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Life history of abyssal and hadal fishes from otolith growth zones and oxygen isotopic compositions

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ABSTRACT

Hadal trenches are isolated habitats that cover the greatest ocean depths (6,500–11,000 m) and are believed to host high levels of endemism across multiple taxa. A group of apparent hadal endemics is within the snailfishes (Liparidae), found in at least five geographically separated trenches. Little is known about their biology, let alone the reasons for their success at hadal depths around the world. This study investigated the life history of hadal liparids using sagittal otoliths of two species from the Kermadec (*Notoliparis kermadecensis*) and Mariana (*Pseudoliparis swirei*) trenches in comparison to successful abyssal macrourids found at the abyssal-hadal transition zone. Otoliths for each species revealed alternating opaque and translucent growth zones that could be quantified in medial sections. Assuming these annuli represent annual growth, ages were estimated for the two hadal liparid species to be from five to 16 years old. These estimates were compared to the shallower-living snailfish *Careproctus melanurus*, which were older than described in previous studies, expanding the potential maximum age for the liparid family to near 25 years. Age estimates for abyssal macrourids ranged from eight to 29 years for *Coryphaenoides armatus* and six to 16 years for *C. yaquinae*. In addition, $^{18}O/^{16}O$ ratios ($\delta^{18}O$) were measured across the otolith using secondary ion mass spectrometry (SIMS) to investigate the thermal history of the three liparids, and two macrourids. Changes in $\delta^{18}O$ values were observed across the otoliths of *C. melanurus*, *C. armatus*, and both hadal liparids, the latter of which may represent a change of > 5 °C in habitat temperature through ontogeny. The results would indicate there is a pelagic larval stage for the hadal liparids that rises to a depth above 1000 m, followed by a return to the hadal environment as these liparids grow. This result was unexpected for the hadal liparids given their isolated environment and large eggs, and the biological implications and plausibility of interpretations of these data are discussed. This study presents a first look at the life history of some of the deepest-living fishes through otolith analyses.

1. Introduction

Hadal trenches cover the greatest ocean depths (6500–11,000 m) and have a distinct fauna from the surrounding deep-sea environment with high apparent levels of endemism (Wolff, 1959; Beliaev, 1989; Jamieson, 2015). A characteristic endemic group known as the snailfishes (Family Liparidae) are prominent members of the hadal community in at least five widely-distributed trenches (Japan, Kermadec, Kurile-Kamchatka, Mariana, and Peru-Chile; Nielsen, 1964; Jamieson et al., 2009; Fujii et al., 2010; Linley et al., 2016). These hadal fishes are notably different from common abyssal species that border the hadal zone in both form and functional role. Hadal liparids have small, translucent bodies and appear to be specialized predators (Linley et al., 2017; Gerringer et al., 2017a). In contrast, characteristic abyssal species such as macrourids have dark coloring and opaque tissues and are generalized benthopelagic predators and scavengers (e.g., Drazen et al., 2008). Observations of large aggregations of these snailfishes that are similar in form, at similar depths, and yet widely dispersed geographically in the seemingly isolated hadal systems, frames the question—why are liparids so successful in the hadal zone?

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A recent and unprecedented collection of otoliths (small aragonitic ear bones; Degens et al., 1969) from hadal snailfishes provided an opportunity to investigate the life history of the deepest dwelling fishes. Otoliths have long been used in fish ecology for age estimation because they usually form annual growth rings (Jackson, 2007). Age, growth, and longevity are traditionally estimated using whole or sectioned otoliths where putative annual growth zones are counted (e.g., Williams and Bedford, 1974). This technique has been applied to fishes from habitats as deep as ~3900 m (Wilson, 1988). Some otolith age estimates indicate that deep dwelling fishes may live longer than shallow living congeners (Cailliet et al., 2001), although the simple older-deeper dichotomy has been called into question (Drazen and Haedrich, 2012). The factors driving depth-related longevity are complicated and may be related to phylogeny, temperature, pressure, oxidative stress, and food availability, among other factors (Cailliet et al., 2001; Drazen and Haedrich, 2012).

In this study, two main life history hypotheses that may factor into the success of liparids near the greatest ocean depths are investigated. First, hadal liparids may be suited to the high-disturbance environment of hadal trenches, which are located primarily at subduction zones and are sites of frequent earthquakes (e.g. Fryer et al., 2003), due to shorter lifespans than groups living on the abyssal plain. Higher-disturbance environments have been shown to select for faster growth rates, for example, in the case of hydrothermal vent organisms (e.g. Lutz et al., 1994; Nedoncelle et al., 2013). Due to the small size of the hadal liparid otoliths (< 1 mm) and the general paucity of data on snailfish age and growth (Falk-Petersen et al., 1988; Orlov and Tokranov, 2011), otoliths of a shallower, common deep-sea liparid *Careproctus melanurus* Gilbert 1892 were investigated. These larger snailfish otoliths allowed the development of a sectioning and age estimation protocol for the family before conducting age estimation on the rare hadal otolith collection. To provide additional context and test whether the deeper-older trend applies in other fish orders, we examined growth patterns in *Coryphaenoides armatus* Hector 1875 and *C. yaquinae* Iwamoto & Stein 1974, which are common deep-abyssal and upper-hadal species (e.g., Linley et al., 2017).

The second hypothesis is that hadal snailfishes do not have a long-range dispersal mechanism that transports larvae out of the trench. Macrourids and many other deep-sea fishes have numerous small eggs and pelagic larvae, some of which occur in the epipelagic (Merrett, 1978; Stein, 1980a; Merrett and Haedrich, 1997; Busby, 2005). In contrast, members of the Liparidae are known to brood, and to have very large eggs (Stein, 1980b) and in some cases, have complex developmental strategies; most notably carcinophyly, whereby they deposit eggs in the gills of lithodid crabs (Yau et al., 2000; Poltev and Steksova, 2010; Poltev, 2013), and even spawn in crab traps (Poltev and Steksova, 2010). In addition, based on the relatively low number of large eggs found in *Notoliparis kermadecensis* Nielsen 1964 and *Pseudoliparis swirei* Gerringer & Linley 2017 (Gerringer et al., 2017c), we expected that larvae and juveniles of snailfishes would remain localized in the trench environment to increase survivorship. These factors of low fecundity, high parental investment, and an apparent lack of pelagic life history stages may have allowed for the radiation of the group into the hadal zone.

Otolith microchemistry provides an opportunity to test both hypotheses regarding early life history. In addition to their value in age estimation, otoliths can incorporate environmental chemistry that can provide clues to a fish's life history (Campana and Neilson, 1985; Campana and Thorrold, 2001; Trueman et al., 2012). By comparing how elemental chemical or isotopic compositions change through the growth of the otolith, it is possible to infer if the fish experienced environmental temperature changes over its lifespan, even with low sample sizes (Trueman et al., 2013). In the case of hadal and abyssal fishes, this is a valuable source of information, because direct observations of these fishes are brief, opportunistic, and historically rare. As otoliths grow in a sequence of deposited rings, their chemical composition reflects the nature of the environment at time of otolith mineralization (Kalish, 1989, 1991). Oxygen isotope ratios in the otoliths change as a function of temperature and $\delta^{18}O$ values of ambient water, allowing thermal history reconstruction when the oxygen isotopic composition of water can be constrained (e.g., Kozdon et al., 2011, 2013; Olson et al., 2012; Befus, 2016). Thus, the ratios of $^{18}O/^{16}O$ can be used to calculate habitat temperatures across the lifespan of individual fish (Thorrold et al., 1997), to within 1 °C precision at a 95% probability level (Høie et al., 2004). Generally, lower $\delta^{18}O$ values indicate higher temperatures at the time of otolith formation, due to thermodynamic effects on oxygen isotope fractionation. Changes in $\delta^{18}O$ values across an otolith are often indicative of an ontogenetic vertical migration or shallow-living planktonic larval stage, and this technique has been used to determine the thermal histories of a number of deep-sea species including slickheads (Shiao et al., 2016), rattails (Lin et al., 2012), cusk eels (Chang et al., 2015), and cutthroat eels (Shiao et al., 2014).

This study aimed to 1) estimate age in hadal snailfishes and abyssal macrourids by counting otolith growth zones; 2) construct ontogenetic temperature profiles to investigate life history through oxygen isotope analysis along the growth axis of otoliths for each species; and 3) discuss the role of life history and growth in driving community structure and endemism in fishes of the hadal zone. We provide the first investigation of the life history of some of the planet's deepest-living fishes to inform discussions of hadal endemism and depth-related trends in growth and longevity.

2. Materials and methods

Otoliths from three liparid and two macrourid species were investigated for age and growth. Sagittal otoliths were extracted from 38 *Notoliparis kermadecensis* specimens collected in April-May of 2014 and from 28 specimens of *Pseudoliparis swirei*, a newly-discovered liparid species from the Mariana Trench, collected in November–December of 2014 (Gerringer et al., 2017c). Sampling was conducted by free-vehicle baited trap. Collection details for both trench locations are provided elsewhere (Linley et al., 2016). Extracted otoliths were initially placed in 75% ethanol and later cleaned and air-dried for storage in 2 ml cryovials. An age estimation protocol for hadal liparids was developed using a confamilial reference species that has more massive otoliths, *Careproctus melanurus*. The 29 *Careproctus melanurus* specimens were collected in the Southern California Bight by trawl in 2013–2015 (Supplementary Table 1). Fish were frozen whole at sea and otoliths were extracted after thawing in the laboratory. *Careproctus melanurus* otoliths were washed in 50% bleach solution to remove remaining tissue, rinsed in deionized water, and then dried. Age estimates for two abyssal macrourids, *Coryphaenoides armatus* and *C. yaquinae*, were made from archived otoliths collected from Station M in the Pacific Ocean at depths around 4000 m, in 1995–1998 (collection details in Drazen, 2002). Total fish mass and standard length were measured at sea on freshly collected specimens for the hadal collections. For the abyssal macrourids, total fish mass was measured in the lab for frozen specimens, and total, head, and pre-anal fin lengths were measured at sea. Sex was determined macroscopically. Hadal otoliths were weighed in the lab using a microbalance (± 0.1 μg precision). Otolith dimensions were measured using fine scale calipers (0.01 mm). Length and width were digitally measured for the hadal liparid otoliths using ImageJ (Schneider et al., 2012).

2.1. Age estimation

The *C. melanurus* otoliths were first polished in the medial plane sulcus-side down by hand. The polished side was mounted on glass slides with resin (Cytoseal 60, Richard-Allan Scientific). The resin cured overnight, and the other side of the otolith was polished using an Isomet lapping wheel (SBT, Model 900) with 600-grit wet-dry carbide paper (Buehler). This polishing revealed growth ring structure across a medial section. Fine polishing was done by hand as needed with diamond lapping film. Success with this approach led to use of the method for the hadal specimens. For the much smaller hadal liparid otoliths, polishing was done in a similar manner to reveal a medial section, but polishing was performed entirely by hand on a smooth glass panel using 6 and 9 µm diamond lapping film (Buehler). Otoliths from *Coryphaenoides armatus* and *C. yaquinae* were cut in the transverse plane to 0.6 mm sections using an Isomet low-speed saw (Buehler), then mounted and polished using the lapping wheel method described above. Otolith sections were aged by two readers (Gerringer, Andrews) and initial estimates were based on various interpretations of the concentric growth zone structure. Refined criteria were determined based on well-defined sections for each species and an examination of length-at-age relationships (irregular patterns pointed to alternative counting criteria). The counting protocol for both abyssal macrourids here followed that detailed by Andrews et al. (1999a) for *Coryphaenoides acrolepis*. Although the importance of age estimate validation is recognized (e.g., Campana, 2001), none of the currently available methods for validation were practical for these species and the counts presented here were assumed to be annual and caused by seasonal fluctuations in organic matter inputs (Morales-Nin and Panfili, 2005).

2.2. Thermal history reconstruction

Otoliths were cleaned in methanol and cast in epoxy (Epoxicure, Buehler, Lake Bluff, IL, USA) in stainless steel bullets (liparids) and aluminum rings (macrourids). These were heated to 80 °C to remove excess moisture and desiccated in a vacuum chamber for ~30 s before curing at 50 °C overnight. Samples were polished to reveal the core using a series of grinding papers and diamond lapping films (Buehler 240, 400, 600 grit; 15, 9, 6, 3, 1, and 0.5 µm). Polished sections were sonicated in methanol, dried, and carbon coated (~250 Å, Cressington Carbon Coater, 208carbon, Watford, UK), then inspected visually with optical microscopy and scanning electron microscopy (SEM; JEOL JSM-5900LV, USA). Oxygen-isotope compositions across the otolith were measured using secondary ion mass spectrometry (SIMS; Cameca ims-1280, University of Hawai‘i at Mānoa, W.M. Keck Research Laboratory). For each measurement, the carbon coat was removed with the application of a 2.5 nA Cs^+ primary ion beam, rastered over a 25 × 25 μm^2 area for 120 s presputtering. For data collection, the raster size was reduced to 15 × 15 μm^2. Each measurement consisted of 30 cycles with 10 s' integration time per cycle. The automatic beam centering routine was applied. A normal incidence electron flood gun was used for charge compensation in an analyzed area. The two oxygen ions, $^{16}O^-$ and $^{18}O^-$, were measured in multicollection mode using two Faraday cups with 10^{10} and 10^{11} Ω registers, respectively. The magnetic field was regulated using a nuclear magnetic resonance controller. Mass resolving power was ~2000, enough to discriminate interference ions. Calcite reference materials (University of Wisconsin Calcite, UWC 1 and UWC 3) were used to determine instrumental isotope fractionation corrections. Although the otoliths are probably aragonite, a different polymorph, the difference in oxygen isotope measurements between calcite and aragonite is likely small (Matta et al., 2013) and no correction was applied in the present study. Data are reported as δ values in parts per thousand (permil; ‰) relative to Vienna Standard Mean Ocean Water (VSMOW, Eq. (1)).

$$\delta^{18}O = 1000*\left(\frac{\frac{^{18}O}{^{16}O}_{sample}}{\frac{^{18}O}{^{16}O}_{VSMOW}} - 1\right) \tag{1}$$

Reproducibilities (2σ) in calcite reference material measurements were 0.15‰ for UWC 1 and 0.15–0.17‰ for UWC 3. Measurement errors are given as 2σ and reflect both the measurement precision (2 standard error) for each analysis and the reproducibility (2 standard deviation) of standard measurements on the analysis day. Measurement spots were then inspected via SEM to ensure quality of the reading. Measurements taken on rough surfaces or those with large visible cracks were discarded and those with potential small scratches were noted. Values were measured relative to VSMOW (Vienna standard mean ocean water), and then converted to VPDB (Vienna Pee Dee Belemnite) based on true ratios.

$$\alpha = \frac{\delta^{18}O_{otolith} + 1000}{\delta^{18}O_{seawater} + 1000} \tag{2}$$

$$1000 \ln \alpha = 16.75\left(\frac{1000}{T}\right) - 27.09 \tag{3}$$

Habitat temperatures were calculated from $\delta^{18}O$ values (‰ vs. VPDB) according to the equations presented by Høie et al. (2004) and reproduced above (Eqs. (2) and (3)), based on otolith carbonate chemistry. Temperature (*T*) was calculated in Kelvin and was converted to °C. Local data on habitat temperatures at collection depth were recorded by free-vehicle lander for the abyssal and hadal species (described Linley et al., 2016) and by CTD at the collection site for *C. melanurus*. Temperature profiles for *C. melanurus* were extracted from the World Ocean Database (WOD; Boyer et al., 2013; Locarnini et al., 2013) for locations within 0.1° of capture site in May and October from two CTD casts (WOD unique ID numbers 8531355 and 8531681). Due to the lack of environmental data at deep abyssal and hadal depths, $\delta^{18}O$ values of seawater were calculated according to the outermost measurements taken from each otolith, which were presumed to reflect the known capture temperature. As a methodological check, these back-calculated values were compared to the few known measurements of seawater $\delta^{18}O$ from the region (Mottl et al., 2004). This manner of calibrating temperature estimates is generally considered accurate to within ± 1 °C (Thorrold et al., 1997; Høie et al., 2004). Based on instrumental reproducibility of UWC 1 and UWC 3 measurements and within-sample measurement variation, temperature error (2σ) in the dataset was between ± 0.8 and ± 2.5 °C (mean ± 1.6 °C).

Data analyses for both age estimation and thermal history reconstruction were conducted using the statistical programming platform R (R Core Team, 2015) and figures were generated using the package *ggplot2* (Wickam, 2009). Tentative von Bertalanffy growth functions (Eq. (4)) were fitted to length-at-age data using the package *fishmethods* (Nelson, 2016), considering the recommendations of Pardo et al. (2013), anchored at zero due to there being few juveniles and limited sample sizes in the collections. Length was standard length for liparids and total length for macrourids. L_∞ is the length at which growth reaches an asymptote, k is the growth rate, and age is age estimate in years.

$$Length = L_\infty - ((L_\infty - L_0)*e^{(-k*Age)}) \tag{4}$$

3. Results

3.1. Age estimation: *Careproctus melanurus*

Twenty-nine *C. melanurus* specimens spanned 11.8–21.8 cm standard length and body masses from 8.1 to 139.5 g (Supplementary Table 1). There were eighteen female, six male, and five unsexed individuals collected from depths of 340–841 m. Otolith mass was between 1.352 and 6.240 mg and dimensions were 1.65–2.72 mm in length, 1.98–3.14 mm in width, and 0.6–1.1 mm in height (otoliths shown in Fig. 1).

There were no significant differences between left and right otoliths within individuals for mass (Welch two-sample *t*-test, $t_{55} = -0.190$, $p = 0.850$), length ($t_{52} = 0.663$, $p = 0.510$), width ($t_{52} = 0.615$, $p = 0.541$), or height ($t_{50} = -0.468$, $p = 0.642$). All metrics (mass, length, width, height) correlated significantly with standard length (Supplementary Table 3), with otolith mass having the strongest slope

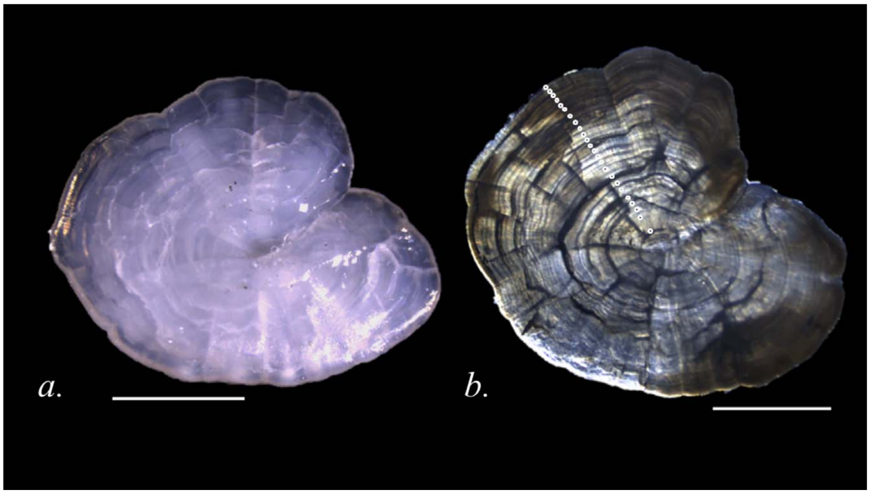

Fig. 1. Two views of *Careproctus melanurus* otoliths that provide details on the growth structure for this species. ***a)*** Whole *C. melanurus* sagittal otolith viewed in reflected light (sample 379#5). ***b)*** Otolith thin section (medial plane), viewed with transmitted light (sample 340#1) with an estimated age of ~24 years for subjective enumeration of annuli. Counted zones are marked. Scale bars 1 mm.

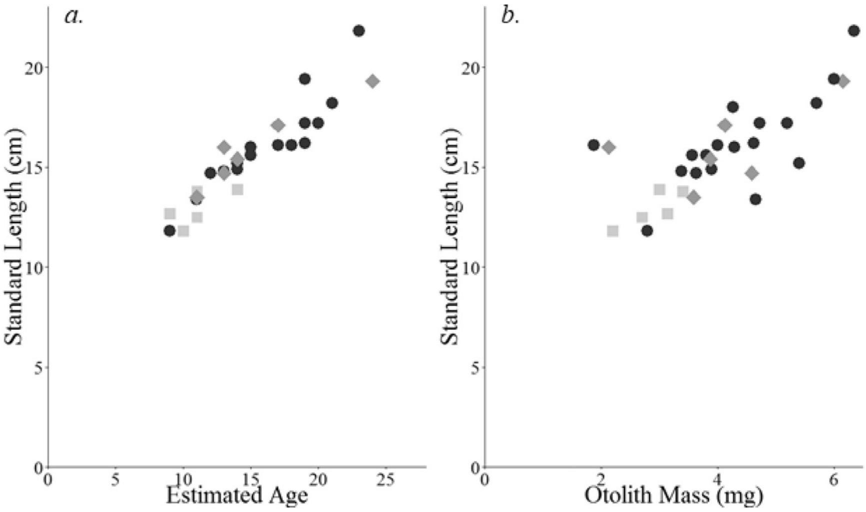

Fig. 2. ***a)*** Length-at-age relationships for *Careproctus melanurus* (n = 29). Results from females shown with circles, males with diamonds, and immature individuals with squares. Estimated age (years) based on otolith growth zones. ***b)*** Length as a function of otolith mass for *C. melanurus* (n = 29) for comparison.

(Supplementary Figure 1). Age estimates for *C. melanurus* were between 9 and 24 years assuming opaque zones represent annual growth rings (Fig. 2).

3.2. Age estimation: hadal liparids

Standard lengths of the 28 *Pseudoliparis swirei* used for age estimation ranged from 10.5 to 28.8 cm. Individual body mass ranged from 8 to 160 g, from capture depths 6914–7966 m. Thirteen of these were females, five males, seven juveniles, and three unsexed. Otoliths (Fig. 3) of this species weighed from 0.3050 to 1.4460 mg, were between 0.827 and 1.547 mm in length, 0.688–1.265 mm in width, and 0.35–0.59 mm in height.

In the 38 *Notoliparis kermadecensis* collected from the Kermadec Trench, depths 6456–7554 m, standard lengths were between 12.9 and 29.0 cm, and body mass ranged from 20 to 230 g. There were 19 females, 12 males, three juveniles, and four unsexed individuals. *Notoliparis kermadecensis* otolith mass was 0.3766–2.0050 mg, length was 0.879–1.539 mm, width was 0.671–1.311 mm, and height was 0.40–0.80 mm. Further collection details and individual results for all liparids can be found in Supplementary Table 1.

All metrics (otolith mass, length, width, and height) increased significantly with both standard length and body mass for both hadal liparid species (Supplementary Table 3; Supplementary Figure 2). Measurements between otoliths of individual fishes were not significantly different in mass, length, width, or height for either *P. swirei* (Welch two-sample *t*-test, $t_{49} = -0.107$, $p = 0.854$; $t_{52} = -0.107$, $p = 0.915$; $t_{51} = -0.241$, $p = 0.811$; $t_{51} = -0.127$, $p = 0.899$) or *N. kermadecensis* (Welch to-sample *t*-test, $t_{69} = 0.124$, $p = 0.901$; $t_{70} = -0.864$, $p = 0.390$; $t_{70} = 0.315$, $p = 0.754$; $t_{70} = -0.093$, $p = 0.926$). Assuming opaque zones represent annual growth, ages for these specimens were estimated to be 5–12 years old for *P. swirei* and 6–15 years old for *N. kermadecensis* (Fig. 4).

3.3. Age estimation: abyssal macrourids

Otoliths from 114 *Coryphaenoides armatus* were sectioned for age estimation (Fig. 5). Individuals ranged in total length from 44.0 to 93.5 cm (head lengths 7.25–15.38 cm) and had body masses between 300 and 3760 g. There were 31 females, 74 males, and nine of unknown sex. Otoliths weighed between 0.0362 and 0.1503 g, were 1.00–2.30 mm in height, 3.60–6.30 mm in width, and 3.50–7.35 mm in length. Forty-four *Coryphaenoides yaquinae* individuals were analyzed, with total lengths ranging from 34.7 to 65.0 cm, weighing 179–1107 g. Head lengths were between 7.4 and 12.0 cm. Of these, 40 were identified as female, two as male, and two of unknown sex. Otoliths of *C. yaquinae* ranged in mass from 0.0246 to 0.0858 g, in height from 1.20 to 1.90 mm, in width from 3.60 to 5.70 mm, and in length from 3.30 to 5.70 mm. Collection details, specimen measurements, and individual age estimates for both macrourids are available in Supplementary Table 2.

Left and right otoliths did not vary significantly in mass (Welch two-

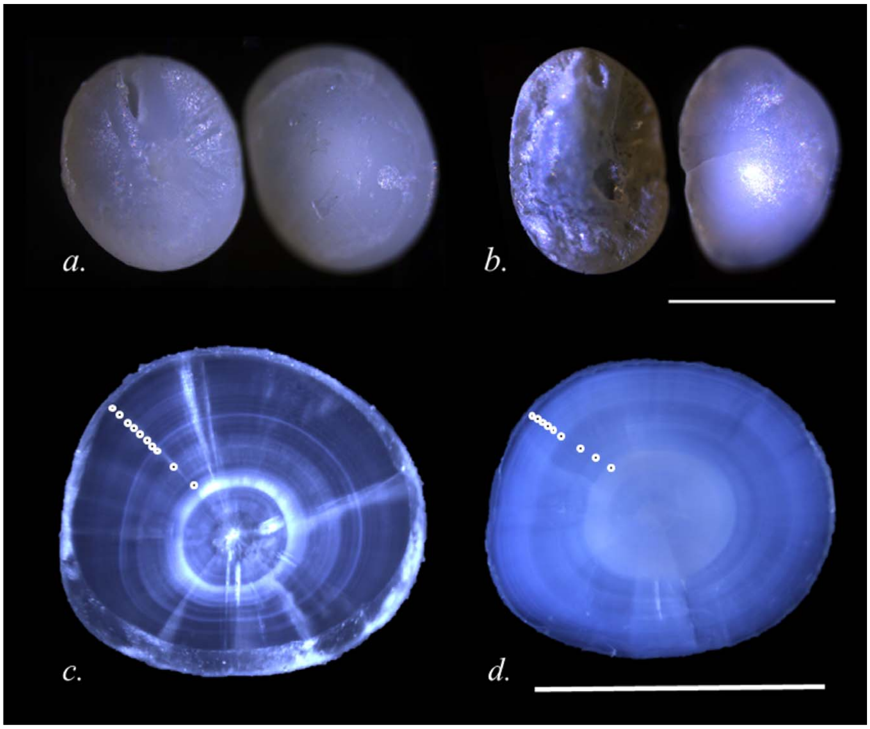

Fig. 3. Hadal liparid otoliths. ***a)*** *Notoliparis kermadecensis*, Kermadec Trench, sample 100326, whole. ***b)*** *Pseudoliparis swirei*, Mariana Trench, sample 200021, whole. ***c)*** *N. kermadecensis*, sample 100219, thin section, estimated age: 10 years. ***d)*** *Pseudoliparis swirei*, sample 200134, thin section, estimated age: 9 years. Counted zones are marked. Scale bars (***a***,***b*** and ***c***,***d***) 1 mm.

sample *t*-test: *C. armatus* $t_{224} = -0.964$, $p = 0.336$; *C. yaquinae* $t_{85} = -0.383$, $p = 0.703$), length (*C. armatus* $t_{224} = -0.413$, $p = 0.680$; *C. yaquinae* $t_{84} = -0.324$, $p = 0.747$), width (*C. armatus* $t_{223} = -1.434$, $p = 0.153$; *C. yaquinae* $t_{84} = -0.045$, $p = 0.965$), or height (*C. armatus* $t_{220} = -0.667$, $p = 0.506$; *C. yaquinae* $t_{85} = -0.706$, $p = 0.482$). Otolith mass, length, width, and height all increased significantly with total length and body mass (Supplementary Table 3) in both *C. armatus* and *C. yaquinae*. Age estimates for *Coryphaenoides armatus* in this collection ranged from eight to 29 years old. Otoliths from *Coryphaenoides yaquinae* had fewer annuli, with ages estimated from six to 16 years old (Fig. 6).

Age estimates, sample sizes, and estimated growth parameters for all study species are presented in Table 1. All fitted von Bertalanffy growth model parameters were significant ($p < 0.001$) except those for the *P. swirei* (L_∞: $p = 0.249$; k: $p = 0.312$). Growth functions fitted for macrourids based on pre-anal fin length also yielded significant results similar to those estimated using total length. For *C. armatus* using pre-anal fin lengths, L_∞ was estimated to be 50.6 ± 5.28 cm, with $k = 0.036 \pm 0.005$. Using pre-anal fin lengths, growth function estimates for *C. yaquinae* were $L_\infty = 20.8 \pm 1.51$ cm and $k = 0.159 \pm 0.028$.

3.4. Thermal history reconstruction

For all samples tested (Table 2), $\delta^{18}O$ values ranged from 28.8 to 33.8‰ relative to VSMOW. Errors (2σ) of individual point measurements ranged from ± 0.18 to ± 0.54‰ (mean 0.35‰) vs. VSMOW. The highest values were found in the deeper-living species (Fig. 7). Significant increases in $\delta^{18}O$ values (corresponding to decreases in habitat temperature) with increasing distance from the core were found for *C. armatus* (ANOVA, $F_{1,8} = 23.2$, $p < 0.05$), *N. kermadecensis* ($F_{1,4} = 18.2$, $p < 0.05$), and nearly significant increases were found for *P. swirei* ($F_{1,4} = 5.9$, $p = 0.073$). *Careproctus melanurus* $\delta^{18}O$ values also varied across the otolith, being lower in the first or second annuli than at the core, and then increasing toward the outer rings. No significant change across the otolith was found for *C. yaquinae* ($F_{1,8} = 0.1$, $p = 0.705$). $\delta^{18}O$ values at points on different sides of the otolith and at similar distances from the core were consistent (Fig. 7). Images of the otolith surface using scanning electron microscopy revealed some measurement points on roughly polished surfaces (triangles in Fig. 7). Based on previous laboratory observations, these values may be expected to be significantly higher (up to 4‰) than the true sample values (Kita et al., 2009). All SEM images can be found in the Supplementary Material. Conversions to VPDB are shown using the true ratios.

For calibration of *P. swirei* $\delta^{18}O$ measurements, we used habitat temperature measured *in situ* and the $\delta^{18}O$ value at the outer otolith edge to solve for the $\delta^{18}O$ of seawater (**Eqs.** 2, 3). Habitat temperature for adults ranged from 1.7 to 1.9 °C (mean 1.8 °C) based on temperature-depth data and specimen collection depth (6914–7966 m, Jamieson and Linley, unpublished data; 13,787 temperature measurements over 14 deployments greater than 6914 m). The mean temperature of 1.8 °C, and the outer edge $\delta^{18}O$ values gave a $\delta^{18}O$ value of −0.86‰ for seawater. Using this value for the thermal reconstruction, the corresponding habitat temperature at the innermost (otolith core) measurement was estimated to be ~6 °C (Fig. 8). This finding suggests a larval phase depth shallower than 1000 m (~430–920 m) in overlying waters. The Kermadec liparid, *Notoliparis kermadecensis*, was collected from depths between 6456 and 7554 m, with a temperature range of 1.2–1.3 °C (mean 1.3 °C; 3929 measurements over 5 deployments, July 2007). Based on the outermost $\delta^{18}O$ value in the otoliths, this would correspond to a $\delta^{18}O$ value of seawater of approximately −1.34‰. Habitat temperature estimates from the core measurements were calculated to be as warm as 8 °C (Fig. 8). This indicates the larval phase was at depths between ~450 and 930 m in overlying waters (Fig. 9).

The abyssal grenadier specimens provided contrasting results (Fig. 7). The *C. yaquinae* specimen was collected from 5255 m at a location near the Mariana Trench. Mean habitat temperature from this individual was estimated to be 1.5 °C (1.4–1.5 °C) for a depth range of 5000–5500 m (4380 CTD measurements over 22 deployments). Hence, the calibrated $\delta^{18}O$ value of seawater was estimated to be −1.52‰. Habitat temperature varied little across the otolith and represented depths below 2000 m. The *C. armatus* specimen was from the abyssal plains near the Kermadec Trench from a depth of 3865 m with temperature range of 1.0–1.6 °C (mean 1.2 °C, depths 3500–4500 m, 2119 temperature measurements over nine deployments, in 2007 and 2014). The calibrated $\delta^{18}O$ value of seawater was −1.74‰, which led to

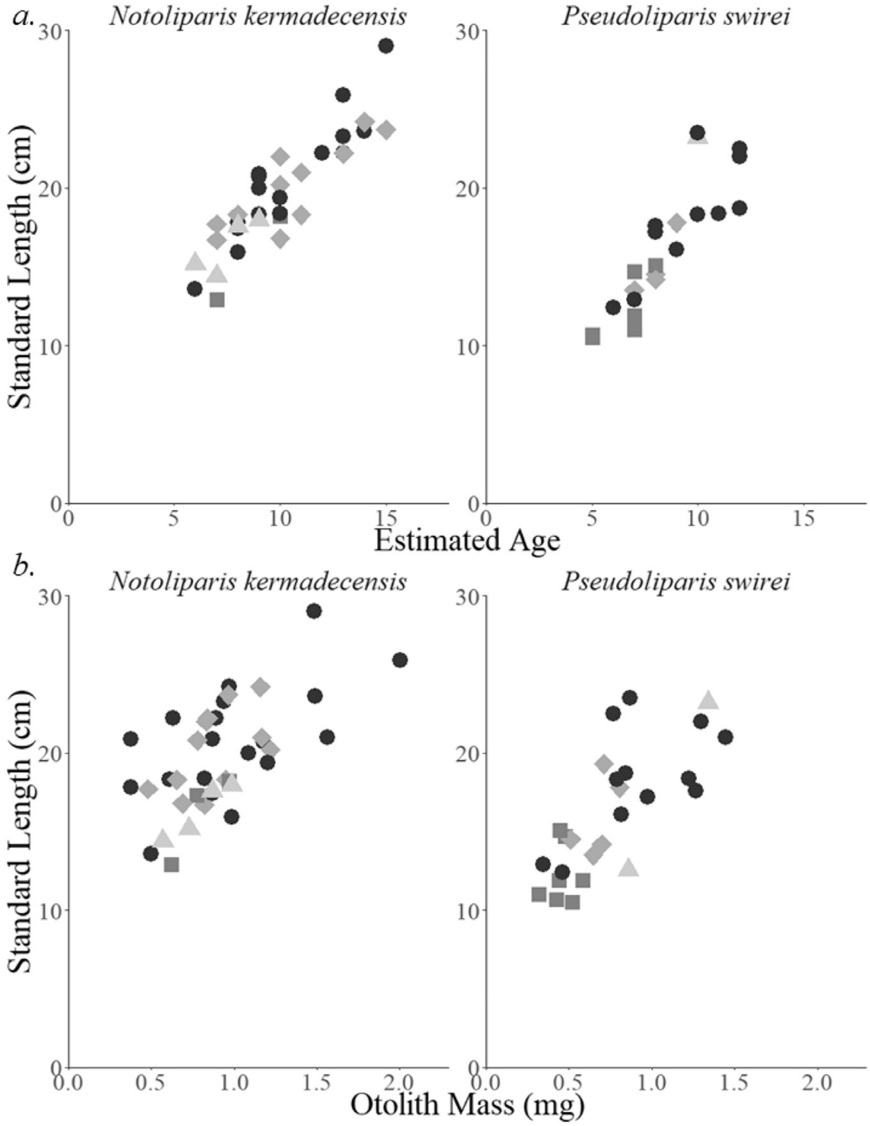

Fig. 4. ***a)*** Length-at-age relationships for two hadal snailfishes, *N. kermadecensis* (n = 34) and *P. swirei* (n = 23). Females (circles), males (diamonds), juveniles (squares), and unknown sex (triangles). Estimated age (in years) assuming opaque rings represent annual growth zones. ***b)*** Standard length (cm) as a function of otolith mass (mg) for comparison.

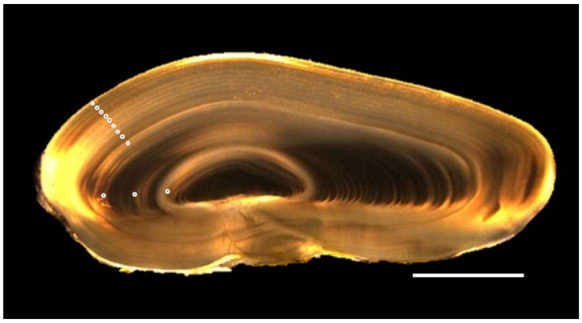

Fig. 5. *Coryphaenoides armatus* thin section. Otolith ID: CA018, estimated age 12 years subjective enumeration of annuli. Counted zones are marked. Scale bar 1 mm.

habitat temperatures ranging from 1 to 4 °C across the otolith. This suggests a change in habitat and a larval phase at depths deeper than 1000 m, but above the bottom.

The collection depth for the *C. melanurus* specimen was 834 m with a corresponding habitat temperature of 5.09 °C. The calibrated $\delta^{18}O$ value of seawater was −3.80‰. Measurements across the otolith provided evidence that habitat temperature increased to approximately ~9 °C, and then returned to ~5 °C. This suggests a pelagic larval phase to depths of 125–300 m, prior to the juveniles and adults subsequently settling at greater depths (Fig. 10). Based on counted rings for age estimation, this largest temperature change would correspond to the first few annuli (Fig. 10**b**).

4. Discussion

4.1. Age estimation

This study sought to compare patterns of life history in abyssal macrourids and hadal liparids through otolith analyses. Here, we focused largely on snailfishes, which appear to be the dominant fish family in multiple trenches worldwide (reviewed by Linley et al., 2016). Information on the age, growth, and longevity of snailfishes is lacking as few studies have been pursued for members of this family. One study that used whole otoliths to estimate the age of *Liparis gibbus* and *Careproctus reinhardti* from off Spitsbergen in the Arctic Ocean led to maximum ages of 6 and 7 years, respectively (Falk-Petersen et al., 1988). The study mentions that the annuli were easy to read. However, it must be considered that sectioned otoliths regularly reveal more growth zone structure not visible in whole otoliths. These finer rings are often annual, presumably reflecting seasonal changes in nutrient inputs, and lead to much greater estimates of age (e.g., Beamish, 1979; Andrews et al., 2002). In our collection, the difference between what was visible in the whole versus sectioned *C. melanurus* otoliths was substantial (Fig. 1).

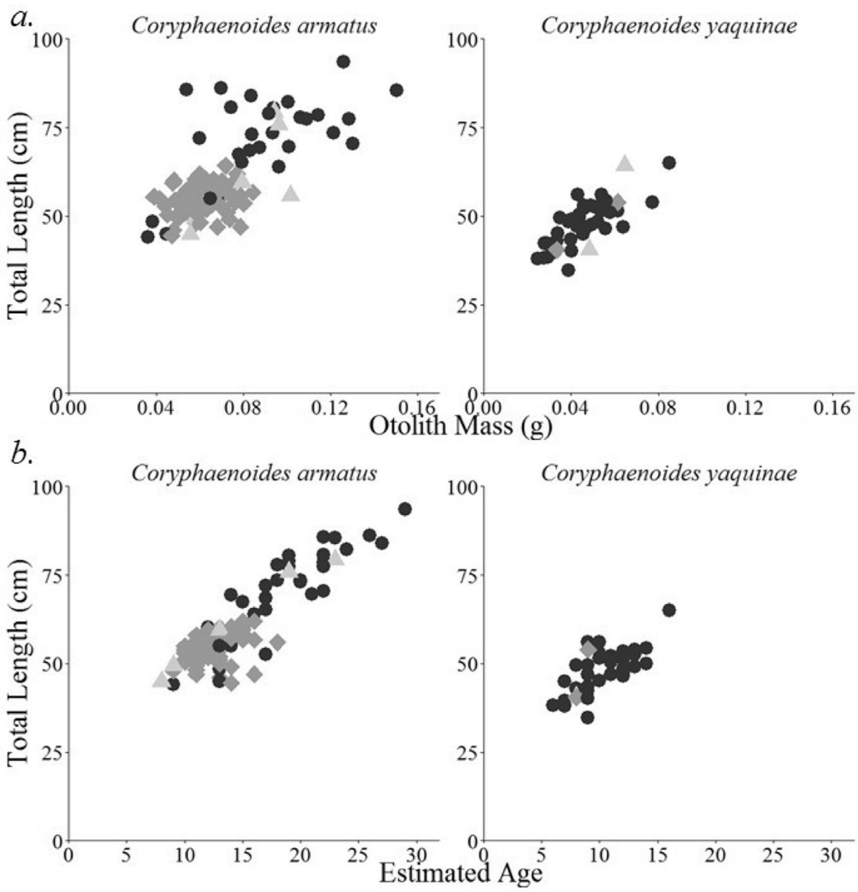

Fig. 6. ***a)*** Length-at-age relationships for two abyssal macrourids, *Coryphaenoides armatus* (n = 107) and *C. yaquinae* (n = 42). Females (circles), males (diamonds), and unknown sex (triangles). Estimated age (in years) assuming opaque rings represent annual growth zones. ***b)*** Total length as a function of otolith mass (g) for comparison.

Table 1
Tentative growth parameters and age estimates for liparids and macrourids. Lengths (cm) are standard length for liparids and total length for macrourids. Number of otoliths used in age estimation (n) shown. Growth coefficient (*k*) and maximum length (L_∞) ± standard errors for von Bertalanffy growth function models are presented. Growth functions fitted based on total length for macrourids, standard length for liparids.

Species	n	Length (cm)	Body Mass (g)	Age Estimates	L_∞ (cm)	*k*
Coryphaenoides armatus	107	44.0–93.5	300–3760	8–29	107 ± 6.33	0.053 ± 0.006
Coryphaenoides yaquinae	42	34.7–52.2	179–1107	6–16	60.5 ± 4.11	0.157 ± 0.026
Careproctus melanurus	29	11.8–21.8	8–140	9–24	22.9 ± 1.39	0.079 ± 0.009
Notoliparis kermadecensis	38	12.9–29.0	20–230	6–15	34.7 ± 4.03	0.086 ± 0.016
Pseudoliparis swirei	28	10.5–28.8	8–160	5–12	75.9 ± 64.0	0.029 ± 0.028

Table 2
Samples used for thermal history reconstruction. Depth in meters and L is standard length in centimeters for liparids and total length in centimeters for macrourids. Number of points measured along otolith were taken in two opposing transects. Mean temperature over the capture depths is listed with ranges in the text. $\delta^{18}O$ values (‰ vs. VSMOW) for seawater estimated based on outermost measurement and capture temperature.

Species	Location	Depth	°C	$\delta^{18}O_{sw}$	L	Sex	Sample ID	Points
Careproctus melanurus	California	834	5.1	−3.80	18.0	female	841#1	8
Coryphaenoides armatus	Kermadec Trench	3865	1.2	−1.74	50.3	male	100038	10
Coryphaenoides yaquinae	Mariana Trench	5255	1.5	−1.52	77.3	female	200152	10
Pseudoliparis swirei	Mariana Trench	7841	1.8	−0.86	11.9	juvenile	200072	6
Notoliparis kermadecensis	Kermadec Trench	7515	1.3	−1.34	18.3	male	100171	6

Otolith sectioning was necessary for age estimation of the smaller liparids used in this study. Maximum age estimates of 10–13 years for the family in general, including previous estimates for *C. melanurus* from the northwestern Pacific Ocean, were based on counting growth zones using the break-and-burn method (Orlov and Tokranov, 2011). Our results suggest that snailfishes in general may be longer-lived, with estimates on the order of twenty years. This discrepancy warrants further investigation, including the use of validation techniques.

The small sample size and narrow specimen length range prevented a reasonable fit of the von Bertalanffy growth function for our study species except as an exploratory tool, especially given the lack of very small/young fish (Horn et al., 2010). In addition, length at maturity for *C. melanurus* remains unknown (Stein, 1980b) and precludes an estimate of age at maturity. However, if the length of each species tends to plateau with increasing otolith mass, we can conclude that fish approaching maximum size were sampled and that estimates of age may

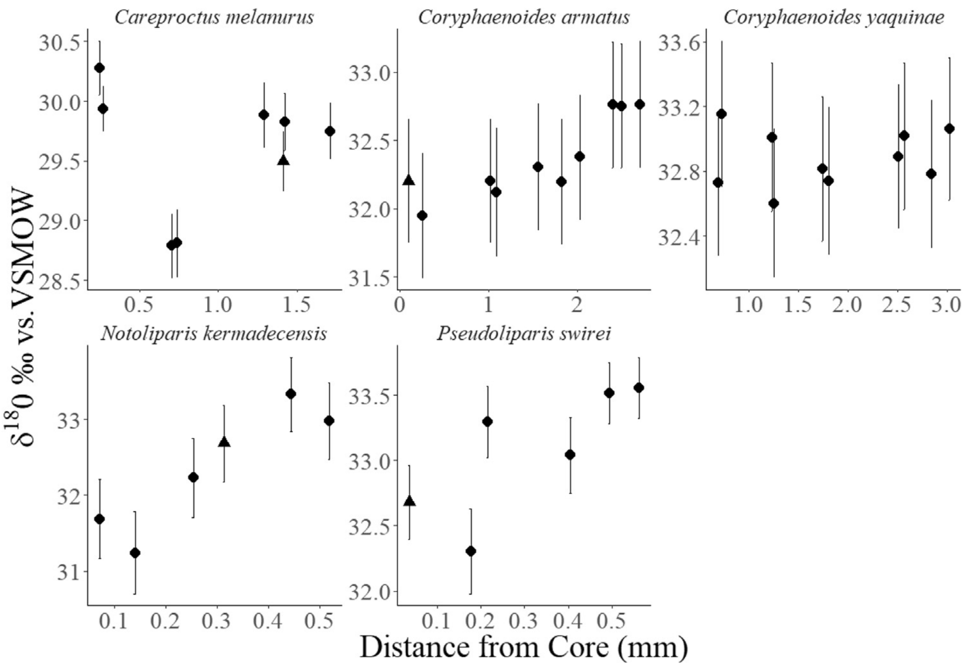

Fig. 7. Measurements of δ^{18}O values (‰ vs. VSMOW) across individual otoliths by species. Triangles indicate measurements that may have imperfections based on SEM inspection. Error bars indicate 2σ. Distance measured from center of the otolith core.

represent maximum age for the species. For *C. melanurus*, growth zones were well defined in the medial sections. Our tentatively-fitted von Bertalanffy function suggested a maximum standard length of near 23 cm, near the maximum size from this collection. Length-at-estimated-age curves for *C. melanurus* did not yet reach a plateau, suggesting a lack of largest individuals in our collection. Subjectivity in age estimation was greatest in the earliest growth because of what appear to be checks (non-annual marks) with spacing that was inconsistent with asymptotic growth. Edge effects were also a problem for the more recent growth. If our age estimation protocol is accurate, *C. melanurus* may approach maximum size in ~15–20 years, with a longevity on the order of 25 years. In addition, the low slope for the increase in size with age for the youngest fish studied implies either early overcounting or a low growth coefficient (*k*). An anchored von Bertalanffy growth function yielded a *k* value of 0.079 ± 0.009 for *C. melanurus*, similar to that found in other upper slope-dwelling fishes (Drazen and Haedrich, 2012).

This study provides the first age estimates for the planet's deepest-living fishes based on otolith growth zones. Age estimates for *Pseudoliparis swirei* were as high as 12 years, and up to 15 years old for *Notoliparis kermadecensis* from the Kermadec Trench. Although sample sizes for liparids in this study were low for a comprehensive quantification of age and growth, similarities between the otolith mass to standard length, and estimated ages to standard length relationships (Fig. 4) provide evidence for consistency in the age estimation protocol. These estimates are much less than may have been predicted according to the older-deeper trend seen in other studies (Cailliet et al., 2001), although as more age estimation work has been done on a variety of deep-sea commercial and bycatch species, a high variability in ages at depth has emerged (e.g., Andrews et al., 1999a, 2009, 2012; Horn et al.,

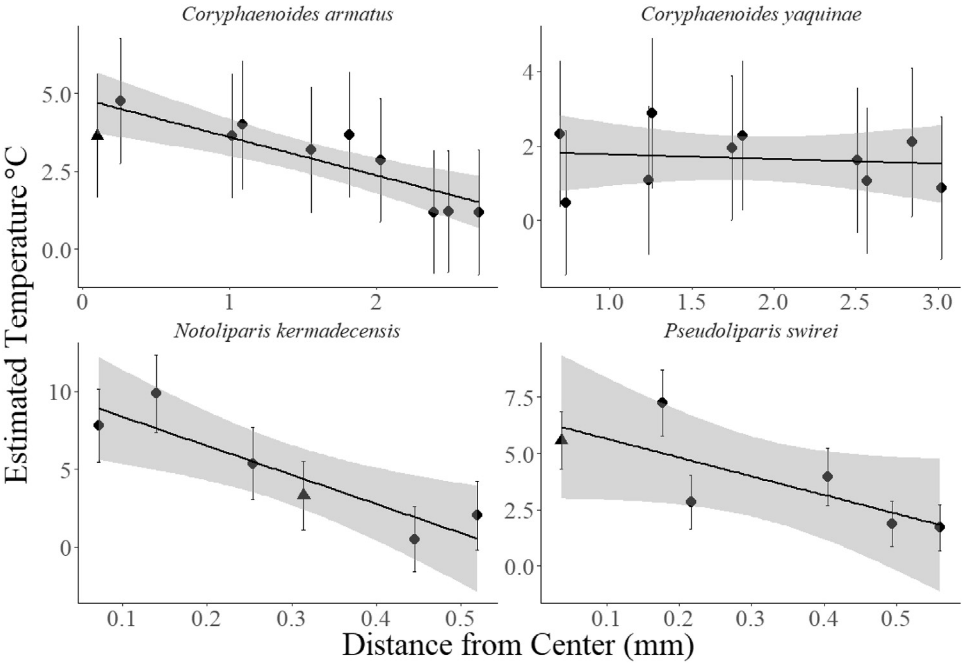

Fig. 8. Estimated temperature changes across the otoliths of the abyssal and hadal fishes of this study. Calculated δ^{18}O for seawater at collection locations was used to calibrate the measured δ^{18}O values through the otolith transects to determine water temperature through ontogeny (Høie et al., 2004). Triangles indicate measurements with potential scratches seen in SEM. Linear fits with 95% confidence intervals shown in gray.

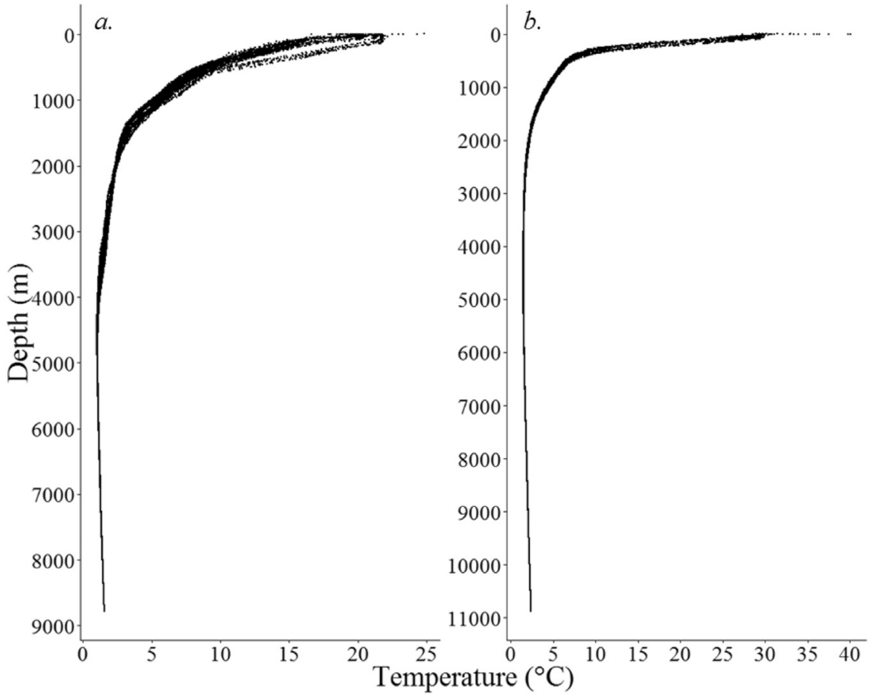

Fig. 9. Temperature-depth profiles for locations near the collections sites within the Kermadec (left) and Mariana (right) trenches (Unpublished data, A. Jamieson and T. Linley, deployment details provided by Linley et al. (2017). Profiles are based on 35,535 measurements over 13 deployments for the Kermadec Trench and 60,627 measurements over 24 deployments for the Mariana Trench (2007–2014).

2012; Tracey et al., 2017). The L_∞, length of asymptotic growth, estimates of 34.7 ± 4.03 cm for *N. kermadecensis* seem reasonable with video observations, collections, and predictions based on depth trends in body size (Priede and Froese, 2013; Linley et al., 2016). For *P. swirei*, however, the predicted L_∞ of 75.9 ± 64.0 cm is not concordant with the known biology of the species and has a very large error range, suggesting that the collection lacks data from the largest individuals and has insufficient sample size. However, if growth of this species is similar to *N. kermadecensis*, as our analysis suggests, the relatively low ages and moderate growth of hadal liparids are concordant with the growing recognition that food supply in trenches may be higher than the surrounding abyssal plains due to accumulation of organic matter through topographic funneling (George and Higgins, 1979; Danovaro et al., 2002; Itoh et al., 2011; Ichino et al., 2015). The presumed shorter lifespans and low age at maturity suggested by the hadal liparid data would be consistent with the hypothesis that liparids are adapted to a higher-disturbance environment than abyssal plain species. The growth coefficient (k) for *Notoliparis kermadecensis* was slightly higher than that

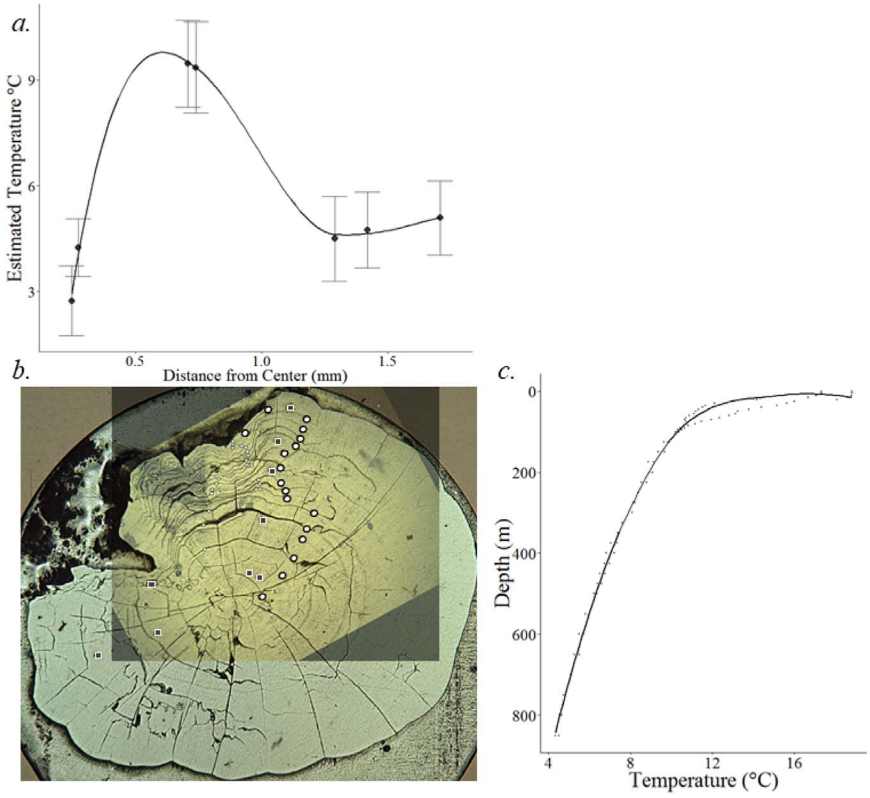

Fig. 10. ***a)*** Estimated temperature changes across the otolith of an adult *Careproctus melanurus* (sample 841#1). Calculated $\delta^{18}O$ for seawater at collection locations was used to calibrate the measured $\delta^{18}O$ values through the otolith transects to determine water temperature through ontogeny (Høie et al., 2004). ***b)*** Growth zones and SIMS spots across *C. melanurus* otolith. Rings counted in age estimates marked in small white circles, SIMS measurements in dark gray squares. ***c)*** Temperature profile for *Careproctus melanurus* collection site. Data extracted from WOD. Profile constructed from 88 measurements in May and October.

found for *C. melanurus*, at 0.086 and 0.079, respectively. The sample size for *P. swirei* was too small for reasonable growth parameters for comparison, as evidenced by the large standard errors for both k and L_∞, as well as the linear shape of the growth curve. Hadal subduction zones are highly susceptible to disturbance (Itou et al., 2000; Oguri et al., 2013) compared to the surrounding abyssal plains, which are considered comparatively stable environments. Seismic activity can cause turbidity flows, which can greatly impact species distributions (Fisher and Raitt, 1962; Richardson et al., 1995; Danovaro et al., 2002). Snailfishes may be adapted to the hadal environment by having faster growth, with less time to reproductive maturity.

Many more age estimates exist for the macrourid fishes (reviewed by Swan and Gordon, 2001), allowing a framework for discussion of the deeper-older trends. Another rattail in the same genus, *Coryphaenoides acrolepis* was validated to reach ages of at least 56 years based on $^{210}Pb/^{226}Ra$ dating, with growth zone age estimates as high as 73 years (Andrews et al., 1999a). Using a similar counting protocol developed by that study, the present maximum age estimates were 29 and 16 years for *C. armatus* and *C. yaquinae*, respectively. Age in *C. armatus* is similar to another study from the population on the Mid Atlantic Ridge (Bergstad, 2013) however, in the present study, neither length-at-age curve for these species reached a plateau, therefore it is possible that maximum ages for both macrourids can be greater than found in this collection given sampling adequacy. While longevity for *C. armatus* and *C. yaquinae* does not appear to be on the order of 100 years, as may have been expected from the deeper-older hypothesis, sampling adequacy and age reading need further investigation. Gadiformes such as the macrourids have been shown to grow more slowly with depth of occurrence in the first thousand meters (Drazen and Haedrich, 2012). This pattern was found to be exponential and the data presented here confirm this pattern at much greater depths because the k coefficients for the abyssal species in this study are similar (*C. armatus*) or higher (*C. yaquinae*) than bathyal species (Table 1). An exponential relationship in growth rates plateauing around 1000 m, mirrors vertical profiles of temperature, strongly suggesting temperature is a driving factor.

Given the available data, age at maturity may be 5–10 years for both hadal snailfish species. Standard length at maturity was approximately 13–15 cm for *P. swirei* and near 13–17 cm for *N. kermadecensis*. While we found clear relationships between size, age, and otolith mass, it could be inaccurate to estimate age from only the otolith mass, as has been found for other species (e.g., Pilling et al., 2003). Two-stage otolith-mass growth relationships are not uncommon in deep-sea species, whereby the otolith-mass growth rate slows with age, often related to the onset of spawning (and close banding representing a 'transition zone') such as for orange roughy *Hoplostethus atlanticus* (e.g., Smith et al., 1995; Francis and Horn, 1997; Horn et al., 1998; Tracey and Horn, 1999) and splitnose rockfish *Sebastes diploproa* (Bennett et al., 1982). Alternatively, for a number of oreo species, the transition zone appears to be related to a change from pelagic to demersal habitat (James et al., 1988; Stewart et al., 1995). These fish have much greater longevity than estimated for hadal liparids, hence the shift in growth pattern may not be as obvious in the hadal snailfishes. However, there did seem to be a shift to finer ring structure indicating a slowing of growth at three to four years for the hadal liparids (Fig. 3). Based on this visible change in the otolith growth pattern, age at maturity may occur relatively early for both hadal liparid species. In *Coryphaenoides armatus*, this shift usually occurred near five years, and close to three years for *Coryphaenoides yaquinae*. However, Stein and Pearcy (1982) found that only the largest *C. armatus* females had developed eggs. Further, for other macrourids, age at maturity is usually 30–50% of maximum age (Drazen and Haedrich, 2012), suggesting our estimates for this family may be too low. Additional collections of small individuals will be needed to better estimate age at maturity.

There are certain limitations to the age estimation method employed here that must be acknowledged. The hypothesis that counted opaque zones represent annual growth for any given fish species requires validation (e.g., Campana, 2001; Cailliet and Andrews, 2008). It is possible that some growth zones represent sub-annual increment structure from unknown environmental signals, such as smaller-scale seasonal changes or stochastic food fall events (e.g., Brothers et al., 1976; Pannella, 1980; Hüssy et al., 2010). In hadal trenches, nutrient inputs may be variable due to seismic activity (Oguri et al., 2013), though the degree to which this could mask a seasonal signal is not yet known. The list of potential age validation techniques (e.g., Campana, 2001) becomes much shorter in deep-sea systems (discussed by Mace et al., 1990; Andrews et al., 1999a). Ship time, sampling equipment, and depth issues make a mark/recapture study impractical for hadal fishes. Most other methods are also challenging for various reasons. One of the more feasible methods is an analysis of growth in the outer most ring collected in different seasons (Gordon and Swan, 1996), but this would require extended temporal sampling opportunities that are not currently available in hadal environments. Validation by radiometric dating has been applied to some deep-sea fishes (Andrews et al., 1999a, 2009), but the amount of material required and the necessity of pooling individuals of similar age precludes this kind of analysis (Andrews et al., 1999b). Only about one hundred hadal liparids have been collected in the fifty years since their discovery (Andriashev, 1955; Nielsen, 1964; Andriashev and Pitruk, 1993; Stein, 2005, 2016; Linley et al., 2016), hence this amount of material is not available. Despite these limitations, the development of a protocol based on a shallower-living liparid species provided some credence to the estimates. Furthermore, the known seasonality of nutrient inputs in the deep sea (e.g., Lampitt, 1985; Morales-Nin and Panfili, 2005; Lutz et al., 2007; Rowe, 2013), presumably even at hadal depths, provides at least a conceptual framework for the formation of annual growth zones. With the present lack of a feasible validation method for hadal snailfishes, we must consider these age estimates as preliminary and note their uncertainty.

4.2. Thermal history reconstruction

Oxygen isotopic compositions across the otolith were used to investigate changes in habitat temperature. For *Careproctus melanurus* we found clear changes (1.5‰) that corresponded to a 5 °C increase within the first few years of growth (~3–4 years), followed by a return to cooler temperatures later in life, although estimated $\delta^{18}O_{seawater}$ values were lower than would be expected. These changes likely reflect an early life history stage that moves upward in the water column, settles to the bottom on the upper slope, which is followed by an ontogenetic downslope migration with increasing size and age. This may not be an unusual circumstance for benthic or benthopelagic species of the continental slope—Pacific grenadier have been collected just below the thermocline and the smallest individuals are collected only on the upper slope (e.g. Matsui and Kato, 1991).

Changes in isotopic composition across the abyssal macrourid otoliths were far less pronounced or absent. There may have been a slight decrease in habitat temperature throughout growth for *Coryphaenoides armatus*, but no change was observed for *C. yaquinae*. These findings may indicate that the vertical migration of larvae before settling back to the bottom is well below the thermocline. A shallow juvenile phase was discovered using oxygen isotope analysis of *Coryphaenoides rupestris* otoliths (Longmore et al., 2011), but this does not seem to be the case for these deepest-dwelling congeners, and abyssal macrourid larvae have not been located. Given the temperature-depth profiles collected for *C. armatus* in the Kermadec Trench, an individual collected near 4000 m with a habitat temperature of 1–2 °C, likely had a larval stage close to 1000 m depth, perhaps accounting for their elusiveness, and also matching a deep downslope migration of juveniles from middle slope to greater abyssal depths (Collins et al., 2005).

Results from the hadal liparid isotopic analyses were surprising, with significant increases in $\delta^{18}O$ values across the otolith for both species. These changes could reflect an up to eight-degree change in habitat temperature, which would place larvae at a surprising depth of shallower than 1000 m, thousands of meters above the adult populations, which appear endemic to their respective trench systems. According to the size of the opaque growth zones, the largest temperature changes for both hadal species seem to be in the first two years of life. Depth differences in various life history stages of deep-sea fishes revealed by isotope analysis are not uncommon, such as reported for bluenose (*Hyperoglyphe antarctica*) off New Zealand by Horn et al. (2010), orange roughy off Ireland (Shephard et al., 2007), and the jellynose fish (*Ateleopus japonicus* and *Ijimaia dofleini*) near Taiwan (Shiao et al., 2017), but the depth differences between pelagic and demersal stages of the hadal liparids suggested here far exceed those of other species. Larvae of the shallow-living snailfish genus *Liparis* have been shown to undergo pelagic planktonic stages before transitioning to life near the benthos (Sokolovskii and Sokolovskaya, 2003), perhaps providing an evolutionary precedent for the planktonic stages of hadal species suggested by the SIMS analyses here.

The SIMS results contradict what may be expected from the extremely large eggs (up to 9.4 mm in *Pseudoliparis swirei*) and low fecundities found in the hadal liparids (Gerringer et al., 2017c; Nielsen, 1964), which both suggest the possibility of parental care and a benthic, developmentally advanced, larval stage. Our results contrast the hypothesis of Priede (2017), who posited that the groups of hadal snailfishes seen at baited cameras might even be family groups with parental care. Gravid females of *Notoliparis kermadecensis* were caught in the Kermadec Trench in both April and November, suggesting continuous or at least a sub-annual periodicity to reproduction (present study collection, HADEEP). Fishes living in the hadal zone are known to exhibit specific adaptations to their *in situ* hydrostatic pressure regimes (Yancey et al., 2014; Gerringer et al., 2017b). The physiological impact of such a dramatic pressure change throughout ontogeny would likely be non-trivial.

The estimation of δ^{18}O values for seawater, given limited environmental data on the deep-sea systems, is approximate and not directly measured as in other studies that have applied this method (e.g., Thorrold et al., 1997). The similarities of estimated δ^{18}O values of seawater between the sites and in different species provides some support for the validity of the method. Our calculated δ^{18}O value of seawater of −0.86‰ (vs. VSMOW) is also very close to those measured by Mottl et al. (2004) in the deep Mariana region (−0.47 ± 0.06‰), supporting findings. These close values also support the choice of the Høie et al. (2004) equation. Even at low temperatures beyond the calibration, this equation yielded reasonable estimates of the δ^{18}O values of bottom water based on *in situ* temperature and isotope analysis of the outer otolith rings. No measurements of δ^{18}O values of seawater were available from the Kermadec Trench for comparison. Further, slight changes in water mass salinity are not expected to change isotopic fractionation patterns substantially (Fowler et al., 1995; Elsdon and Gillanders, 2002). Thus, it is likely that changes in δ^{18}O values across the otolith indeed reflect changes in habitat temperature. The measurement of organic material, rather than the aragonitic portion of the otolith, can cause significant differences in isotopic values measured via SIMS (e.g., Matta et al., 2013); however, these differences are usually ~5‰ (vs. VPDB) below expected values and relatively easy to identify as outliers (Shiao et al., 2014). Matta et al. (2013) did find differences in the oxygen isotopic compositions of charred and uncharred otoliths, with the latter having relatively low in δ^{18}O values. However, our calculated δ^{18}O values of seawater for the hadal species were consistent with those measured directly, as discussed above, suggesting that the organic material did not significantly alter results. For *C. melanurus*, calculated δ^{18}O values of seawater were anomalously low, perhaps due to the measurement of uncharred vs. charred otoliths and the remaining organic material (Matta et al., 2013). Hadal pressures also do not explain the data because pressure effects on oxygen isotope fractionation are only significant at pressures tenfold higher than those seen at hadal depths (Clayton et al., 1975; Polyakov and Kharlashina, 1994). The fact that changes in δ^{18}O values in the present study followed a consistent trend and were highly reproducible within the spot measurements of the same annulus on a corresponding side of the otolith provides support for measurement precision. Although the absolute temperatures reported are approximate, the change in isotopic composition across the otolith should reflect relative ontogenetic change in habitat temperature. It is possible that the Høie et al. (2004) equation is overly sensitive to changes in delta values or that additional biological effects are confounding results. Results are similar to those found by Linzmeier et al. (2016) who showed that changes in δ^{18}O values of *Nautilus* shell rings corresponded to depth-related temperature changes of ~12 °C. Our data provide intriguing initial insight and further investigation of otolith microchemistry is warranted.

5. Conclusions

Age estimates based on opaque zones in otolith thin sections for *Coryphaenoides armatus* and *C. yaquinae* were lower than may have been expected from bathyal species, but growth rates may be similarly slow (e.g. Andrews et al., 1999a; Drazen and Haedrich, 2012). Analysis of oxygen isotopic composition across the otoliths of *C. armatus* revealed changes in habitat temperature of ~1–2 °C throughout ontogeny, suggesting deep pelagic larval stages for this species. No significant changes in δ^{18}O values were found across the otoliths of *C. yaquinae*, suggesting stable temperatures in larval and juvenile phases and throughout adulthood. Larvae for these deepest-living macrourids have yet to be found, likely because of their great depths of occurrence, below most trawling activity.

This study provides the first age estimates for fishes from hadal depths. Age estimates suggested that hadal liparids do not seem to fit the deeper-older trend seen for shallower-living fishes (e.g., Cailliet et al., 2001), although this study had low sample sizes. The reason for their potential moderate growth rates and relatively young ages could be adaptations to the greater food levels in the seismically active, high disturbance environment of the hadal zone. Results from oxygen isotope measurements across the otolith suggest that hadal snailfishes have a shallower pelagic larval stage. This contradicts expectations that a benthic life history could enable isolation and the development of hadal endemism in addition to allowing them to benefit from the absence of predators at hadal depths. The success of the snailfishes in the hadal zone may be related to other factors, such as trophic ecology and pressure adaptation.

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Contributors

JCD, AJJ, TDL, and MEG collected abyssal and hadal fish specimens. NDG collected *Careproctus melanurus* samples. MEG and AHA developed the sectioning protocols and estimated ages. MEG, GRH, and KN conducted oxygen isotope analyses. All authors contributed to the discussion and interpretation of the ideas presented and the writing and editing of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2017.12.002.

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