

AGE OF BLACK CORAL (*ANTIPATHES DENDROCHRISTOS*) COLONIES, WITH NOTES ON ASSOCIATED INVERTEBRATE SPECIES

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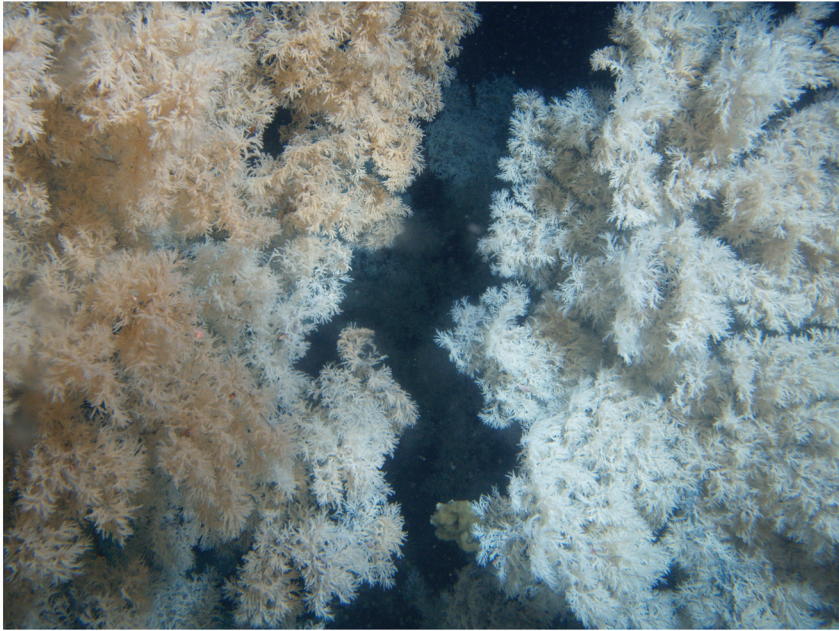
ABSTRACT

In 2005, a dead 2.1-m high colony of the Christmas tree black coral, *Antipathes dendrochristos* Opresko, 2005, was collected from 106 m of water off southern California. Based on growth increment counts, a radiocarbon (^{14}C) analysis, and an indirect corroboration by lead-210 dating from a second, live colony, the colony was about 140 yrs old when it died. The dead skeleton was heavily colonized by invertebrates with 2554 individuals living on the colony. Corophioid amphipods, sea anemones, brittle stars, and crinoids dominated this assemblage. Thus, along with living colonies, it is arguable that the destruction of dead antipatharian colonies may have as yet unknown effects on a range of deep-water organisms.

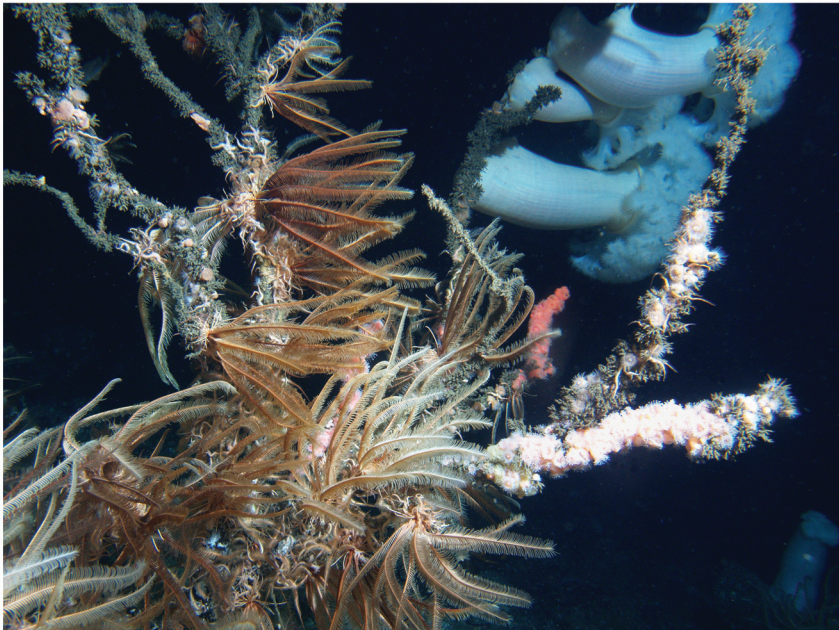
Antipatharians (black corals) are found in all oceans, with the greatest number of species living in the subtropics and tropics. Worldwide, there are about 250 species in six families. Although a few species occur in shallow waters, most live at depths of 20 m and deeper, and the deepest record is > 8000 m. Black corals develop a variety of growth forms, including arborescent, fan-shaped, unbranched, and symmetrically branched (Opresko, 2001, 2002, 2003b, 2004; D. Opresko, Oak Ridge National Laboratory, pers. comm.; Species 2000). Most of these corals live on hard substrata, such as rock ridges and walls, boulders, and cobble (Grigg, 1965; Miller, 1998; Tissot et al., 2006). As with most other groups of deep-water corals, the role that black corals play in benthic ecology, and particularly their role as habitat for other species, is poorly understood (Buhl-Mortensen and Mortensen, 2004; Boland and Parrish, 2005).

The Christmas tree coral, *Antipathes dendrochristos* Opresko, 2005 (Fig. 1A), lives in southern California waters in depths of about 90 m to at least 360 m. This irregularly arborescent species grows to about 2.5 m tall and predominantly inhabits low-relief mixed rock areas, primarily on offshore banks (Opresko, 2005; Yoklavich and Love, 2005; Tissot et al., 2006). Little else is known of the biology of this organism. From direct observations using a small manned submersible, about 15% of live colonies have invertebrates, including galatheid crabs, brittle stars, barnacles, and polychaetes, living among the polyps. A small percentage (1%–2%) of the colonies are either entirely dead or have dead branches (Tissot et al., 2006), and large numbers of sessile animals, including crinoids, basket stars, anemones, and brittle stars, live on these dead branches and trunks (Yoklavich and Love, 2005).

In 2005, we collected a large dead colony and (1) estimated how long it had lived, (2) estimated its growth rate, and (3) characterized what organisms currently were living on it. In addition, we collected a second, live, colony and estimated its growth rate and age.



a.



b.

Figure 1. (A) Living *Antipathes dendrochristos* colony, Santa Cruz Island, southern California Bight. (B) The upper trunk and branches of the dead *Antipathes dendrochristos* colony with its typical invertebrate assemblage.

MATERIALS AND METHODS

A dead colony of *A. dendrochristos*, measuring 2.1 m tall \times 0.9 m wide \times 1.0 m deep with a base of 4.5 cm in diameter, was collected on 13 October 2005 in 106 m of water near the shallowest part of the "Footprint," a rocky feature located seaward of the Santa Cruz–Anacapa Island Passage, southern California (Fig. 2). The colony (located at 33°57.906'N, 119°29.434'W) was in a field of small boulders, most of which were 0.25–0.75 m in diameter. This was the only *A. dendrochristos* colony (living or dead) that we observed in this area, although living colonies of this species are common in deeper water on the Footprint. Using the collecting arm of the research submersible DELTA, the colony was pulled free of an underlying boulder at its base and carried to the surface. On the support ship's deck, the colony was placed on a white sheet to allow for detection of those organisms that fell off as the colony warmed and began to dry. The colony was cut into pieces and frozen in plastic bags, along with all associated organisms. Near this location, a living colony was also collected that provided an opportunity to estimate age from a smaller living colony.

AGE ESTIMATION.—Age estimation was made from cross sections taken near the base of each colony (both dead and living). For the dead colony, two cross-sections (1 mm thick) of the colony's trunk were cut about 2 cm up from the base of the colony. Cross sections were not taken at the lowermost part of the colony because the base splayed outward and downward over the rock.

Growth increment age estimations were made (by B.A.B.) from cross sections of black coral mounted on glass slides. These sections were polished with increasingly fine lapping film, up to a maximum of 15- μ m grit, until viewing was optimal. Both transmitted and reflected light were used to examine the sections under a Leica MZ95 dissecting microscope at 50–75 \times magnification. Ultimately, reflected light provided the greatest resolution of the banding patterns. Age initially was estimated in two ways with the smaller living coral section from: (1) counts of very fine, subordinate growth increments, and (2) counts of much more dominant, yet less frequent, growth increments. The difference between these age estimates was the basis for applying the lead-210 (^{210}Pb) dating technique (30 vs 300 yrs).

To estimate growth rates, measurements were made along four radial paths from the center to the outside edge of the cross-section in both the dead and living specimens. Care was taken to ensure that each radial path was clear of irregularities, such as branching scars, that may distort growth estimates. Growth rate was estimated using the range of measured diameter or radius vs estimated age.

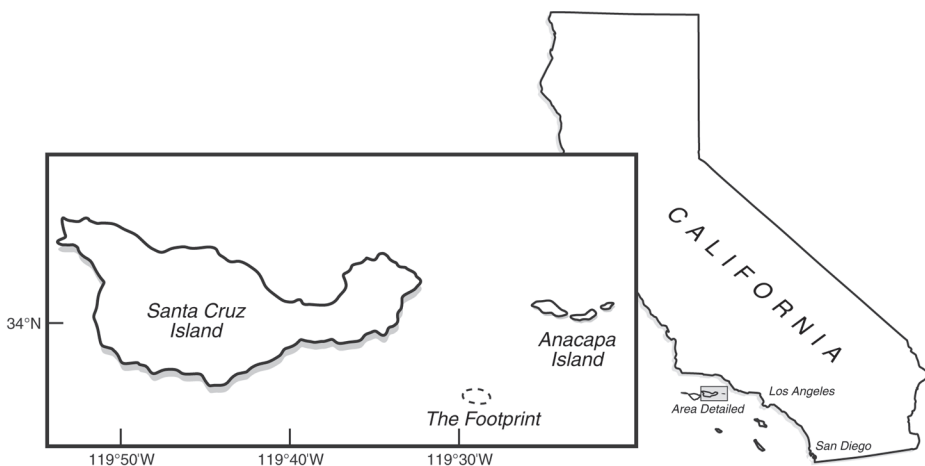


Figure 2. Location of the Footprint, a rocky area located just seaward of the Santa Cruz–Anacapa Island Passage, southern California, and site of the collection of a dead *Antipathes dendrochristos* colony.

AGE CORROBORATION.—We corroborated the growth increment age using ^{210}Pb and ^{14}C dating. Core material from the living colony was analyzed for ^{210}Pb and ^{226}Ra at Moss Landing Marine Laboratories (MLML). From a portion of the colony, 25 mm in length (along the axis) core material was extracted from a series of cross-sections using a New Wave[®] micro-milling machine. The 25 mm length of coral was sectioned into 15 pieces to allow for (1) locating the center of the skeleton throughout the length of the portion, and (2) control over use of the drill bit to extract precisely the center of the skeleton. With this instrument, core samples were accurately removed with a Brasseler[®] 1400 μm bit.

The approach using a single core sample in determining the more plausible age estimate (30 vs 300 yrs) was related to two possible scenarios for exogenous levels of ^{210}Pb . For a sample that was extracted from the center of a 300-yr-old coral, the ratio of ^{210}Pb to ^{226}Ra should be in secular equilibrium for levels that are typical of the marine environment. Hence, extraction of a core sample with a diameter of 1.4 mm would have removed the first 56–70 yrs of growth (calculated based on the variation of diameter and the age estimate) and would have been deeply buried in over 200 yrs of growth; secular equilibrium is achieved at about 120 yrs (within about 98% of equilibrium). For a sample extracted from the center of a 30-yr-old coral, secular equilibrium would not have been attained, given typical exogenous levels of ^{210}Pb were present at the time of growth. Hence, extraction of a core sample with a diameter of 1.4 mm would have removed the first 6–7 yrs of growth (calculated as stated above) and would have been buried in only 24–25 yrs of growth; formation of this material would have occurred too recently to be in equilibrium. Measurement of ^{210}Pb and ^{226}Ra from the sample was performed using well-established techniques at MLML, the details of which are described in Andrews et al. (2002).

One cross section of the dead coral was analyzed for radiocarbon (^{14}C) at Keck Carbon Cycle Accelerated Mass Spectrometry (KCCAMS) Facility at the University of California, Irvine. The surface of the cross section was scraped off with a scalpel and discarded. The cleaned surface of both the axial center and the cross section edge was drilled using a diamond dental burr to extract about 10 mg of material. An organic ^{14}C -free sample (for background correction) and a wood standard were also processed. Carbonates were removed with a 1N HCl treatment for 30 min. Samples were rinsed twice with MilliQ water and dried on a heating block at 80 °C. Sample CO_2 was produced by combustion at 900 °C in evacuated, sealed quartz tubes in the presence of CuO and silver wire, which was reduced to graphite, as described in Santos et al. (2004), in preparation for AMS analysis.

ASSOCIATED ORGANISMS.—In the laboratory, each frozen piece of the colony was thawed in cold water and stripped of associated organisms. The wash water was passed through a 63- μm sieve and the trapped material collected and preserved in formalin. After about 2 wks, this material was rinsed in fresh water, transferred to 50% ethanol, examined under a dissecting microscope, and sorted into taxonomic groups.

RESULTS

AGE ESTIMATION.—The radius of the living coral cross section ranged from about 3 to 3.75 mm and growth increment age estimates, as stated previously, were 30 ± 1 (SD) and 300 ± 10 (SD) yrs depending on the technique. The resultant growth rates were 0.100–0.125 mm yr^{-1} for the 30-yr estimate, and 10 times slower for the 300-yr estimate. The growth rate based on the 30-yr estimate was in agreement with the growth rate of the larger dead colony section.

The radius of the dead coral cross section ranged from 14.1 to 21.8 mm, and the resultant growth increment counts were made at a radius of 14.3 mm, 15.7 mm, 18.2 mm, and 19.8 mm (mean of 17.0 mm, SD = 2.47). Age, estimated visually from growth increment counts in the dead coral cross section, was 140 ± 5 (SD) yrs. Radial growth rate of the dead colony, assuming an average radius of 17.0 mm and an age of

Table 1. Ages of the center and edge of dead *Antipathes dendrochristos* colony collected in 106 m depth, October 2005, in southern California. All values are given as means with one standard deviation. Radiocarbon concentrations are given as fractions of the modern standard, $D^{14}C$, and conventional radiocarbon age, following the conventions of Stuiver and Polach (1977). Sample preparation backgrounds have been subtracted based on measurements of ^{14}C -free coal. ^{13}C values were measured on prepared graphite using the AMS spectrometer. These can differ slightly (typically by 1‰–3‰) from those of the original material if fractionation occurred during sample graphitization of the AMS measurement. BP = before present.

UCIAMS #	Sample name	^{13}C (‰)	±	Fraction modern	±	$D^{14}C$ (‰)	±	^{14}C age (BP)	±
23185	Black coral (center)	-24.7	1.2	0.9083	0.0020	-91.7	2.0	770	20
23186	Black coral (edge)	-25.7	1.3	0.9258	0.0021	-74.2	2.1	620	20

140 yrs, was estimated to be 0.121 mm yr^{-1} (range of 0.102 – 0.141 mm yr^{-1}). Overall growth rate (linear tip extension rate) was estimated to be 1.5 cm yr^{-1} , assuming a total colony height of 2.1 m.

AGE CORROBORATION.—The 30-yr age estimate for the living colony was supported by ^{210}Pb dating, and the 300-yr age estimate was not. ^{210}Pb activity was $1.54 \pm 2\%$ (SE) dpm g^{-1} and ^{226}Ra activity was $0.094 \pm 21\%$ (SE) dpm g^{-1} , as measured from a total core sample weight of 0.0168 g. The ^{210}Pb : ^{226}Ra ratio for this sample was 16.4, far exceeding secular equilibrium; hence, the findings indicate an average initial uptake of ^{210}Pb (over the core formation period) would need to be on the order of 6230 dpm g^{-1} to achieve a measured unsupported level (1.48 dpm g^{-1}) in the core. This was calculated by subtracting the average estimated core age (32 yrs) from the estimated age of 300 yrs and back calculating to the average initial activity necessary to decay to the measured level in that amount time for a core that was 56–70 yrs old. An initial activity on the order of 1000s of dpm g^{-1} is not a reasonable estimate for this environment. Given the sample was 30 yrs old, the average initial ^{210}Pb levels, for a core 6.5 yrs in age, would have been 3.4 dpm g^{-1} ; this activity level is reasonable for this environment.

Both visual and ^{14}C age estimates yielded similar estimates of life span for the dead colony. From the visual assessment of the cross section, 140 ± 5 (SD) growth increments were counted. The ^{14}C analyses indicated the colony had lived 110–190 yrs, with a mean value of 150 yrs (SD ± 20 ; Table 1). This finding is in agreement with the age and growth estimates supported by lead-dating from the living colony.

ASSOCIATED ORGANISMS.—In total, 2554 organisms were found living on the dead colony (Fig. 1B, Table 2). Tubiculous corophioid amphipods, *Erichthonius rubricornis* (Stimpson, 1853), were the most abundant organisms, followed by sea anemones [primarily *Corynactis californica* Carlgren, 1936 and *Metridium* sp.], brittle stars (*Ophiacantha diplasia* Clark, 1911, and *Ophiacantha bakeri* McClendon, 1909, and the crinoid *Florometra serratissima* (Clark, 1907)]. The 2554 individuals represent a conservative estimate of the total number of organisms occupying the dead colony. It is likely that some of the more mobile organisms, such as the brittle stars and crinoids, had fallen or swum off the colony as it was being lifted off the seafloor.

DISCUSSION

Based on mutually supportive data from traditional enumeration of rings and radiometric age estimations, it is likely that *A. dendrochristos* produces annual growth increments. The linear-tip-extension growth rate of this colony (1.5 cm yr^{-1}) was

Table 2. Invertebrates living on a dead black coral colony collected in southern California. The colony was collected in a depth of 106 m on 13 October 2005. For all organisms, we report a general classification (Column 1) and, when possible, the lowest taxa identified (Column 2).

Gammarid amphipods	<i>Erichthonius rubricornis</i> (Stimpson, 1853)	1,445
Sea anemones	<i>Corynactis californica</i> Carlgren, 1936, <i>Metridium</i> sp.	644
Brittle stars	<i>Ophiacantha bakeri</i> McClendon, 1909 <i>Ophiacantha diplasia</i> Clark, 1911	381
Crinoids	<i>Florometra serratissima</i> (Clark, 1907)	46
Polychaetes	<i>Glycera</i> sp. <i>Pholoides aspera</i> Fauchald, 1977 <i>Phyllodoce</i> sp. <i>Eunice multipectinata</i> Moore, 1911	9
Snails	<i>Amphissa reticulata</i> Dall, 1916 <i>Babelomurex oldroydi</i> (I. S. Oldroyd, 1929) <i>Calliostoma variegatum</i> Carpenter, 1864	6
Isopods		8
Chitons	<i>Lepidozona scabricostata</i> (Carpenter, 1864)	3
Brachiopods		3
Tunicates		2
Nudibranchs	<i>Aeolidia papillosa</i> (Linnaeus, 1761)	2
Sipunculids		2
Solitary coral	<i>Desmophyllum dianthus</i> (Esper, 1794)	1
Hydroid colony		1
		Total: 2,554

within the general range of that of two Hawaiian species studied by Grigg (2004) (6.12 cm yr^{-1} for *Antipathes grandis* Verrill, 1928 and 6.42 cm yr^{-1} for a species identified as *Antipathes dichotoma* Pallas, but now considered to be a different species [Opresko 2003a]), and one temperate species from New Zealand (1.6 cm yr^{-1} for *Antipathella fiordensis* [Grange and Goldberg, 1993]). Hence, the estimated growth rate of 1.5 cm yr^{-1} is not unrealistic. The radial growth rate calculated in this study ($0.10\text{--}0.14 \text{ mm yr}^{-1}$) was somewhat slower than the $0.18\text{--}1.14 \text{ mm yr}^{-1}$ calculated for *A. dichotoma* from 50 m depths in Hawaiian waters (Roark et al., 2006) and similar to a number of other deep-water corals (e.g., Druffel et al., 1990, Andrews et al., 2005, Roark et al., 2005). Given that the *A. dendrochristos* colony lived for about 140 yrs, our observations of larger living colonies indicate that some colonies can live even longer.

The use of ^{210}Pb dating in this manner and for these purposes is supported by several assumptions. Because the marine environment is not known to provide unsupported activities (by ^{226}Ra) on the order of 1000's of dpm, we are reasonably certain that the core material from the living colony could not have been on the order of 200–300 yrs old. A much more plausible scenario is that the section was on the order of 30 yrs old, provided there was an initial activity near 3 dpm g^{-1} . Unsupported ^{210}Pb activities determined from other deep-water corals typically range from about 0.1 to 1.0 dpm g^{-1} (e.g., Druffel et al., 1990; Andrews et al., 2002, Adkins et al., 2004; Thresher et al., 2004). The levels calculated for *A. dendrochristos* would be more representative of sediments (e.g., Lewis et al., 2002). Because these colonies were taken in an area where currents may be strong, sediments may be frequently resuspended, potentially making elevated levels available for uptake.

Both living and dead *A. dendrochristos* colonies provide habitat for a range of organisms. While some groups of invertebrates are found in high densities on both live and dead colonies, others appear to be mostly limited to either living or dead colonies. For instance, both tube-dwelling gammarid (corophioid) amphipods and anemones may live only on dead colonies or on the dead parts of colonies. We have noted that the dead branches of otherwise living colonies are often encrusted with anemones and that some dead colonies are completely covered by these cnidarians. On the other hand, living colonies are most often inhabited by barnacles, polychaetes, crinoids, and less often by sponges and galatheid crabs (Tissot et al., 2006; M. Love, pers. obs.). In particular, it is notable that two organisms, the barnacle *Oxynaspis rossi* Newman, 1972 and an undescribed genus and species of polynoid polychaete (L. Harris, Natural History Museum of Los Angeles County, pers. comm.), both of which seem to be nearly ubiquitous on living *A. dendrochristos* colonies, were not encountered on the dead colony. The Oxynaspididae are found almost exclusively on antipatharians (Newman, 1972), and worms of the family Polynoidae are symbiotic on a variety of deep-water corals (Buhl-Mortensen and Mortensen, 2004). It appears that whatever benefits accrued to these species by living on live *A. dendrochristos* are absent from dead ones.

In summary, *A. dendrochristos* colonies provide shelter for a range of invertebrate organisms, both when colonies are alive and after their deaths. While recent research has emphasized the role that fishing may play in the deaths of living, deep-water corals (Koslow et al., 2001; Roberts et al., 2006), it is arguable that the destruction and removal of dead coral colonies, at least of the antipatharians, also may have effects on associated invertebrate assemblages.

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