



Variability in growth rates of long-lived black coral *Leiopathes* sp. from the Azores

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ABSTRACT: Five colonies of black coral *Leiopathes* sp. were collected as bycatch from depths of 293 to 366 m from the Condor, Açor, and Voador seamounts (Azores region). The colonies had axial diameters between 4.9 and 33.1 mm and heights between 43 and 175 cm. Their ages and radial growth rates were estimated using radiocarbon dating. Results indicated that the smallest and largest colonies had similar radial growth rates of 5 to 7 $\mu\text{m yr}^{-1}$, whereas the other 3 colonies had grown more rapidly by a factor of 3 to 5 at ~ 20 to 30 $\mu\text{m yr}^{-1}$. Colony lifespan ranged between 265 ± 90 and 2320 ± 90 yr. Fine-scale sampling along a radial transect from the edge to the center of the 2320 yr old *Leiopathes* sp. revealed variable growth rates throughout the colony lifespan. Slower radial growth rates of ~ 4 to 5 $\mu\text{m yr}^{-1}$ were recorded over the initial 1600 yr and the last 300 yr of its life span, and a period of more rapid growth (20 $\mu\text{m yr}^{-1}$) over the intermediate 400 yr of its life. Variability in radial growth rates among colonies resulted in colony ages that were not linearly correlated to colony axis diameter or height. Our findings of great longevity and slow growth rates for *Leiopathes* sp. agree with other *Leiopathes* sp. age and growth studies, indicating that colony and population recovery from damage or removal may take centuries to millennia.

KEY WORDS: Antipatharia · Cold-water corals · Deep-sea · Growth · Longevity · Radiocarbon · Northeast Atlantic

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INTRODUCTION

Deep-sea or cold-water coral ecosystems have been recognized as important biodiversity hotspots in the deep sea (Roberts et al. 2009). The structural complexity of cold-water corals provides essential habitat that is used during feeding and spawning and as nursery grounds for a range of organisms, including commercially important fish species (Husebø et al. 2002, Reed 2002, Costello et al. 2005, Metaxas & Davis 2005, Roberts et al. 2009). An added factor that creates a sense of urgency in protecting these unique organisms is their extreme vulnerability to disturbance. Several studies have shown that bottom fishing can damage or destroy cold-water corals,

reducing the 3-dimensional complexity of the bottom topography and leading to decreased faunal biodiversity and biomass (Koslow et al. 2001, Hall-Spencer et al. 2002, Morgan et al. 2005, Althaus et al. 2009, Clark & Rowden 2009).

Despite the realization of damage to these communities, the recovery of cold-water coral ecosystems from bottom fishing impacts is poorly known (Althaus et al. 2009). An understanding of cold-water coral life history traits, such as age, growth rates, and longevity, is essential to appreciate the nature and extent of these effects and to evaluate the time scale of recovery. Cold-water corals can attain ages on the order of decades to millennia (e.g. Druffel et al. 1995, Adkins et al. 2004, Andrews et al. 2009, Roark et al.

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2009). Some antipatharians or black corals are particularly long-lived, with estimated ages in the thousands of years. At the extreme end of longevity is an estimate exceeding 4000 yr for a *Leiopathes* sp. colony in Hawaii (USA), representing the longest-lived invertebrate to date (Roark et al. 2009).

The Azores harbor diverse cold-water coral garden communities, dominated by gorgonians, stylasterids, and black corals, predominantly inhabiting rocky hard-bottom areas in island slopes and seamounts (OSPAR Commission 2010a, Braga-Henriques et al. 2012, Tempera et al. 2012). Local artisanal fisheries have continually targeted some of these coral-rich areas in the seamounts for several decades, mostly using bottom-tending longline and handline gears. The bycatch of bottom longline fisheries revealed that *Leiopathes* sp. are often damaged and captured during fisheries operations (Sampaio et al. 2012), raising concerns on the extent of these impairments and their recovery potential.

The aim of the present study was to estimate age and growth rates of *Leiopathes* sp. in the Azores region using radiocarbon dating. Additional objectives were to (1) determine the variability in growth rates within and between black coral colonies from the same and different geographic regions; and (2) measure the correlation between colony age and skeletal axis diameter and height as a basis for bycatch census purposes and video transect analyses. Ultimately, the goal is to gather information to better evaluate the vulnerability of these species to fisheries impacts and the capacity of *Leiopathes* sp. for recovery from damage or removal.

MATERIALS AND METHODS

Specimen collection and identification

Black coral colonies were obtained from bycatch material from the local longline fishing fleet. Two specimens were collected from Condor seamount at depths of 293 and 366 m, 2 other from the Açor seamount at depths of 302 and 366 m, and a fifth from the Voador seamount at a depth of 366 m (Fig. 1, Table 1). The material was deposited in the collection of the Department of Oceanography and Fisheries of the University of the Azores (DOP-UAz).

All colonies were identified as belonging to the genus *Leiopathes* (Family Leiopathidae) based on the presence of an irregular sympodial corallum with multi-directional branching and uniserial to biserial

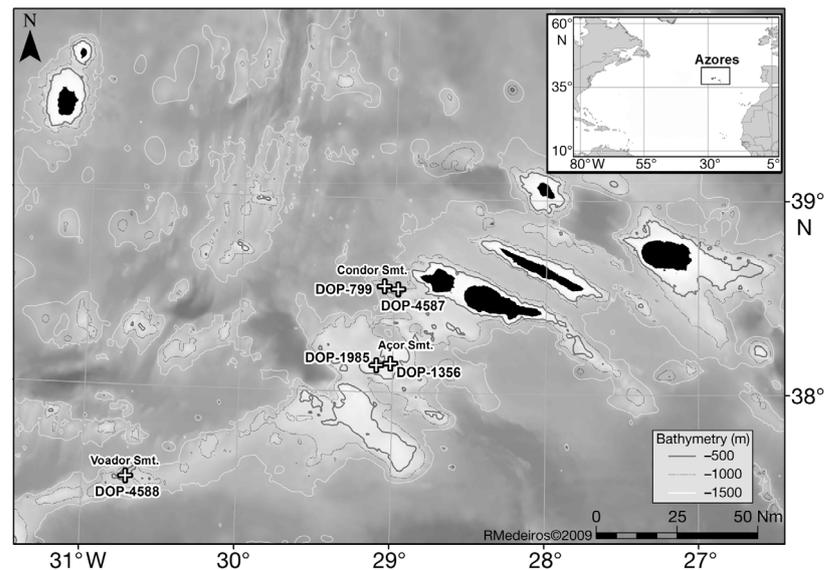


Fig. 1. Collection sites of *Leiopathes* sp. in the Condor (DOP-799, DOP-4587), Açor (DOP-1985, DOP-1356), and Voador (DOP-4588) seamounts, within the Azores region

Table 1. *Leiopathes* sp. Data of the 5 specimens used in this study. Collection year and site (bank) were known for all specimens, with the exception of DOP-1985, where collection year was estimated as 1985 by the fishermen. Axis diameter: minimum and maximum values at the sample extraction plane. Height: vertical colony height. ^a: Collection year may not be representative of the final year of formation for this colony based on observation of encrusting organisms on exterior of basal portion. ^b: Base axis was at an angle, making a diameter measurement difficult

Specimen ID	Date	Site	Latitude, longitude	Depth (m)	Axis diameter (mm)	Height (cm)	Morphotype
DOP-1985	1985	Açor Bank	38° 17' N, 28° 52' W	366	28.9–33.1	175	2
DOP-1356	23 Mar 2007 ^a	Açor Bank	38° 17' N, 28° 52' W	307	16.5–17.8	155	1
DOP-4588	Jan 2009	Voador Bank	37° 32' N, 30° 43' W	366	25–26 ^b	137	1
DOP-799	17 Sep 2006	Condor Bank	38° 08' N, 29° 05' W	293	11.4–14.2	113	1
DOP-4587	Jan 2009	Condor Bank	38° 08' N, 29° 05' W	366	4.9–5.2	43	3

branchlets with a scorpioid arrangement. These branchlets bear small, simple, and smooth-surfaced spines reduced in size or absent on larger branches and stems (Opresko 1998). Careful examination of some of these morphological characters (e.g. gross morphology, size of the colony; length, diameter, and shape of the terminal branches, dimension and distribution of the spines and polyps on the axial skeleton) suggested that the studied specimens belonged to 3 morphotypes: (1) DOP-799, DOP-1356, DOP-4588, (2) DOP-1985, and (3) DOP-4587. Because the species currently classified under the genus *Leiopathes* in the NE Atlantic require revision (D. Opresko pers. comm.), we refrain from assigning these morphotypes to specific species. Genetic identification of these specimens was not possible due to the lack of freshly preserved material.

Sample preparation

Cross sections 1 cm thick were taken from the bases of the colonies with a hand saw (Fig. 2). The portions of each colony were examined to locate the best position for cross sectioning to optimize alignment of the skeletal axis with the vertical orientation of the micromilling machine (*z*-axis). A sample series of skeletal anti-pathin (a structural protein), oriented along the radius, was extracted using the micromilling machine for each colony section. Sample extraction began at the edge and progressed along radial lines successively toward the axial core. Each extraction was made with a 500 μm carbide cutter bit with a spherical shape (Brasseler USA®, Part No. H71.11.005). The bit was guided through the skeletal material at a depth near the bit radius (~ 250 μm), and multiple passes were made to obtain enough sample mass. Near-edge samples were ~ 250 μm in radial thickness because of overlapping extraction paths. Samples extracted closer to the core, and separated from the successive near-edge samples, had an extraction path thickness using the full bit diameter (500 μm). Each extraction was removed successively with a fine-tipped blade under magnified viewing



Fig. 2. *Leiopathes* sp. (A) Complete type-specimen (height: 62 cm; axis diameter: 18 mm) assigned to morphotype 3 (DOP reference collection). Estimated age is 300 to 1700 yr based on the growth rates provided in this study. (B) Colony section used in sample extractions for DOP-1985. (C) Frame grab from micromill computer showing the sample series taken from the edge of DOP-1985, with an overlap of extraction paths (0.5 mm bit width). (D) Post-extraction surface of the coral section showing the narrower sample series at the edge, 3 intermediate radial samples (full bit width at 0.5 mm), and the axial core extraction

conditions. Target extraction mass was near 3 mg at a minimum for radiocarbon analyses. Because samples were extracted along radial lines, some extraction paths were full circle, sampling the entire radius, to increase sample mass for the period of formation. In order to obtain enough sample mass, core samples were typically >500 μm in diameter and deeper than the near-edge radial extraction.

The selection of sample areas within each colony depended on the size of the colony and the potential analysis, either radiocarbon dating or bomb radiocarbon dating. Rough estimates of age from growth zone counting and growth rates from other studies on similar corals (e.g. Roark et al. 2006) provided a basis for the limits of the extraction series (working to encompass pre-bomb to post-bomb $\Delta^{14}\text{C}$ levels). For most colonies, the edge was sampled at the finer scale, stated previously, to evaluate the application of bomb radiocarbon dating. The locations of older samples ranging to the core were selected based on the regu-

lar spacing and avoidance of fractures or separations in the skeletal structure. Pre-bomb samples from the fine scale series near the edge (determined later) and the older samples ranging to the core were used in radiocarbon dating. Extraction of coral material from the 5 coral colonies successfully produced >50 samples to provide a selection of measurement locations in each colony section. Samples were analyzed in successive sets, the results of which were used to make educated decisions for the next set of samples. Ultimately, 25 samples were selected and analyzed with sample mass ranging from 1.0 to 7.3 mg and the number per colony ranging from 1 in the smallest colony to 10 in the largest colony (Table 2).

Analytical measurements

Extracted samples were submitted as powder to the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratories, Livermore, California, USA, for radiocarbon analysis. Sample CO₂ was generated via combustion, converted to

graphite and measured for radiocarbon (¹⁴C) content using an accelerator mass spectrometer (AMS). The ¹⁴C values were reported as Δ¹⁴C (Stuiver & Polach 1977) and were corrected for isotopic fractionation using measured δ¹³C values and an assumed δ¹³C value of −17‰, rounded off from a mean of the measured values (n = 9, 17.4 ± 0.8‰ SD). For bomb radiocarbon dating, the Δ¹⁴C measured in the latest samples were used to determine rough estimates of age and growth from post-bomb to pre-bomb levels. For radiocarbon dating, the full series of pre-bomb Δ¹⁴C values were used to determine colony age, and were reported as conventional radiocarbon age (CRA) and calendar year before present (BP, relative to 1950 AD) corrected reservoir effects (ΔR). A calculated reservoir age of 399 ± 17 ¹⁴C yr was determined from a mean Δ¹⁴C value of −49 ± 2‰ (n = 9), reported for 1955 from the North Atlantic Ocean (Stuiver 1980), which was converted to the fraction modern (Fm) for 1950 (Fm = 0.9516), and then ¹⁴C years with the following conversion (¹⁴C yr = −8033 × ln(Fm)). A global marine reservoir correction age of 464 ± 23 ¹⁴C yr (from the Marine09 supplementary material in Reimer et al. 2009)

Table 2. *Leiopathes* sp. Results from radiocarbon assays separated by colony (Specimen ID) and into the consecutive sample series taken along each radial axis (CAMS ID = Center for Accelerator Mass Spectrometry lab number and Sample ID = laboratory record). Provided are assumed (−17‰) and measured (given to 0.1‰) δ¹³C values, with the measured radiocarbon fraction modern (Fm), calculated Δ¹⁴C, and conventional radiocarbon age (CRA). >Modern: >1950 AD. ^a: Samples combined to increase sample extraction mass

Specimen ID	CAMS ID	Sample ID	δ ¹³ C (‰)	Fm ± 1 SD	Δ ¹⁴ C ± 1 SD (‰)	CRA ± 1 SD (yr)
DOP-1985	147817	AA 09	−17	0.9549 ± 0.0035	−52.0 ± 3.5	370 ± 30
	147381	AA 10	−17	0.9509 ± 0.0049	−55.9 ± 4.9	405 ± 45
	147382	AA 11	−16.6	0.9357 ± 0.0028	−71.1 ± 2.8	535 ± 25
	147383	AA 12	−17	0.9330 ± 0.0029	−73.8 ± 2.9	555 ± 30
	147384	AA 14	−17	0.9299 ± 0.0031	−76.8 ± 3.1	585 ± 30
	147385	AA 15	−17	0.9241 ± 0.0029	−82.6 ± 2.9	635 ± 25
	147818	AA 17	−17	0.9049 ± 0.0040	−101.6 ± 4.0	800 ± 40
	147819	AA 18	−16.4	0.8705 ± 0.0036	−135.8 ± 3.6	1115 ± 35
	147820	AA 19	−17	0.7862 ± 0.0030	−219.5 ± 3.0	1935 ± 35
	147386	AA 20	−17	0.7283 ± 0.0025	−277.0 ± 2.5	2545 ± 30
DOP-1356	147824	AA 44	−17.6	0.9520 ± 0.0028	−54.9 ± 2.8	395 ± 25
	147825	AA 46	−17	0.9445 ± 0.0033	−62.4 ± 3.3	460 ± 30
	147829	AA 45	−17.4	0.9387 ± 0.0034	−68.1 ± 3.4	510 ± 30
	147830	AA 47	−17.2	0.9354 ± 0.0027	−71.3 ± 2.7	535 ± 25
	147823	AA 43	−17	0.9259 ± 0.0030	−80.8 ± 3.0	620 ± 30
DOP-4588	147826	AA 21+22 ^a	−18.9	1.0945 ± 0.0036	86.6 ± 3.6	>Modern
	147831	AA 23	−17	1.1006 ± 0.0034	92.7 ± 3.4	>Modern
	147821	AA 33	−16.6	0.9303 ± 0.0039	−76.4 ± 3.9	580 ± 35
	147827	AA 34	−18.1	0.9196 ± 0.0028	−87.0 ± 2.8	675 ± 25
	147387	AA 35	−17	0.9046 ± 0.0028	−102.0 ± 2.8	805 ± 30
DOP-799	147388	AA 37	−17	1.1040 ± 0.0142	96.0 ± 14.2	>Modern
	147828	AA 40	−18.2	0.9562 ± 0.0033	−50.7 ± 3.3	360 ± 30
	147822	AA 36	−17	0.9459 ± 0.0035	−61.0 ± 3.5	445 ± 35
	147389	AA 39	−17	0.9372 ± 0.0030	−69.5 ± 3.0	520 ± 30
DOP-4587	147390	AA 42	−17	0.9323 ± 0.0041	−74.4 ± 4.1	565 ± 40

was subtracted from the reservoir age (399 ± 17 ^{14}C yr) for a ΔR value of -65 ± 29 ^{14}C yr. The negative result is consistent with more centrally located ocean positions, such as Hawaii ($\Delta R = -28 \pm 4$ ^{14}C yr; Roark et al. 2006; cf. coastal regions affected by upwelling with positive ΔR values, e.g. Sherwood et al. 2008, Soares & Martins 2010). Calibrated calendar age was determined using the calculated ΔR value in Calib 6.0 (<http://calib.qub.ac.uk>) with the Marine09 calibration record (Reimer et al. 2009). Because the sample extraction was composed of material formed over several decades of deposition, the Calib 6.0 calculation option of a 'sample calendar year span' was chosen in the Calib 6.0 analysis (Stuiver & Reimer 1993). This option performs a moving average of the calibration curve and is the best option for this kind of sample design, and the final reported age for each sample was the median probability age. Final sample age determinations were corrected to the time of collection by adding 35 to 59 yr, depending on the sample. Based on these age data, long-term average growth rates for full colonies and within colonies were determined and plotted for interpretation.

RESULTS

Radiocarbon age

Fm measured for ^{14}C ranged, as expected, from a low ratio in the core of the largest colony to >1.0 ($>$ Modern) for the most recent and post-bomb affected samples near or at the edge of 2 of the 5 colonies (Table 2). Calculated $\Delta^{14}\text{C}$ values ranged from a low of $-277.0 \pm 2.5\%$ (mean \pm SD) from the core of DOP-1985 to post-bomb elevated values approaching 100‰ in the near-edge material of DOP-799 and DOP-4587. Change in $\Delta^{14}\text{C}$ across the radial transects of each colony revealed a variable rate of decline with 3 of the 5 colonies having similar rates of decline (Fig. 3). This corresponded to conventional radiocarbon ages ranging from near 500 to 600 ^{14}C yr for the smallest colonies to >2000 ^{14}C yr for the largest colony.

The age of individual extracted samples and total colony age (lifespan of the colony) were determined using the calibrated radiocarbon ages (Table 3). Only measured $\Delta^{14}\text{C}$ values less than the value used to determine a ΔR could be used in determining a calendar year before 1950; hence, some pre-bomb values were deemed 'Modern' and likely formed close to 1950, but were not used in the determination of sample age. The age of the 2 smallest colonies was near 300 yr, and the oldest was ~ 2320 yr old. Dis-

tances to the center of the extraction path (cut width) were plotted with radiocarbon age to reveal differences and similarities in growth rates over time, both within and between colonies (Fig. 4).

Growth rates

Growth rates differed among the *Leiopathes* sp. specimens studied. The smallest and largest colonies had similar growth rates of 5 to 7 $\mu\text{m yr}^{-1}$, whereas the other 3 colonies grew more rapidly by 3 to 5 times, with growth rates of ~ 20 to 30 $\mu\text{m yr}^{-1}$ (Table 4). The largest colony was the slowest-growing overall, but the within-colony rates differed over time (Fig. 5). The earliest and latest growth rates were similar at 4

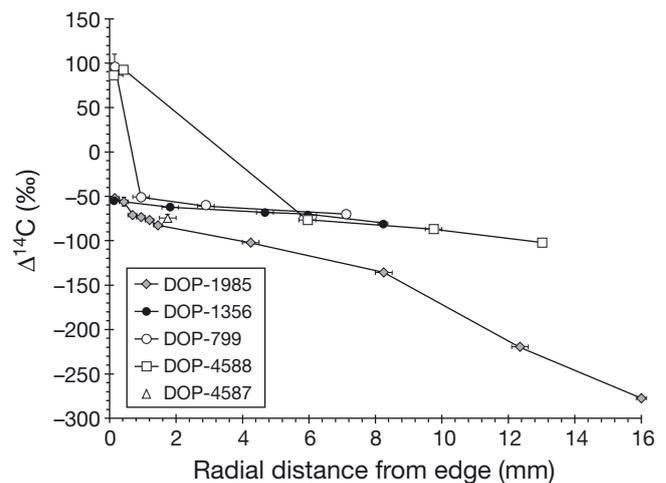


Fig. 3. *Leiopathes* sp. Radial distance from axis to outer edge (mm) versus $\Delta^{14}\text{C}$ determinations for the 5 colonies studied

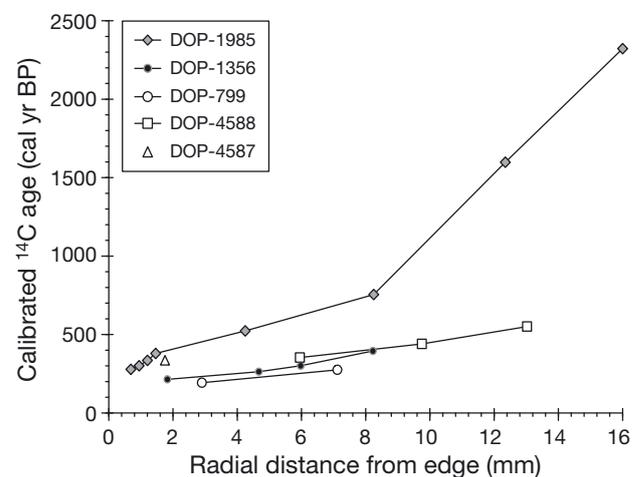


Fig. 4. *Leiopathes* sp. Radial distance from axis to outer edge versus reservoir-corrected calendar age for the 5 colonies studied

Table 3. *Leiopathes* sp. Synopsis of radial samples extracted from the coral axis, given as the distance from the section edge toward the center (distance to the center of extraction width for mean growth zone radius), with the width of the cut from milling based on the bit diameter and extraction (successive radial path or single path using full tip diameter). Listed are the calculated calendar years before present (BP; median probability age) with the uncertainty from Calib 6.0 (moving average) with a reservoir age (ΔR) of -65 ± 29 yr (ca. $\Delta^{14}C = -49 \pm 2$; Stuiver 1980; mean \pm SD). Age was corrected to time of collection from the calibration year of 1950. Data in parentheses are 1 SD calibrated age ranges. >Modern: >1950 AD. ^a: $\Delta^{14}C$ value too close to the pre-bomb reference used in determining ΔR , which leads to an error in Calib 6.0 age calculations

Specimen ID	Sample ID	Distance (mm)	Cut width (mm)	Calendar years BP	Age (yr)
DOP-1985	AA 09	0.15	0.30	Modern	Modern
	AA 10	0.43	0.26	95 (5–135)	130 (40–170)
	AA 11	0.69	0.26	245 (195–295)	280 (230–330)
	AA 12	0.95	0.26	265 (215–320)	300 (250–355)
	AA 14	1.20	0.26	300 (255–350)	335 (290–385)
	AA 15	1.46	0.26	345 (300–390)	380 (330–425)
	AA 17	4.25	0.50	490 (450–525)	525 (485–560)
	AA 18	8.25	0.50	720 (675–765)	755 (710–800)
	AA 19	12.35	0.50	1560 (1500–1620)	1600 (1540–1660)
	AA 20	16.00	0.30	2290 (2230–2340)	2320 (2270–2380)
DOP-1356	AA 44	0.15	0.30	74 (0–100)	130 (60–160)
	AA 46	1.83	0.50	160 (105–240)	215 (160–300)
	AA 45	4.68	0.50	205 (180–270)	265 (235–325)
	AA 47	5.98	0.50	245 (195–290)	300 (250–350)
	AA 43	8.23	0.30	340 (285–380)	395 (340–440)
DOP-4588	AA 21+22	0.28	0.28	>Modern	–
	AA 23	0.70	0.14	>Modern	–
	AA 33	5.95	0.50	295 (250–355)	355 (305–415)
	AA 34	9.75	0.50	380 (330–430)	440 (385–485)
	AA 35	13.03	0.30	490 (465–520)	550 (520–580)
DOP-799	AA 37	0.15	0.30	>Modern	–
	AA 40	0.95	0.50	Modern ^a	–
	AA 36	2.90	0.50	135 (75–230)	195 (130–285)
	AA 39	7.12	0.26	220 (185–275)	275 (240–335)
DOP-4587	AA 42	1.75	0.50	275 (220–340)	335 (280–395)

to $5 \mu\text{m yr}^{-1}$, with a period of more rapid growth at $\sim 20 \mu\text{m yr}^{-1}$ through the upper middle ages of the colony (2 to 8 mm in radius and ~ 400 to 750 yr ago). In addition, growth rates of the other 3 colonies were consistent with the faster growth period of the largest colony. Colony ages across the 5 specimens used in this study did not significantly correlate with the main axis diameter of the colony ($r = 0.76$, $p = 0.14$, $n = 5$) or their height ($r = 0.59$, $p = 0.29$, $n = 5$), meaning that axis diameter and colony height did not increase linearly with colony age based on our limited number of samples.

Use of bomb radiocarbon dating provided estimates of age and growth that support the conventional radiocarbon dating, but the findings were not well defined. Because of low growth rates and the relatively short time frame for bomb radiocarbon dating (~ 50 yr), there was not enough material for good temporal resolution. Based on changes in $\Delta^{14}C$ from what can be classified as pre-bomb to post-bomb values near the edge of the coral section, 2 colonies provided estimates of age. For DOP-799, the assumption was made that sample extraction was before and

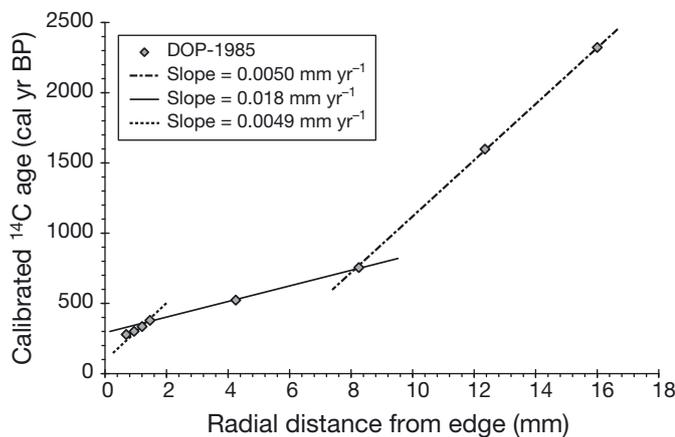


Fig. 5. *Leiopathes* sp. Radial distance from axis to outer edge versus reservoir-corrected calendar age for the largest colony studied (DOP-1985), with variable growth rates

near the initial rise of bomb $\Delta^{14}C$ and a limit of calendar year 1955 was chosen. Support for this determination comes from the measured value of $-50.7 \pm 3.3\%$, similar to the value (mean \pm SD) determined for the North Atlantic Ocean pre-bomb levels ($-49 \pm 2\%$; Stuiver 1980). A conservative growth rate estimate based on the extremes of extraction radius provided a rate of ~ 10 to $20 \mu\text{m yr}^{-1}$. For DOP-4588, it was assumed that the second sample measurement ($92.7 \pm 3.4\%$) encompassed the rise and peak for bomb $\Delta^{14}C$. Given that the sample crossed the peak years, 1965 was arbitrarily chosen as the year of formation. A conservative growth rate estimate was approximately 10 to $25 \mu\text{m yr}^{-1}$. Bomb radiocarbon dating estimates for 2 of the other 3 colonies was not possible because elevated levels were not measured due to other factors (edge not sampled or no post-bomb growth).

Table 4. *Leiopathes* sp. Mean colony growth rates based on the maximum age estimate. Mean radius and radius range were determined to account for radial growth variation. ^a: Estimated last year of formation at 1950 leads to a calculated growth rate of 0.024 (0.021–0.030) mm yr⁻¹ (consideration for evidence that no post-bomb growth occurred)

Specimen ID	Maximum age (yr)	Mean radius (mm)	Radius range (mm)	Mean growth rate (mm yr ⁻¹)	Growth rate range (mm yr ⁻¹)
DOP-1985	2320 (2270–2380)	16.00	15.60–16.40	0.0069	0.0066–0.0072
DOP-1356	395 (340–440)	8.23	7.95–8.50	0.021 ^a	0.018–0.025 ^a
DOP-4588	550 (520–580)	13.03	12.97–13.07	0.024	0.022–0.025
DOP-799	275 (240–335)	7.12	6.17–8.07	0.026	0.018–0.033
DOP-4587	335 (280–395)	1.75	1.55–1.95	0.0052	0.0039–0.0070

DISCUSSION

Radiocarbon dating

Radiocarbon dating indicated that some *Leiopathes* sp. black corals in the Azores have been continuously growing for at least 2300 yr with growth rates as low as 5 $\mu\text{m yr}^{-1}$. These findings corroborate previous reports of high longevity and slow growth rates for *Leiopathes* sp. in the Pacific and NW Atlantic (Roark et al. 2006, 2009, Williams et al. 2006, Prouty et al. 2011), demonstrating that these life history traits are consistent across oceanographic regions of the world.

Our age estimates for *Leiopathes* sp. fall within the lower to middle range of reported values for other *Leiopathes* sp. studies (198 to 4265 yr: Roark et al. 2006, 2009, Williams et al. 2006, Prouty et al. 2011). However, the maximum age reported here was not from the tallest and thickest colony recorded from the region, suggesting that *Leiopathes* sp. in the Azores may attain ages exceeding this estimate. A large specimen that was collected from Condor Seamount had a height of 3 m and an axis diameter of 40 mm. Unfortunately, this specimen belonged to a private collection and we were unable to sample it for radiocarbon dating. However, 1 of the goals of this study was to estimate age for colonies in the field from axis diameter. Although correlation between age estimates and axis diameter resulted in a wide range of uncertainty, an age interval for this specimen was calculated using the range of growth rates of the largest colony aged in this study (DOP-1985; 6.6 to 7.2 $\mu\text{m yr}^{-1}$ radial growth rate). Assuming the observed changes in growth rate over the lifespan would be similar for a colony of this size, an estimate of 2800 to 3000 yr was determined. Given the full range of measured radial growth rates in this study (5.2 to 26.0 $\mu\text{m yr}^{-1}$), age could be between 700 and 3900 yr. However, it is likely that a mean growth rate is most applicable to a colony this large and an age near 3000 yr is likely. According to this estimation the

theoretical maximum age of *Leiopathes* sp. in the Azores is similar to the maximum age reported for *Leiopathes* sp. in Hawaii.

Growth rates of our samples were comparable to those reported for the Gulf of Mexico (8 to 22 $\mu\text{m yr}^{-1}$: Prouty et al. 2011), but greater than those given for Hawaii (2 to 13 $\mu\text{m yr}^{-1}$: Roark et al. 2006, 2009). The reasons for these differences are uncertain, but may be related to factors such as food availability discussed in more detail in the next section. Despite these differences, growth rates in *Leiopathes* sp. are generally lower and lifespans greater than in other deep-sea coral species. For example, the deep-sea antipatharian species *Stauropathes arctica* off Newfoundland (Canada) grows faster and has a shorter lifespan than *Leiopathes* sp. (growth rate = 33 to 66 $\mu\text{m yr}^{-1}$, maximum reported lifespan = 82 yr: Sherwood & Edinger 2009). Octocorals in general have more rapid growth rates and lower lifespans than *Leiopathes* sp., with growth rates between 50 and 440 $\mu\text{m yr}^{-1}$ and an estimated longevity in hundreds of years (Andrews et al. 2002, Sherwood et al. 2006, Watling et al. 2011). The only other species with comparable growth and longevity to *Leiopathes* sp. is the zoanthid *Gerardia* sp. (lifespan in the order of millennia with growth rates as low as 5 $\mu\text{m yr}^{-1}$: Druffel et al. 1995, Parrish & Roark 2009, Roark et al. 2009).

Variability in growth rates

We estimated age and growth rates of 5 *Leiopathes* sp. colonies of different sizes to explore whether variations in age and growth were related to colony size. Growth rates differed among the colonies, with the largest and smallest colonies presenting the slowest mean growth rates (5 to 7 $\mu\text{m yr}^{-1}$), and 3 intermediate sized colonies presenting 4 to 5 times higher mean growth rates (21 to 26 $\mu\text{m yr}^{-1}$). This may be related to differences in colony size, colony collection site, or species-specific differences.

The morphological characters of the coral colonies indicated 3 distinct morphotypes. The largest, the smallest, and the 3 intermediate sized colonies represented 1 morphotype each. Because the species classified under the genus *Leiopathes* in the NE Atlantic require revision (D. Opresko pers. comm.), and we did not have enough freshly preserved material for genetic identification, we were unable to determine whether the 3 morphotypes were different species. Recent molecular phylogenetic studies on deep-sea bamboo corals have demonstrated high lability in morphological characters traditionally used for their classification (Dueñas & Sanchez 2009) i.e. deep-sea corals may show considerable phenotypic plasticity within species.

If the 3 morphotypes correspond to different species, then the observed differences in growth rates may correspond to species-specific rates. Considerable growth rate differences have been reported for closely related antipatharian species of the genus *Antipathes* (Roark et al. 2006, Love et al. 2007). Growth rates of *A. dichotoma* from 50 m depth off Hawaii (Roark et al. 2006) were up to 8 times greater than growth rates reported for *A. dendrochristos* collected at 106 m depth off southern California (Love et al. 2007).

Alternatively, different growth rates may reflect differences in food availability around the seamount. The differences in growth rates were recorded for specimens collected within the Açor (DOP-1985, DOP-1356) and Condor Seamounts (DOP-799, DOP-4587, Table 4). Isotopic evidence indicates that antipatharian corals feed on suspended matter derived from surface production (Roark et al. 2006, 2009, Sherwood et al. 2008), which can be influenced by local hydrographic patterns. In the Azores, information on near-bottom oceanographic conditions (currents, temperatures, and biogeochemical parameters) is scarce and regional models provide only coarse information; however, there is evidence that current circulation and local upwelling–downwelling patterns around seamounts are distinct from the surrounding ocean in the Northeast Atlantic Ocean, producing a diverse and complex physical environment (Vilas et al. 2009, Mendonça et al. 2012). Preliminary data on particulate organic carbon (POC) influx for Condor Seamount suggest that POC concentrations can be nearly 2 orders of magnitude greater on the northern slope relative to the southern slope (A. Colaço pers. comm.). This spatial heterogeneity in particle flux at the microhabitat scale could explain differences observed in coral growth rates on a seamount. Large intra-seamount variability in POC

concentrations and plankton biomass has also been recorded at the Sedlo and Seine Seamounts located in subtropical waters of the northeast Atlantic Ocean, related to differences in local circulation around the seamount (Vilas et al. 2009).

Growth rate comparisons of *Leiopathes* from different oceanographic regions suggest that surface-layer productivity, and thus food availability, may influence coral growth rates. We measured, rates similar to those reported for the Gulf of Mexico, and greater than those calculated for Hawaii. Primary productivity estimates in the Azores region ($385 \text{ mg C m}^{-2} \text{ d}^{-1}$) are similar to the Gulf of Mexico ($417 \text{ mg C m}^{-2} \text{ d}^{-1}$), but are nearly 2 times greater than for the Hawaii region ($228 \text{ mg C m}^{-2} \text{ d}^{-1}$, www.seararoundus.org), reflecting similarities in the trends observed for *Leiopathes* growth rates among these regions. Regional differences in growth rates of bamboo coral in New Zealand have also been attributed to differences in oceanographic conditions and food availability (Tracey et al. 2007).

A third potential explanation relates to variations in growth rates throughout the life span of the coral, rather than to species-specific growth rates. Roark et al. (2006) found greater radial growth rates over the initial 400 yr of a 2370 yr old *Leiopathes* sp. from Hawaii. More recently, Prouty et al. (2011) reported an inverse relationship between colony age and growth rates based on measurements in 5 colonies with different axis diameters. Our results show a contrasting pattern, with lowest growth rates (4 to $5 \text{ } \mu\text{m yr}^{-1}$) recorded over the initial 1600 yr and the last 300 yr of lifespan of the 2320 yr old *Leiopathes* sp., with a period of more rapid growth ($20 \text{ } \mu\text{m yr}^{-1}$) during the intermediate 400 yr of life. Similar growth rates were recorded for our smallest specimen with a lifespan of 300 yr. These results suggest low growth rates in young and old colonies. Low initial growth rates could be related to low surface area exposed to the currents delivering organic particles on which the polyps are feeding, thus capturing only few resources for growth, as suggested for bamboo corals from the Gulf of Alaska (Roark et al. 2005). In this scenario, the growth rate would increase as the coral surface area and feeding efficiency increased, but may slow down as the colony reaches a maximum size. Studies on the growth and modularity of colonial cnidarians suggest that growth rates and colony maximum sizes are controlled by size-dependent interactions between the colony and the environment, such as the balance between metabolic rate and resource capture (e.g. Sebens 1982, Kim & Lasker 1998). As the size of the colony increases, the

amount of resources captured by different parts of the colony are reduced by colony self-shading. In addition, energy allocation to reproduction and other physiological functions may be favored in relation to growth (Kim & Lasker 1998).

An additional consideration with the observed growth rate variability is the reliance of radiocarbon dating on the stability of the ^{14}C reference record over time. It is important to note that a series of assumptions are necessary in this instance because time-specific radiocarbon records, extending back 2000 yr, do not exist as a reference in the region. It is assumed that the calculated ΔR value for the mixed layer is relatively consistent over time, but minor variations due to upwelled dissolved inorganic carbon or POC (depending on the primary source for skeletal growth) could change the reservoir age for unknown periods of time. A minor depression of $\Delta^{14}\text{C}$ on the order of 10‰ can lead to a positive change in reservoir age of 85 ^{14}C yr for this study. This factor was described for the northeast Atlantic from historical samples, primarily from the ocean margin, and was attributed to the North Atlantic Oscillation (Tisnérat-Laborde et al. 2010). A problem with age estimates determined in this study is unlikely because (1) sample extraction covered decades of growth and likely normalizes such minor variations (>10 yr period) and (2) the Azores are more closely associated with the structural stability of the North Atlantic Gyre; nevertheless, it is important to mention this potential complication when making age determinations on deep-sea corals.

Management and conservation

As is the case with old-growth forests of terrestrial environments, our findings indicate that *Leiopathes* are particularly vulnerable to natural and anthropogenic disturbance. Once removed, these colonial organisms will not return to their former structural and ecological significance within our lifetime. Disturbance and removal from bottom trawling is among the most significant threats to cold-water corals (Althaus et al. 2009), and recent studies have demonstrated that other bottom-set fishing gears, such as longlines, can also significantly impact these communities in areas of intense fishing (Duran Muñoz et al. 2011, Sampaio et al. 2012). In the Azores, bottom trawling and deep-sea netting are forbidden and only bottom long lining is allowed (European Council Regulation [EC] No. 1568/2005 of 20 September 2005; see also Probert et al. 2007, Santos et al. 2009).

Recent studies on bycatch during longline fishing experiments revealed that 33% was composed of corals, and ~7% of the corals caught were antipatharians (DOP-UAz unpublished data).

Anecdotal reports from fishermen suggest a progressive reduction in the accidental capture of *Leiopathes* after 20 yr of bottom-longline fishing on insular slopes and seamounts. Large *Leiopathes* colonies (>2 m tall), and previously collected by fishermen, were not recorded in video surveys recently conducted in the Azores (A. Braga-Henriques pers. obs.). This finding could indicate that the largest and oldest colonies have already been removed from the population in heavily fished areas. These observations suggest that bottom longlines have had a destructive effect, and management strategies to reduce impacts to these ancient corals should be implemented.

The Government of the Azores recently created 4 deep-sea marine protected areas for the conservation of particularly sensitive benthic habitats, such as coral and sponge reefs and gardens. These protected areas are the Sedlo Seamount (Santos et al. 2009, 2010), and 3 high seas areas claimed by Portugal to the Commission on the Limits of the Continental Shelf (Altair and Antialtair Seamounts, and an area of the Mid-Atlantic Ridge north of the Azores), of which all are part of the OSPAR network of Marine Protected Areas (OSPAR Commission 2010b). The present study on *Leiopathes* contributes to this conservation effort by providing estimates of growth and longevity for an important structural member of these habitats, one of the longest-lived corals known. This information must be considered for the classification of additional vulnerable habitats that harbor ancient communities and deserve protection.

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