}}$ the isotope ratio of prey organisms of the fish, $\delta^{13}\text{C}_{\text{DIC}}$ is the isotope ratio of dissolved inorganic carbon in ambient waters, and ε is the total isotope fractionation factor from ambient waters to otolith aragonite assumed to be not different from 0 (Solomon et al. 2006). Due to the absence of deep local DIC studies, the mean $\delta^{13}\text{C}_{\text{DIC}}$ values were calculated from data compiled by Becker et al. (2016) using 3 stations in the eastern proximity of the Azores. Section-dependent values were based on the mean depth values derived from the otolith thermometry (Table S1). Lipid corrected muscle mean $\delta^{13}\text{C}$ values and SD of the 3 study species were used as $\delta^{13}\text{C}_{\text{Diet}}$ ratios (see Solomon et al. 2006).

Following Chung et al. (2019b), the standard metabolic rate (SMR), was estimated from statistical allometric relationships as:

$$\text{SMR} = B_0 \times (\text{Body mass})^\alpha \times e^{-\frac{0.65}{(8.62 \times 10^{-5} \times (T_{\text{oto}}))}} \quad (5)$$

where B_0 is the normalised constant of 1.64×10^{13} determined for 79 species by Killen et al. (2010), alpha is the allometric mass-scaling exponent for mass-specific metabolic rate (a value of -0.1 was used; Clarke & Johnston 1999, White et al. 2006, Killen et al. 2010), and T_{oto} is the temperature calculated from $\delta^{18}\text{O}$ thermometry in Kelvin. This equation is based on 3 assumptions: a common, statistically derived metabolic level (' B_0 ' term in Chung et al. 2019b), accurate reconstructions of fish size from otolith age counts, and body mass scaling of SMR with an exponent of -0.1 .

C_{resp} values are a proxy for field metabolic rate; however, most ecophysiological studies use oxygen consumption rates as a proxy for metabolic rate. Statistical calibrations to convert C_{resp} values to equivalent oxygen consumption rates have been determined experimentally for Australian snapper *Chrysophrys auratus* (Martino et al. 2020) and Atlantic cod *Gadus morhua* (Chung et al. 2019b) and presented in the form of exponential decay models:

$$C_{\text{resp}} = C \times (1 - e^{-k \times \text{FMR}_{\text{oto}}}) \quad (6)$$

where the C and k terms are model fitted values, and FMR_{oto} is the oxygen consumption rate in $\text{mgO}_2 \text{kg}^{-1} \text{h}^{-1}$. However, with increasing data from a wider range of fishes (Alewijnse 2021) it is becoming clear that the decaying exponential component may in part reflect experimental artefacts, specifically inclusion of additional metabolic components to SMR at high induced temperatures. The linear form of the calibration model presented in Chung et al. (2019b) avoids these potential artefacts. We have therefore estimated effective oxygen consumption rates according to the linear form of the calibration model:

$$\text{FMR}_{\text{oto}} = (C_{\text{resp}} - 0.041)/0.000971 \quad (7)$$

Given the uncertainties of the equations and the subsequent error propagation, both the thermometry and metabolism calculations were constructed using a Monte Carlo framework with 1000 iterations, drawing each variable randomly from a normal distribution constrained by estimates of uncertainty (SDs around parameter estimates). For temperature determination, we estimated uncertainty in $\delta^{18}\text{O}_{\text{water}}$ values with an SD of 0.1‰, and uncertainty around measured $\delta^{18}\text{O}_{\text{oto}}$ values of 0.2‰. Uncertainties around temperature equation parameters are taken from Høie et al. (2004)

(Eq. 2). For estimation of C_{resp} values, SDs of 0.1, 0.5, and 0.5‰ were applied to $\delta^{13}C_{oto}$, $\delta^{13}C_{Diet}$, and $\delta^{13}C_{DIC}$ values, respectively. All data analysis was performed using the statistical environment R (R Core Team 2013). After confirming the normal distribution of the residual errors and homogeneous variances, differences between group means were assessed using 1-way analysis of variance (ANOVA) and post-hoc Tukey tests for data that met the assumptions. Non-parametric Kruskal-Wallis tests with Wilcoxon rank sum post-hoc comparisons were used for non-normally distributed groups. To compare between the different species, a permutational multivariate analysis of variance (PERMANOVA) was used, implementing depth as a function of species and otolith region nested within species (999 permutations and Bray-Curtis similarity index). Additionally, the individual rate of change (IRC) was computed as the difference between adjacent otolith regions of each individual to provide a metric of the intra-individual difference between adjacent sections. To test interspecific differences in metabolic regressions we compared the Akaike information criterion of a generalized linear model with C_{resp} as a function of fish mass and temperature with and without species as a factor.

3. RESULTS

3.1. Overview

The otolith thermometry using $\delta^{18}O$ ratios revealed consistent and marked differences in inferred temperature between otolith regions in all 3 taxa (ANOVA p-values < 0.003). The derived tempera-

tures showed similar differences with overall decreases of mean temperatures with increasing otolith radius, size, and age with differing patterns between the species (Table 2).

For rockfish the core $\delta^{18}O_{oto}$ values recorded higher mean temperatures (mean = 15°C) than the 2 overlapping regions middle and edge (Fig. 2). This was paralleled by a -4.3°C mean individual rate of change between the core and middle regions (Fig. 2, Table 2). The maximum inferred temperature was 18.5°C, found in a core region, while the minimum temperature found was 5.9°C of an edge region. Correlating the calculated temperatures to Azorean mean temperature–depth profiles, core rockfish otolith regions (corresponding to the smallest mean size) exhibited a

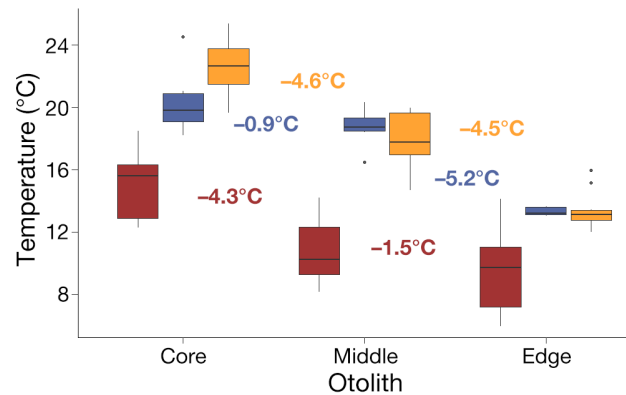


Fig. 2. Boxplot of the calculated temperature of otolith regions of rockfish (red), wreckfish (blue), and seabream (yellow), with coloured boxes showing the interquartile range, horizontal lines the median value, and vertical lines the last maximum and minimum value before the upper and lower fence, respectively, with points indicating outliers. Coloured numbers denote the mean individual rate of change between the 2 equally coloured adjacent otolith regions of each species

Table 2. Mean back-calculated total length (TL) and age with corresponding temperature (temp.), depth, metabolism rates, and 95% confidence intervals (CI) of the 3 otolith regions of rockfish, wreckfish and seabream. C_{resp} : metabolically derived carbon in the otolith aragonite

		Mean TL (cm)	Mean age (yr)	Thermometry				Metabolism			
				Mean temp. (°C)	CI	Mean depth (m)	CI	Mean C_{resp}	CI	Oxygen consumption (mg O ₂ kg ⁻¹ h ⁻¹)	CI
Rockfish	Core	3.1	0.4	15	13.2–16.8	214	72–356	0.3	0.3–0.37	161	121–201
	Middle	15.8	3.6	10.8	9.2–12.4	631	435–827	0.2	0.2–0.27	85	67–103
	Edge	28.9	7	9.5	6.8–12.1	804	467–1141	0.2	0.15–0.25	67	44–90
Wreckfish	Core	53.8	2.3	20.3	18.9–21.7	5	0–13	0.37	0.34–0.39	196	165–228
	Middle	77.6	6.2	18.7	17.6–19.8	16	0–37	0.31	0.28–0.34	138	109–167
	Edge	99.2	11	13.3	13.0–13.6	326	279–374	0.19	0.15–0.22	61	47–74
Seabream	Core	11	0.7	22.6	21.4–23.8	2	0–2	0.41	0.38–0.43	327	230–425
	Middle	24.8	3.6	17.7	16.3–19.2	49	4–94	0.33	0.28–0.39	169	124–215
	Edge	38.4	7.7	13.4	12.5–14.3	333	237–429	0.21	0.17–0.26	77	53–101

mean depth of ca. 200 m while values of the middle and edge regions of larger individuals, corresponded to higher depth estimates of ca. 600 and 800 m, respectively (Table 1).

In wreckfish the mean $\delta^{18}\text{O}$ values of the core and middle regions overlapped while the edge region recorded a lower mean temperature (13.3°C) with a pronounced mean IRC decline between middle and edge regions (-5.2°C). The maximum derived temperature was 24.5°C of a core region. Derived depths for core and middle regions of wreckfish indicated mean depths of below 50 m for both, while values of edge regions correspond to significantly deeper depths of ca. 300 m (Table 2, Fig. 3).

For seabream the otolith thermometry showed a decrease of mean temperatures with increasing otolith radius, size, and age (Table 2). Values ranged from 12.0°C (edge region) to 25.3°C (core region). The IRC between the regions was similarly negative between both the core and middle regions and the middle and edge regions (Fig. 2). The corresponding depths of the regions showed clear differences between the 3 regions (Fig. 3, Tukey $p < 0.001$) and increasing depth with increasing otolith radius (corresponding to larger sizes and older animals). The core section exhibited the shallowest derived depths, between the surface and 2 m, significantly shallower than 50 m, extending above the SD of the mean temperatures.

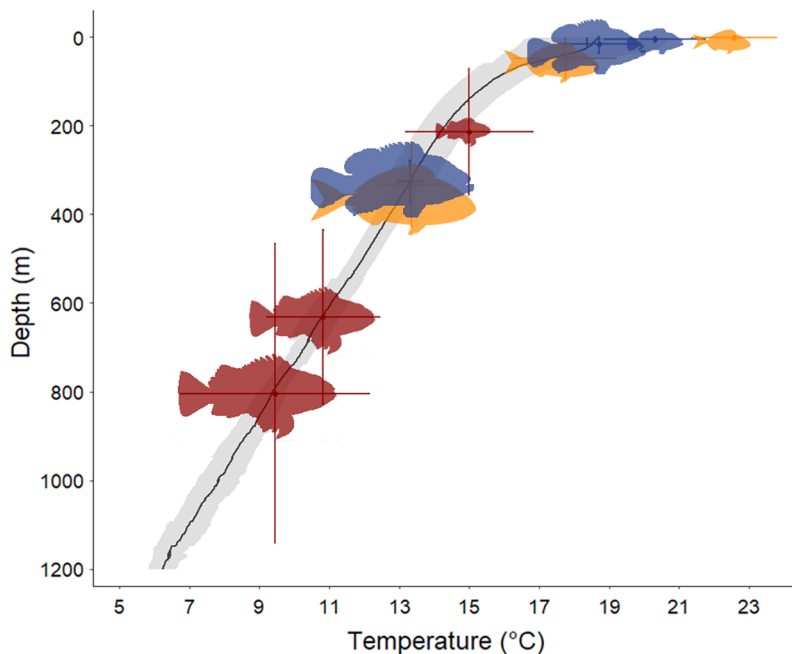


Fig. 3. Mean depth and temperature of the life stages of rockfish (red), wreckfish (blue), and seabream (yellow) (small fish symbols represent younger and larger ones older life stages), with the mean temperature–depth profile from the Azores (black line) and its SD (grey area)

Values of the middle region revealed deeper values (ca. 50 m) and edge regions with the deepest mean of ca. 300 m, with maximum estimated depth past 400 m.

Regarding metabolism, C_{resp} values indicated a consistent decrease in mass-specific field metabolic rate with increasing distance from the otolith core (and thus increasing age and body size) across all 3 taxa (Table 2). Estimated equivalent oxygen consumption ranged from 106 to $375 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ for rockfish, 116 to $380 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ for wreckfish, and 112 to $419 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ in seabream (Table 2).

3.2. Interspecific comparison

The comparison between the 3 study species showed clear differences in realised habitat temperature, field metabolic rates, and ontogenetic dynamics of these deep-sea fishes. The otolith thermometry indicated different depth distributions of the different species (PERMANOVA pseudo- $F(2) = 22.7$, $p < 0.001$) and life stages of the species (PERMANOVA pseudo- $F(6) = 14.8$, $p < 0.001$). The highest temperature (and therefore shallowest derived depth) was exhibited by small seabream, with a temperature exceeding the mean and SD of the local temperature profiles. Differences between the 3 species were largest between core otolith regions (Kruskal-Wallis $H(2) = 23.6$, $p < 0.0001$) with only wreckfish and seabream showing similar depth values (Fig. 3, Wilcoxon post-hoc test $p > 0.05$). With increasing depth inter-specific differences decreased, with all 3 species revealing more similar ranges at the edge region (Kruskal-Wallis $H(2) = 7.9$, $p < 0.02$).

Regarding metabolism, all 3 species showed decreasing C_{resp} values with increasing body size, reflecting a combination of body size and temperature effects on mass specific metabolic rates with differences between the species (improved generalized linear model performance with species included as factor). Relative C_{resp} values showed consistent relative positions in core and middle regions, with rockfish displaying the lowest C_{resp} values and seabream displaying highest C_{resp} values. At the edge region, corresponding to the largest size of individuals, the C_{resp} ranges overlap for all 3 species.

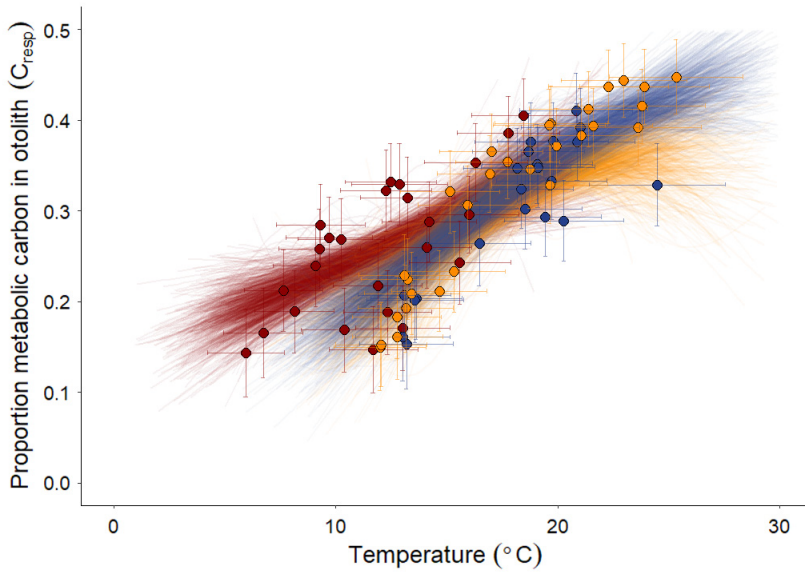


Fig. 4. Scatter plot of metabolically derived carbon in the otolith aragonite (C_{resp}) as function of temperature, i.e. field metabolic rate in rockfish (red), wreckfish (blue), and seabream (yellow). Points are the mean individual values of Monte Carlo iterations with SD denoted as error bars, lines being the 1000 respective loess regressions

3.3. Thermal sensitivity of FMR

In all 3 species, C_{resp} values (and therefore FMR) increased with increasing temperature (Fig. 4). The apparent thermal sensitivity of FMR, given by the slope of the relationship between C_{resp} values and experienced temperature (Fig. 5 bottom), was similar across taxa, but this relationship is complicated by the inverse covariation between experienced temperature and ontogenetic increases in body size. In wreckfish and, to a lesser extent, seabream, the rate of increase in C_{resp} values with increasing temperature fell faintly as temperatures approach 25°C, potentially implying a thermal maximum beyond which metabolic performance declines.

FMR values converted to oxygen consumption rates were compared to SMR

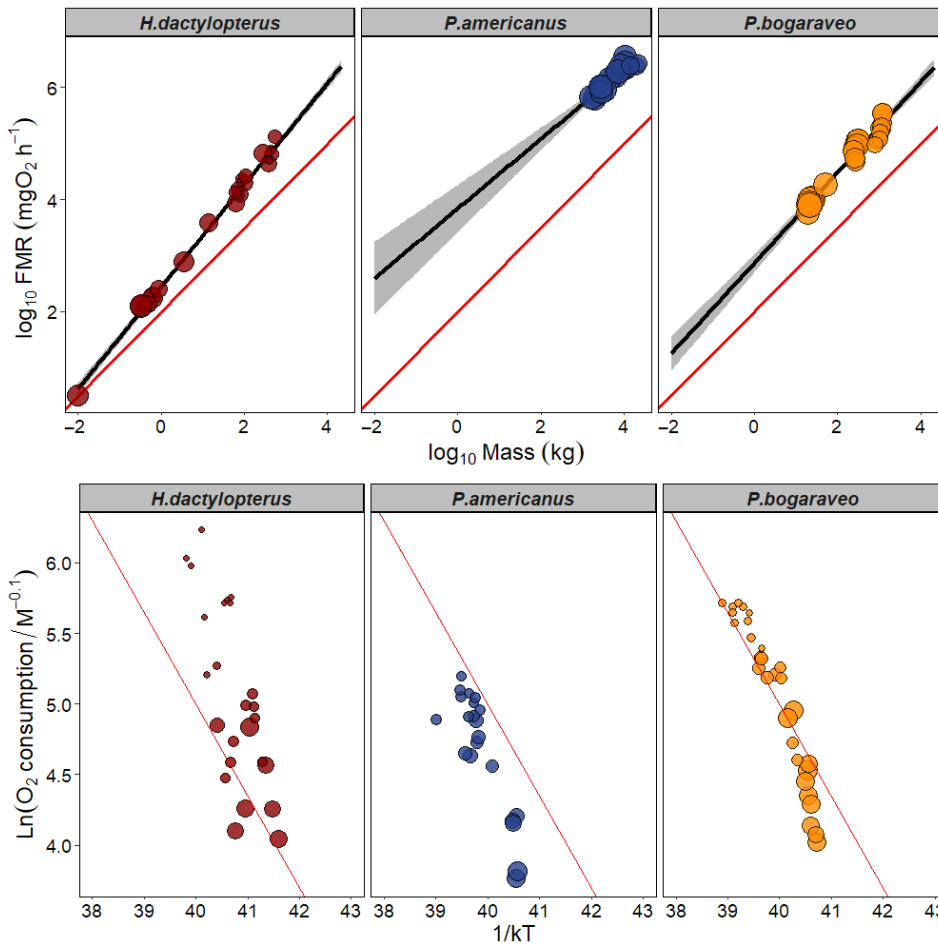


Fig. 5. Mass- (top) and temperature- (bottom) scaling of field oxygen consumption rates inferred from otolith isotopes (*Helicolenus dactylopterus*, *Polyprion americanus*, and *Pagellus bogaraveo*). (Top) Mass scaling of whole organism oxygen consumption rates. Red lines: mass scaling with an exponent of 0.79; point size shows mean temperature. (Bottom) Arrhenius plot showing thermal sensitivity of the field metabolic rate (FMR) values accounting for body size. Red lines: temperature scaling with a thermal sensitivity of 0.65eV; point size shows relative mass. kT : k is Boltzmann's constant, and T is temperature in Kelvin against the natural log of mass-corrected respiration

predicted by metabolic theory (Eq. 5), considering variations in reconstructed body size and experienced temperature (Fig. 6). FMR values estimated from otolith isotope compositions covaried closely with variations in SMR predicted from temperature and body size approximating 3 times modelled SMR in all cases except for juvenile samples from rockfish, where measured FMR values lay between 1 and 3 times estimated SMR (Fig. 6). However, the estimates of SMR values are based on 3 assumptions: a common, statistically derived metabolic level (' B_0 ' term in Chung et al. 2019b), accurate reconstructions of fish size from otolith age counts, and body mass scaling of SMR with an exponent of -0.1 . We are unable to confirm that any of the assumptions underlying SMR estimation (see Section 3.4.) are valid for the 3 species in this study; therefore, apparent differences in the relationship between inferred FMR and SMR for rockfish compared to wreckfish and seabream could reflect violations of the assumptions above rather than differences in species' physiology. The resulting inferred mass scaling exponents for whole body oxygen consumption rates are (with SE of the regression slope in parentheses): rockfish: 0.91 (0.02), wreckfish: 0.62 (0.05), *Pagellus bogaravo*: 0.81 (0.03). The estimated slope for wreckfish is low compared to expected mass scaling exponents between 0.65 and 1 (Glazier 2014, Norin preprint <https://doi.org/10.1101/2021.03.29.437465>), likely reflecting additional reduction in field metabolic rates associated with increasing inhabited depth. Arrhenius plots (Fig. 5 bottom) were used to explore the effect of varying apparent body mass scaling

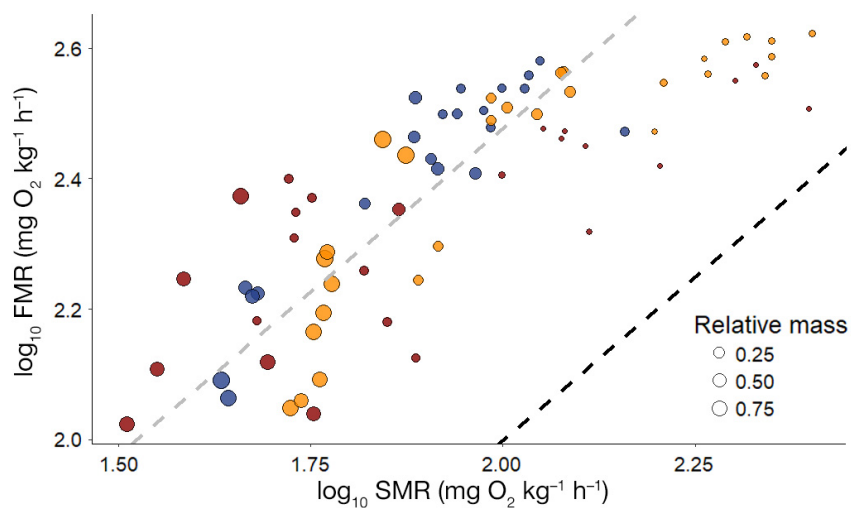


Fig. 6. Comparison between standard metabolic rates (SMR) inferred from reconstructed body mass and experienced temperature and field metabolic rates (FMR), both expressed as oxygen consumption rates ($\text{mg O}_2 \text{ mg}^{-1} \text{ h}^{-1}$). Color indicates species (rockfish: red; wreckfish: blue; seabream: yellow); symbol size indicates reconstructed body mass relative to the largest sampled body size for each species. Sustained FMR values are expected to lie between 1 (black dashed line) and 3 (grey dashed line) times SMR

on inferences of thermal sensitivity. We explored the relationship between mass-scaled oxygen consumption rates and temperature drawing on 3 alternative values for mass scaling exponents, the statistically inferred exponents given above, a common exponent of -0.25 (as implied by strict metabolic theory) and a steeper mass scaling exponent of -0.1 . For low (relatively shallow) mass scaling exponents, inferred relationships between temperature and FMR are negative, indicating over-correction of body mass effects (Figs. S1 & S2). Applying a common body mass scaling exponent of -0.1 (close to the mass exponent of -0.12 inferred for rockfish) removed systematic body size effects, resulting in the following apparent thermal sensitivities of FMR: rockfish -0.98 (0.19), *Polyprion americanus* -0.85 (0.11), *Pagellus bogaravo* -0.93 (0.05).

4. DISCUSSION

4.1. Overview

The life cycles of deep-sea fish are often presented as generalized and oversimplified models because ecological and biological data is typically limited, restricting our understanding of multi-specific fisheries management. The analysis of stable isotope data, as a retrospective proxy of life history and environmental conditions experienced through the ontogeny, was used in this study to further investigate the life cycles of rockfish, wreckfish and seabream. The results provide novel information in support of the hypothesis that all 3 species undergo pronounced ontogenetic shifts in metabolism and across vertical habitat use, while revealing important differences among species (Fig. 7). The contrasting results among the 3 study species, highlight the ecological differences not only in their overall distribution but also in the dynamics throughout the life history of these deep-sea fishes. At the same time, the depth data strengthen the species distribution information used for fisheries management decisions, while the metabolism estimates provide novel data for estimating energetic needs of the species and parameterise food web models. As such, these findings have implications for the conservation and sustainable management of these key species in the Atlantic.

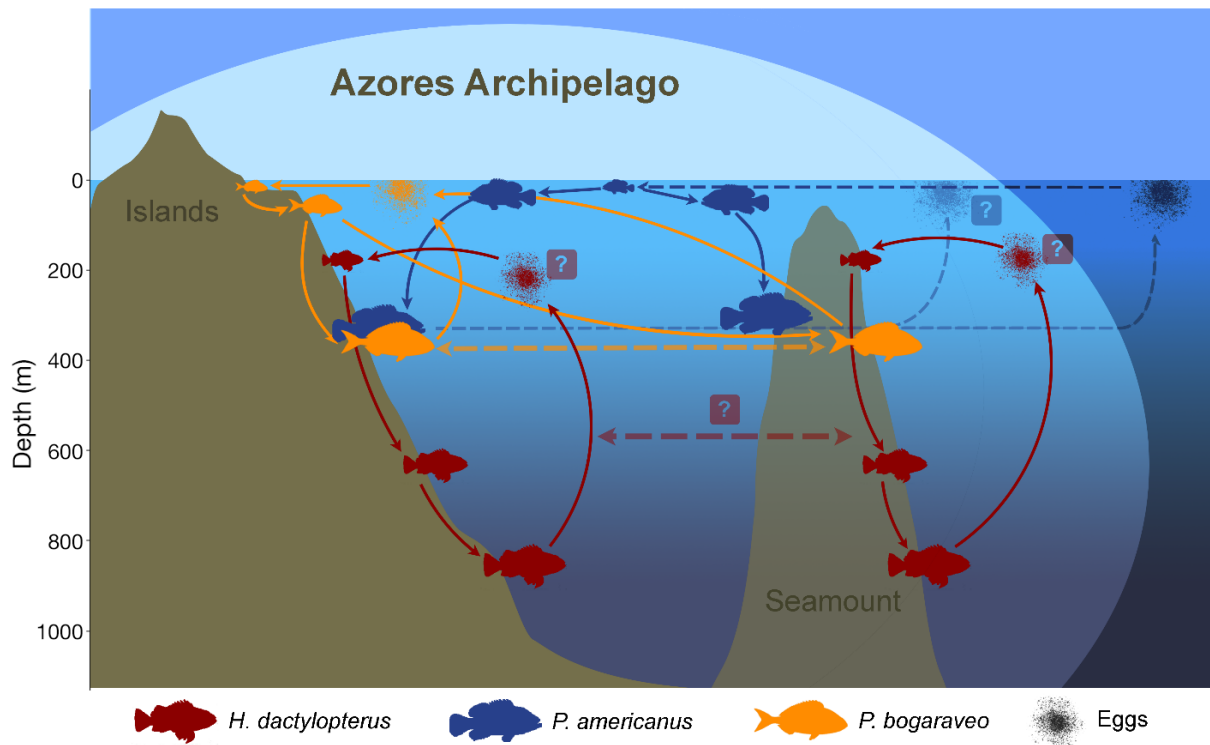


Fig. 7. Conceptual model of the life cycles of the 3 study species (*Helicolenus dactylopterus*, *Polyprion americanus*, and *Pagellus bogaraveo*) in the Azores study area (light blue ellipse). Sizes of fish silhouettes represent the different life stages (early juveniles, sub-adults, and mature fish); arrows represent theorised ontogenetic habitat shifts. Dashed arrows and question marks illustrate remaining knowledge gaps

4.2. Rockfish

The distribution of the sampled rockfish revealed by the otolith thermometry (17 to 7°C and water depths of 100 to 1100 m) are closely comparable to the distribution of rockfish found in catch-based studies of other Atlantic populations (Kelly et al. 1999, Allain & Lorange 2000, Consoli et al. 2010, Capezzuto et al. 2020) and the Azores (Menezes et al. 2006, Santos et al. 2020). Here, Menezes (2003) found a maximum catch depth of 1085 m with a minimum temperature of 7°C. Thus, the relative temperature and depth changes inferred in this study provide relevant insights into the ontogenetic shifts of the species.

The mean derived depths of the different life stages indicate an ontogenetic shift to deeper waters after the shallow water juvenile life stage. The ontogenetic migration across depth and associated temperature reduction during its life history is associated with a decrease in mass-specific metabolic rate with age and size in rockfish, consistent with expectations from metabolic ecology (Clarke & Johnston 1999, Drazen & Seibel 2007); however, the apparent thermal sensitivity of FMR is greater than the canonical activation energy of -0.65eV (Brown et al. 2004), implying ad-

ditional reduction in activity as fish move from warm shallow to deeper waters. We observed no evidence for reduced metabolic performance at either cold or warm boundaries of the experienced temperature range. Inferred field metabolic rates were similar across all 3 species where experienced temperatures overlap at around 16–20°C (the warmer water experienced within the temperature range for rockfish). The temperatures below 15°C and higher C_{resp} values of rockfish compared to the other species may in part reflect small relative body sizes of rockfish compared to adult wreckfish and seabream (body sizes of rockfish and seabream being more comparable). It is therefore likely that rockfish have relatively high field metabolic rates in colder waters compared to the other 2 study species. Otolith-inferred FMR for rockfish is much lower than SMR inferred from metabolic theory based on the core samples, which, together with associated shallow mass scaling slopes for whole body FMR, likely implies that the body sizes inferred for the otolith core samples are underestimated.

The estimated core region temperatures observed for rockfish are difficult to interpret from the ontogenetic and early life history perspective. Conversely, the estimated core temperature would suggest that

larvae and juveniles are not surface oriented, where warmer waters are found. However, rockfish spawning occurs in the coldest time of the year, with temperatures down to 15°C and little thermal stratification within the first 150–200 m present in the region (Locarnini et al. 2018). In addition, the early life stage of rockfish is poorly known, and the fate of the internally fertilized embryos, released embedded on a gelatinous matrix is unknown (Sequeira et al. 2011 and references therein). It remains unclear if the egg masses will remain benthic or may drift at specific depth. In summary, the early life history, in particular the larval stage habitat-use and dispersal of rockfish, remains unknown as does the understanding of vertical ontogenetic habitat use at the earlier stages (see question marks in Fig. 7). In contrast, the observed shifts in metabolism are consistent with morphologic and diet shifts from more streamlined juveniles with a more active foraging behaviour (probably associated with pelagic hunting) to benthic ambush predators in later life stages (Rodríguez-Mendoza et al. 2011 and references herein). Similar to the findings of Santos et al. (2020), large rockfish reveal a broad depth range suggesting the availability of suitable habitats across a wide vertical window in the Azores (Pham et al. 2015), yet the location and extent of their essential fish habitats remain to be identified.

4.3. Wreckfish

The results of wreckfish otolith regions indicate a shallow pelagic phase throughout juvenile life stages (otolith core and middle). The elevated temperatures estimated for the juveniles, exceeding local average surface temperatures, might result from the higher temperatures potentially experienced in the Gulf Stream along which the wreckfish larvae and juveniles are expected to live before reaching the Azores. We detected a pronounced ontogenetic habitat shift from warm shallow surface waters to colder and deeper waters of around 300 m (Fig. 3), consistent with the hypothesis proposed by several authors (Sedberry et al. 1996, 1998, Ball et al. 2000, Machias et al. 2003). The overall depth distribution is also in agreement with catch data from the Azores (Menezes 2003) and other parts of the Atlantic (Ray & Robins 2016).

Contrary to preceding studies, the intra-individual variability we found suggests that at least some individuals shift to deeper habitats between 77 and 99 cm TL and thus close to the size of maturity (Peres & Klippel 2003). Still, inter-individual plasticity may be high, and the timing of the shift likely influenced by

the presence of suitable demersal habitat. Interestingly, the longline catch data used to provide *a priori* depth distributions shows the highest catch of juveniles (same size as regions core and middle) at depths of 350 to 500 m on average. Such variability would probably be detected on catch-biased data while being potentially masked by the time integrated signal of our study as suggested previously (G. Menezes pers. comm.).

This study also provides the first estimates of field metabolic rate of wreckfish. The low allometric scaling exponents found for whole organism FMR are potentially associated with changes in activity levels linked to ontogenetic depth changes. As such, wreckfish might transition from a more active predation of the intermittently available epipelagic prey to a reduction in activity after the ontogenetic shift to demersal habitats with more stable prey availability. The thermal sensitivity of C_{resp} (and therefore FMR) indicates a potential non-linear response of wreckfish; however, a larger sample size with a wider temperature range would be necessary to draw robust inferences. The broad inter-individual variation of metabolic rates at high temperatures (particularly visible around 19°C) could be evidence of the large variability of prey availability and composition while the wreckfish juveniles disperse along the epipelagic current systems of the North Atlantic Ocean.

The otolith thermometry and derived depth data of this study supports, for the first time, the pronounced habitat shift of this data deficient species, providing new insights into the stochasticity of the timing of vertical migration as reflected by intra-individual data. The recurrent catch of mature adults in the region reinforces the suggested importance of the Azores for the north Atlantic population of wreckfish (Ball et al. 2000). Further research needs to be conducted to identify whether mature adults return to the west Atlantic to spawn, or if the Mid-Atlantic constitutes an alternative spawning ground (see Fig. 7).

4.4. Seabream

The otolith thermometry of seabream shows a wide temperature and associated depth range, agreeing with catch depth distribution recorded in the Azores and the Mediterranean (Menezes et al. 2006, Mytilineou et al. 2013). There was a significant gradual ontogenetic shift in temperature and depth from warmer shallow waters to colder deeper waters as the individual grows, with adults occupying the coldest and deepest layers. Early juvenile life stages display

high temperatures exceeding the average of Azores surface waters. After hatching in spring, the young of the year have been found to aggregate in coastal areas using the inshore habitats as nurseries for approximately 1 yr in the Azores and continental European waters (Santos et al. 1995, Lorange 2011, Pinho et al. 2014). With summer sea surface temperatures between 20.5 and 23.5°C (Amorim et al. 2017), the thermometry of the juveniles thus provides realistic values for the study area. These results support the hypothesis that the black spot seabream life cycle includes an obligatory shallow water recruitment stage followed by a post-recruitment phase of several months as suggested by several authors (Afonso et al. 2012, Félix-Hackradt et al. 2013, Teixeira 2013, Pinho et al. 2014). The question remains, however, whether this recruitment is exclusively coastal or may also be epipelagic (marked as question marks in Fig. 7). Additional studies using amino acid compound specific isotopic analysis should clarify this question by determining the source of post-recruitment diet, i.e. coastal vs offshore.

FMR in seabream reveal significant ontogenetic differences with lower mass-specific metabolism in larger individuals residing in deeper and colder waters (Fig. 5). Seabream show a non-linear relationship between FMR and temperature (Fig. 4), with a slight inflection at around 18°C. As in all 3 species, the apparently high thermal sensitivities for mass-corrected FMR likely imply a reduction in activity levels associated with ontogenetic depth migrations (Fig. 5).

4.5. Contrasting ontogenetic dynamics of deep-sea fishes

While rockfish shift from benthopelagic juveniles to deep benthic ambush predators relatively early, both wreckfish and seabream start their life in shallow waters, shifting to the deep-sea habitat only at or close to attaining maturity. Yet, even the shallow juvenile life stages of the 2 latter species could hardly differ more in their habitat use, with solitary juvenile wreckfish being transported in epipelagic waters across ocean basins, often in association to floating debris (Sedberry et al. 1996), while seabreams seek shelter in inshore coastal nurseries.

In all 3 species, the ontogenetic shift to deeper habitats around maturity is associated with a relative reduction in metabolism, a proxy for activity. At low temperatures, rockfish maintain higher metabolic and thus higher activity levels (Figs. 4 & 5).

4.6. Potential of otolith chemistry for deep-sea fish ecology

While absolute values for both temperature and field metabolic rate inferred from otoliths are subject to uncertainty, otolith chemistry offers a unique tool to elucidate life history characteristics of deep-sea species using relatively few samples. Due to the integrative nature of the otolith tissue matrix and temporal and spatial variation in parameters included in calculations, our results cannot be used to infer more detailed assumptions about exact timings of ontogenetic shifts. Furthermore, owing to remaining parameter uncertainties, absolute depths and metabolic rates should be interpreted with caution. The calculated C_{resp} values fall within the wide range of values reported in the literature (Chung et al. 2019a and references herein) yet are higher than the those reported for 4 other deep-sea species (Chung et al. 2019b). Inferences of FMR show high sensitivity for the source values (especially $\delta^{13}\text{C}$ values of ambient seawater) used in the mixing models. We highlight the need for studies of the water isotope–depth profiles or proxies for the respective calculations. Nevertheless, this study demonstrates that otolith stable isotope analyses can yield significant new knowledge about broad shifts of habitat and metabolic activity using relatively small sample sizes, making it a highly powerful method to fill existing essential knowledge gaps concerning the life cycles of deep-sea fishes. Further research of otolith biogeochemistry is necessary to determine the degree of inter- and intraspecific differences in fractionation and to provide accurate parameters for wider application in the future.

The differences in metabolism among species highlight the heterogeneity of the evolutionary traits these species have developed to adapt to the challenging conditions of the deep-sea throughout their ontogeny. Current management strategies tend to oversimplify and generalize patterns to aid complex decision making, even more when concerning elusive organisms in remote ecosystems. Yet, with high market value and vulnerable life history characteristics (low fecundity, slow growth, etc.), the understanding of the life cycles and essential fish habitats of commercially exploited species is essential for sustainable management. The harvest of coastal juvenile seabream arguably has considerable impacts on the population and subsequent commercial yields (Pinho et al. 2014). Fishing mortality has not been assessed for the data-scarce wreckfish, but increasing commercial and recreational exploitation of juvenile wreckfish around fish aggregation devices could significantly

impact the reproductive capacity in future years (similar to tuna as detailed in Hallier & Gaertner 2008). Based on the heterogeneity of depth distribution and habitat use, we stress the need for appropriate differentiation in management and further research. The use of accessible, cost effective, and robust methods such as retrospective otolith chemistry has the potential to complement the existing catch-based data and contribute to fill knowledge gaps about elusive deep-sea species.

5. CONCLUSIONS

The retrospective otolith stable isotope analysis of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ published here provides new and supporting data for otherwise data-poor commercial demersal species. The otolith thermometry contributes thermal niche and depth distribution data which clearly compliment catch biased methods to coerce a more realistic image of the species ecology. The metabolism proxies supply information about the species' adaptations to the ambient conditions in the deep sea and bioenergetic consequences. Rockfish exhibit the deepest distribution of the 3 study species with larger specimen inhabiting deeper waters than juveniles. The metabolic rate decreases with increasing age and habitat depth, while size-specific metabolism is the highest of the 3 species. Wreckfish reveal an abrupt ontogenetic shift to deep waters after a pelagic juvenile stage, with size-specific metabolism rates declining faster with increasing size. Seabream indicate a shallow coastal juvenile stage before shifting gradually to deeper habitats. Similar to wreckfish, the non-linear slope of metabolic rate decline indicates a change in physiology and/or behaviour in the older individuals inhabiting deeper and colder waters. The contrasting life cycles of the 3 species provided herein reiterates the evolutionary complexity of deep-sea species that ought to be considered for sustainable management of multi-specific fisheries.

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LITERATURE CITED

- ✦ Abecasis D, Costa A, Pereira J, Pinho M (2006) Age and growth of bluemouth, *Helicolenus dactylopterus* (Delaroché, 1809) from the Azores. *Fish Res* 79:148–154
- ✦ Afonso P, Graça G, Berke G, Fontes J (2012) First observations on seamount habitat use of blackspot seabream (*Pagellus bogaraveo*) using acoustic telemetry. *J Exp Mar Biol Ecol* 436–437:1–10
- ✦ Alewijnse SR, Stowasser G, Saunders RA, Belcher A, Crimmen OA, Cooper N, Trueman CN (2021) Otolith-derived field metabolic rates of myctophids (Family Myctophidae) from the Scotia Sea (Southern Ocean). *Mar Ecol Prog Ser* 675:113–131
- Allain V, Lorance P (2000) Age estimation and growth of some deep-sea fish from the northeast Atlantic Ocean. *Cybius* 24:7–16
- ✦ Amorim P, Perán AD, Pham CK, Juliano M, Cardigos F, Tempera F, Morato T (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* 4:56
- ✦ Ball A, Sedberry G, Zatzoff M, Chapman R, Carlin J (2000) Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers. *Mar Biol* 137:1077–1090
- ✦ Becker M, Andersen N, Erlenkeuser H, Humphreys MP, Tanhua T, Körtzinger A (2016) An internally consistent dataset of $\delta^{13}\text{C}$ -DIC in the North Atlantic Ocean—NAC13v1. *Earth Syst Sci Data* 8:559–570
- ✦ Bergstad OA (2013) North Atlantic demersal deep-water fish distribution and biology: present knowledge and challenges for the future. *J Fish Biol* 83:1489–1507
- ✦ Bradbury IR, Laurel B, Snelgrove PV, Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc R Soc B* 275:1803–1809
- ✦ Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- ✦ Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Mar Ecol Prog Ser* 188:263–297
- ✦ Capezuto F, Ancona F, Calculli C, Sion L, Maiorano P, D'Onglia G (2020) Feeding of the deep-water fish *Helicolenus dactylopterus* (Delaroché, 1809) in different habitats: from muddy bottoms to cold-water coral habitats. *Deep Sea Res* 159:103252
- ✦ Chung MT, Trueman CN, Godiksen JA, Grønkjær P (2019a) Otolith $\delta^{13}\text{C}$ values as a metabolic proxy: approaches and mechanical underpinnings. *Mar Freshw Res* 70:1747–1756
- ✦ Chung MT, Trueman CN, Godiksen JA, Holmstrup ME, Grønkjær P (2019b) Field metabolic rates of teleost fishes are recorded in otolith carbonate. *Commun Biol* 2:24
- ✦ Clark MR (2009) Deep-sea seamount fisheries: a review of global status and future prospects. *Lat Am J Aquat Res* 37:501–512
- ✦ Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA (2016) The impacts of deep-sea fisheries on benthic communities: a review. *ICES J Mar Sci* 73: i51–i69
- ✦ Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol* 68:893–905

- Consoli P, Battaglia P, Castriota L, Esposito V, Romeo T, Andaloro F (2010) Age, growth and feeding habits of the bluemouth rockfish, *Helicolenus dactylopterus dactylopterus* (Delaroche 1809) in the central Mediterranean (southern Tyrrhenian Sea). *J Appl Ichthyology* 26:583–591
- Craig H, Gordon LI (1965) Deuterium and oxygen 18 variations in the ocean and the marine atmosphere. In: Tongiorgi E (ed) *Stable isotopes in oceanographic studies and paleotemperatures*. Consiglio Nazionale delle Ricerche Laboratorio di Geologia Nucleare - Pisa, Spoleto, p 9–130
- Drazen JC, Haedrich RL (2012) A continuum of life histories in deep-sea demersal fishes. *Deep Sea Res I* 61:34–42
- Drazen JC, Seibel BA (2007) Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. *Limnol Oceanogr* 52:2306–2316
- Drazen JC, Sutton TT (2017) Dining in the deep: the feeding ecology of deep-sea fishes. *Ann Rev Mar Sci* 9:337–366
- Félix-Hackradt F, Hackradt C, Treviño-Otón J, Segovia-Viadero M, Pérez-Ruzafa A, García-Charton J (2013) Environmental determinants on fish post-larval distribution in coastal areas of south-western Mediterranean Sea. *Estuar Coast Shelf Sci* 129:59–72
- Gerringer M, Andrews A, Huss G, Nagashima K and others (2018) Life history of abyssal and hadal fishes from otolith growth zones and oxygen isotopic compositions. *Deep Sea Res I* 132:37–50
- Glazier D (2014) Metabolic scaling in complex living systems. *Systems* 2:451–540
- Hallier JP, Gaertner D (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Mar Ecol Prog Ser* 353:255–264
- Høie H, Otterlei E, Folkvord A (2004) Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). *ICES J Mar Sci* 61: 243–251
- Isidro E (1987) Contribuição para o estudo da biologia e pesca de Boca Negra, *Helicolenus dactylopterus* (De la Roche, 1809) dos Açores. Relatório da 7ª Semana das Pascas dos Açores, Secretaria Regional da Agricultura e Pescas. Direção Regional das Pescas, Horta
- Kalish JM (1991) ^{13}C and ^{18}O isotopic disequilibria in fish otoliths: metabolic and kinetic effects. *Mar Ecol Prog Ser* 75:191–203
- Kelly C, Connolly P, Bracken J (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
- Killen SS, Atkinson D, Glazier DS (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol Lett* 13:184–193
- Krug H (1989) The Azorean blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) (Teleostei: Sparidae): age and growth. *Cybio* 13:347–355
- Krug H (1998) Variation in the reproductive cycle of the blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) in the Azores. *Arquipélago Ciênc Biol Mar* 16:37–47
- Locarnini RA, Mishonov AV, Baranova OK, Boyer TP and others (2018) *World ocean atlas 2018, Vol 1. Temperature*. NOAA Atlas NESDIS 81, Silver Spring, MD
- Lorance P (2011) History and dynamics of the overexploitation of the blackspot sea bream (*Pagellus bogaraveo*) in the Bay of Biscay. *ICES J Mar Sci* 68:290–301
- LOTAÇOR - Serviço de Lotas dos Açores SA (2020) *Pescado Descarregado na R.A.A.*
- Machias A, Somarakis S, Papadroulakis N, Spedicato MT, Suquet M, Lembo G, Divanach P (2003) Settlement of the wreckfish (*Polyprion americanus*). *Mar Biol* 142:45–52
- Martino JC, Doubleday ZA, Chung MT, Gillanders BM (2020) Experimental support towards a metabolic proxy in fish using otolith carbon isotopes. *J Exp Biol* 223: jeb217091
- McConnaughey TA, Gillikin DP (2008) Carbon isotopes in mollusk shell carbonates. *Geo-Mar Lett* 28:287–299
- Menezes G (2003) Demersal fish assemblages in the Atlantic Archipelagos of the Azores, Madeira, and Cape Verde. Universidade dos Açores, Ponta Delgada
- Menezes GM, Sigler MF, Silva HM, Pinho MR (2006) Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). *Mar Ecol Prog Ser* 324:241–260
- Mindel BL, Neat FC, Trueman CN, Webb TJ, Blanchard JL (2016) Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea. *PeerJ* 4:e2387
- Mytilineou C, Tsagarakis K, Bekas P, Anastasopoulou A and others (2013) Spatial distribution and life-history aspects of blackspot seabream *Pagellus bogaraveo* (Osteichthyes: Sparidae). *J Fish Biol* 83:1551–1575
- Norse EA, Brooke S, Cheung WW, Clark MR and others (2012) Sustainability of deep-sea fisheries. *Mar Policy* 36: 307–320
- Peres MB, Haimovici M (2004) Age and growth of southwestern Atlantic wreckfish *Polyprion americanus*. *Fish Res* 66: 157–169
- Peres MB, Klippel S (2003) Reproductive biology of southwestern Atlantic wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae). *Environ Biol Fishes* 68:163–173
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Pham CK, Vandepierre F, Menezes G, Porteiro F, Isidro E, Morato T (2015) The importance of deep-sea vulnerable marine ecosystems for demersal fish in the Azores. *Deep Sea Res I* 96:80–88
- Pinho M, Diogo H, Carvalho J, Pereira JG (2014) Harvesting juveniles of blackspot sea bream (*Pagellus bogaraveo*) in the Azores (Northeast Atlantic): biological implications, management, and life cycle considerations. *ICES J Mar Sci* 71:2448–2456
- Pinho M, Medeiros-Leal W, Sigler M, Santos R, Novoa-Pabon A, Menezes G, Silva H (2020) Azorean demersal longline survey abundance estimates: procedures and variability. *Reg Stud Mar Sci* 39:101443
- Pitcher TJ, Clark MR, Morato T, Watson R (2010) Seamount fisheries: Do they have a future? *Oceanography (Wash DC)* 23:134–144
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Ray C, Robins CR (2016) *A field guide to Atlantic coast fishes: North America, Vol 32*. Houghton Mifflin Harcourt, Boston, MA
- Rodríguez-Mendoza R, Muñoz M, Saborido-Rey F (2011) Ontogenetic allometry of the bluemouth, *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaenidae), in the Northeast Atlantic and Mediterranean based on geometric morphometrics. *Hydrobiologia* 670:5–22
- Santos RS, Hawkins S, Monteiro LR, Alves M, Isidro EJ (1995) Marine research, resources and conservation in the Azores. *Aquat Conserv* 5:311–354
- Santos R, Pabon A, Silva W, Silva H, Pinho M (2020) Population structure and movement patterns of blackbelly rose-

- fish in the NE Atlantic Ocean (Azores archipelago). *Fish Oceanogr* 29:227–237
- ✦ Schwarcz H, Gao Y, Campana S, Browne D, Knyf M, Brand U (1998) Stable carbon isotope variations in otoliths of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 55: 1798–1806
- ✦ Sedberry G, Carlin J, Chapman R, Eleby B (1996) Population structure in the pan-oceanic wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae), as indicated by mtDNA variation. *J Fish Biol* 49:318–329
- Sedberry G, Carlin JL, Menezes GM (1998) Movements of a pelagic-phase wreckfish, *Polyprion americanus* (Schneider, 1801), as indicated by tag and recapture. *Arquipélago Ciênc Biol Mar* 16:69–72
- Sedberry GR, Andrade CAP, Carlin JL, Chapman RW and others (1999) Wreckfish *Polyprion americanus* in the North Atlantic: fisheries, biology, and management of a widely distributed and long-lived fish. In: Musick JA (ed) *Life in the slow lane: ecology and conservation of long-lived marine animals*. Symposium 23, p 27–50, American Fisheries Society, Bethesda, MD
- ✦ Sequeira V, Vila S, Neves A, Rifes P and others (2011) The gelatinous matrix of the teleost *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) in the context of its reproductive strategy. *Mar Biol Res* 7:478–487
- ✦ Sequeira V, Neves A, Paiva RB, de Lima JP, Vieira AR, Gordo LS (2012) Life history parameters as possible discriminators of bluemouth *Helicolenus dactylopterus* (Delaroche, 1809) populations in Portuguese waters. *Fish Res* 125-126:69–76
- ✦ Shephard S, Trueman C, Rickaby R, Rogan E (2007) Juvenile life history of NE Atlantic orange roughy from otolith stable isotopes. *Deep Sea Res I* 54:1221–1230
- ✦ Sherwood GD, Rose GA (2003) Influence of swimming form on otolith $\delta^{13}\text{C}$ in marine fish. *Mar Ecol Prog Ser* 258: 283–289
- ✦ Smoliński S, Denechaud C, von Leesen G, Geffen AJ, Grønkvær P, Godiksen JA, Campana SE (2021) Differences in metabolic rate between two Atlantic cod (*Gadus morhua*) populations estimated with carbon isotopic composition in otoliths. *PLOS ONE* 16:e0248711
- Sobrinho-Gonçalves L, Isidro E (2001) Fish larvae and zooplankton biomass around Faial Island (Azores archipelago). A preliminary study of species occurrence and relative abundance. *Arquipélago Ciênc Biol Mar* 18A:35–52
- ✦ Solomon CT, Weber PK, Cech J, Joseph J, Ingram BL and others (2006) Experimental determination of the sources of otolith carbon and associated isotopic fractionation. *Can J Fish Aquat Sci* 63:79–89
- Teixeira JPN (2013) Recruitment dynamics and early life history of the blackspot seabram, *Pagellus bogaraveo* (Perciformes: Sparidae). Universidade dos Açores, Ponta Delgada
- ✦ Thorrold SR, Campana SE, Jones CM, Swart PK (1997) Factors determining $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ fractionation in aragonitic otoliths of marine fish. *Geochim Cosmochim Acta* 61:2909–2919
- ✦ Treberg JR, Killen SS, MacCormack TJ, Lamarre SG, Enders EC (2016) Estimates of metabolic rate and major constituents of metabolic demand in fishes under field conditions: methods, proxies, and new perspectives. *Comp Biochem Physiol A Mol Integr Physiol* 202:10–22
- ✦ Trueman CN, MacKenzie KM, Palmer MR (2012a) Identifying migrations in marine fishes through stable-isotope analysis. *J Fish Biol* 81:826–847
- ✦ Trueman CN, MacKenzie KM, Palmer MR (2012b) Stable isotopes reveal linkages between ocean climate, plankton community dynamics, and survival of two populations of Atlantic salmon (*Salmo salar*). *ICES J Mar Sci* 69: 784–794
- ✦ Trueman CN, Rickaby REM, Shephard S (2013) Thermal, trophic and metabolic life histories of inaccessible fishes revealed from stable-isotope analyses: a case study using orange roughy *Hoplostethus atlanticus*. *J Fish Biol* 83: 1613–1636
- ✦ Trueman CN, Johnston G, O’Hea B, MacKenzie KM (2014) Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proc R Soc B* 281: 20140669
- ✦ Trueman CN, Chung MT, Shores D (2016) Ecogeochemistry potential in deep time biodiversity illustrated using a modern deep-water case study. *Philos Trans R Soc Lond B Biol Sci* 371:20150223
- ✦ Trueman CN, Artetxe-Arrate I, Kerr LA, Meijers AJS and others (2023) Thermal sensitivity of field metabolic rate predicts differential futures for bluefin tuna juveniles across the Atlantic Ocean. *Nat Commun* 14:7379
- ✦ Watson RA, Morato T (2013) Fishing down the deep: accounting for within-species changes in depth of fishing. *Fish Res* 140:63–65
- ✦ White CR, Phillips NF, Seymour RS (2006) The scaling and temperature dependence of vertebrate metabolism. *Biol Lett* 2:125–127

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