



Axial rod growth and age estimation of the sea pen, *Halipteris willemoesi* Kölliker

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Abstract

Halipteris willemoesi is a large octocoral commonly found in the Bering Sea. It is a member of a ubiquitous group of benthic cnidarians called sea pens (Octocorallia: Pennatulacea). Sea pens have a skeletal structure, the axial rod, that in cross section exhibits growth rings. Pairs of adjacent rings, or ring couplets, were assumed to be annuli and were used to estimate the age and growth of *H. willemoesi*. Twelve axial rods, extracted from *H. willemoesi* collected in the Bering Sea, were selected to represent small (25–29 cm total length), medium (97–130 cm TL) and large (152–167 cm TL) colonies. Each rod resembled a tapered dowel; the thickest part (0.90–6.75 mm in diameter) was at about 5–10% of total length from the base tip, the distal part was more gradually tapered than was the base. The number of ring couplets increased with rod size indicating their utility in estimating age and growth. Estimated age among rods was based on couplet counts at the thickest part of each rod; the average estimated age (\pm SE) was 7.1 ± 0.7 , 19.3 ± 0.5 , and 44.3 ± 2.0 yr for small, medium and large-size rods, respectively. Based on these estimated ages, average growth rate in total length was 3.9 ± 0.2 , 6.1 ± 0.3 , and 3.6 ± 0.1 cm yr⁻¹ for small, medium, and large-size colonies. The average annual increase in maximum rod diameter among all colonies was 0.145 ± 0.003 SE mm yr⁻¹; therefore, age prediction from maximum rod diameter was calculated (estimated age (yr) = $7.0 * (\text{maximum rod diameter, mm}) - 0.2$; $R^2 = 0.99$). At maximum diameter, the average couplet width was relatively constant among the three colony sizes (0.072 ± 0.05 mm). X-ray diffraction and electron microprobe analyses revealed that the inorganic portion of the rod is composed of a high-magnesium calcite. Radiometric validation of these age and growth rate estimates was attempted, but high amounts of exogenous ²¹⁰Pb precluded using the disequilibria of ²¹⁰Pb:²²⁶Ra. Instead, ²¹⁰Pb activities were measured in a series of cores extracted along the axial rod. These activities ranged from 0.691 ± 0.036 (SE) to 2.76 ± 0.13 dpm g⁻¹, but there was no pattern of decay along the length of the rod; therefore, the growth rates and corresponding ages could not be validated. Based on estimated age from ring couplet counts, growth in total rod length is slow at first, fastest at medium size, and slows toward maximum size, with an estimated longevity approaching 50 yr.

Introduction

Sea pens and whips (Octocorallia: Pennatulacea) are colonial organisms that inhabit soft-bottom areas over a broad range of depths (intertidal – 6200 m) in all oceans (Williams, 1995, 1999). They can form vast

forest-like patches of biogenic habitat that may play an important role as fish habitat (Krieger, 1993). Each colony stands erect and is secured to the sea floor by peristaltic burrowing of the peduncle, a slightly swollen basal (proximal) part of the fleshy tissue. The upper or distal part, the rachis, is populated with feed-

ing polyps (autozooids). Sea pens are considered to be sessile (Williams, 1999), but movement by detaching, drifting, and re-attaching has been noted in the shallow-water species *Ptilosarcus gurneyi* (Birkeland, 1974) and *Renilla kollikeri* (Kastendiek, 1976), and the deep-water sea pen *Umbellula lindahli* (Flores, 1999). Despite this potential for movement, sea pens may contain useful records of environmental conditions stored in the skeletal tissues.

The endoskeleton of sea pens is a simple unbranched structure called an axial rod. The axial rod of the sea pen *Veretillum cynomorium* consists of a matrix of longitudinally oriented collagen fibrils embedded in columns of calcite that radiate out from a nodular core (Franc & Chassagne, 1974; Ledger & Franc, 1978). At the base (inferior) end, a calcification gradient exists between the non-calcified tip and the rest of the rod. The autoradiography (^3H -proline labeling) results of Franc et al. (1985) indicate that deposits are made onto the rod exterior; the interior is closed to deposition. Chia & Crawford (1977) found evidence of initial axial rod formation in *P. gurneyi* primary polyps soon after settlement of the planula. Birkeland (1974) found that growth rings in the axial rods of young sea pens (*P. gurneyi*) were formed annually, based on observed growth, and averaged 0.1 mm in width. Some colonies were estimated to be 15 years old based on rod diameter but, because of core degeneration, these estimates remain unvalidated. Linear extension rates and radiometric age determination provide evidence that skeletal growth rings in other octocorals are formed annually (Grigg, 1974; Szmant-Froelich, 1974; Andrews et al., 2002).

In September 1997, numerous large sea pens (*Halipterus willemoesi*) were collected as bycatch during bottom-trawl sampling in the Bering Sea prompting an investigation of the structure of the axial rod as a tool for determining age. Transverse sections revealed many growth rings in the axial rods indicating that *H. willemoesi* colonies may be slow growing and long lived; therefore, anthropogenic disturbance or removal of sea pen 'forests' could have a lasting effect on the structure of soft-bottom communities. In addition, chronologically ordered sequences of ring widths may be useful for constructing a history of variation in the surrounding environment. This concept is supported by studies on other organisms that indicate skeletal microstructure can be used as a record of age and environmental variability; for example trees (Stokes & Smiley, 1996), fish (Woodbury, 1999), bivalves (Cerrato, 2000), and other colonial anthozoans (Druffel et

al., 1995; Cole et al., 2000; Andrews et al., 2002; Risk et al., 2002). Despite the cosmopolitan distribution and large size of *H. willemoesi* (Williams, 1995), we found no literature describing colony age or the growth of its axial rod. Therefore, the focus of this study was to: (1) describe the structure of different-size axial rods; (2) estimate colony age from axial rod ring counts; (3) create growth models from estimated ages; and 4) attempt to validate colony age and growth estimates using radiometric age validation.

Material and methods

Twelve *H. willemoesi* colonies were selected from two trawl samples collected in the eastern Bering Sea (Fig. 1). Species identification was based on the recent revision of the order Pennatulacea (Williams, 1995). Colonies were selected by total rod length to form three size groups (small, 25–29 cm; medium, 98–130 cm; large, 153–167 cm) consisting of four colonies each (Table 1). The largest colonies were from Pribilof Canyon (11 September 1997, 56°16.8' N, 169°25.8' W, 248 m depth, 3.5°C bottom temp.), the others were collected farther northwest (28 July 1998, 60°0.6' N, 177°56.4' W, 142 m, 2.0°C). Soft tissue surrounding the axial rod was easily removed because it was securely attached only to the rod base.

Each rod was allowed to dry for 1 month at room temperature before measuring and sectioning. Rod diameter along the full length of each rod was measured with a micrometer to the nearest 0.05 mm. Cross sections were cut at set distances from the base tip with a diamond blade saw and mounted onto slides with LR White resin. Each mounted section was ground down to a thickness of approximately 0.3 mm using 320 and 600 grit wet/dry sand paper and coated with immersion oil for viewing. Sections were viewed through a dissecting microscope with transmitted light to make all counts and measurements at a magnification of 16 times. Although higher magnification revealed rings nested within rings, these finer rings were often hard to distinguish. Growth rings were evident as couplets, each consisting of one translucent and one adjacent opaque band.

For each cross section, the number of couplets was counted three non-consecutive times. In addition, radial measurements of cross sections of the rod base were made to quantify and construct a longitudinal view of the thickness of a core of smooth rings and the overlaying layer of rough material. These measure-

Table 1. Axial rod measurements and age estimates at maximum rod diameter for twelve *Halipertis willemoesi* colonies collected in the eastern Bering Sea, with calculated total length and diameter growth rates

Size-group and colony	Total length (cm)	Maximum diameter (mm)	Average increment width (mm) ^a	Estimated age (yr ± SD) ^b	Length growth rate (cm yr ⁻¹) ^c	Diameter growth rate (mm yr ⁻¹) ^d
Small						
BS-G	25.3	0.90	0.075	6.0 ± 1.0	4.21	0.150
BS-E	26.2	0.95	0.079	6.0 ± 1.7	4.36	0.158
BS-F	29.0	1.15	0.075	7.7 ± 1.2	3.78	0.150
BS-H	29.3	1.05	0.060	8.7 ± 0.6	3.38	0.121
Medium						
BS-D	97.8	2.55	0.070	18.3 ± 0.6	5.33	0.139
BS-B	118.4	2.80	0.074	19.0 ± 1.0	6.23	0.147
BS-A	124.4	2.85	0.075	19.0 ± 2.6	6.54	0.150
BS-C	130.3	3.05	0.074	20.7 ± 2.1	6.30	0.148
Large						
PC-C	152.6	5.85	0.073	40.0 ± 5.3	3.81	0.146
PC-D	156.9	6.35	0.076	41.7 ± 2.1	3.76	0.152
PC-B	162.6	6.75	0.072	47.0 ± 1.7	3.45	0.144
PC-A	166.7	6.40	0.066	48.3 ± 1.5	3.44	0.132

^aCalculated as half the diameter divided by increment count.

^bTriplicate count of the growth increments resulting in an average age at the maximum rod diameter.

^cTotal length divided by the estimated age.

^dMaximum diameter divided by the estimated age.

ments were also repeated three non-consecutive times. Triplicate counts and measurements were averaged before calculating the average and standard error (SE) for each rod size group and cross-section position. Cross-section positions were constant within each size group and were determined by distance from the base tip. Average couplet width was calculated as one-half rod diameter divided by couplet count.

Rod length and diameter measurements and growth increment counts (estimated age) were used to estimate growth rates. In addition, growth rates were calculated for the change in colony size, from small to medium and from medium to large, by dividing the difference of the average rod lengths by the difference of the average estimated age.

To gain a better understanding of the composition and structure of the carbonate matrix, X-ray diffraction was performed at the Department of Geology and Geophysics at the University of Alaska, Fairbanks.

To attempt a validation of age and growth estimates, a radiometric age-validation technique was applied to the calcified axial rod among and within colonies. Skeletal material from three sea pen colonies was used in these analyses. Whole and core skeletal material from one colony was used in a preliminary analysis to determine the levels of ²¹⁰Pb and ²²⁶Ra.

Core material at the center of the rod was exposed when the rod exterior was removed using a milling machine. The result was a 1-mm diameter, 3-cm long core estimated to be the first few years of growth. Extracted samples were cleaned and processed for ²¹⁰Pb and ²²⁶Ra using well established protocol as described by Andrews et al. (1999 a, b). Two approaches were utilized to attempt to validate age and growth. First, to determine radiometric age using the disequilibria of ²¹⁰Pb and ²²⁶Ra, core material from the thickest, and presumably oldest, part of the axial rod in two colonies was analyzed. The aim of this approach was to age individual cores using the disequilibria of ²¹⁰Pb and ²²⁶Ra. Second, core material at locations along the axial rod (base to tip) was analyzed for ²¹⁰Pb only. The aim of this approach was to measure the decay of ²¹⁰Pb activity along the rod from the apical tip to near the base tip that presumably corresponds with a young-to-old gradient.

Results

The axial rods of *H. willemoesi* resembled a thin tapered dowel, and extended the length of the colony (Fig. 1). The upper part of the rod was white, well

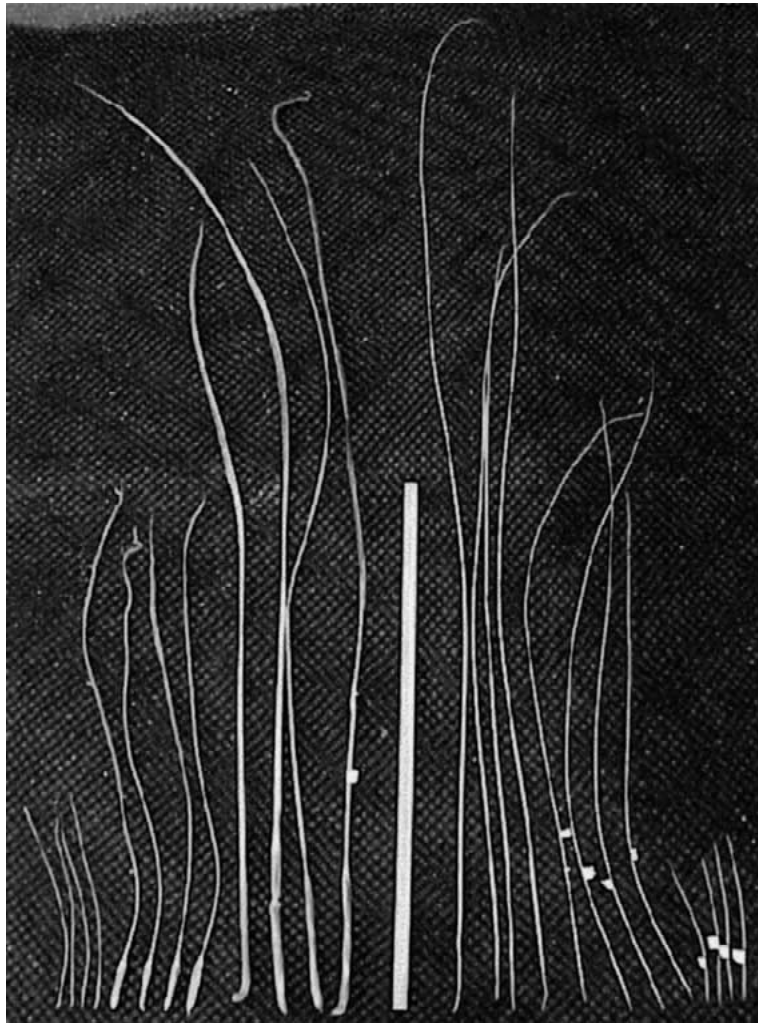


Figure 1. Twelve intact *Halipteris willemoesi* colonies from the Bering Sea (left of meter stick) next to the twelve axial rods from similar-size colonies. The cleaned rods on the right were used to describe rod structure, and to estimate colony age and growth rate.

calcified, and smooth and circular in cross section (Fig. 2A). Soft tissue easily sloughed off this part. The lower part, hereafter referred to as the base, comprised about 10% of the total rod length and differed from the upper part by having a rough exterior and by being irregular in cross section (Fig. 2B). Except at its very tip, which was brown and pliable when wet, the base was also white and well calcified. Soft tissue was securely attached to the base, particularly the tip.

Transverse sections of the rod base revealed that the rough material overlays a core of smooth, concentric growth rings that are similar in cross-section appearance to the rings in the upper part of the rod (Fig. 2). Series of radial measurements of this core were used to construct longitudinal views to show how core thickness decreases toward the base tip (Fig. 3).

Comparing core thickness among different size rods helps to illustrate how the rod base may grow. Assuming no structural variation after deposition, the core of small rods corresponds in thickness to the lower part of the core in large rods indicating that the youngest part of large rods is probably close to the base tip.

Rod shape was similar among the different size groups (Fig. 4A). From the point of maximum diameter, rod thickness decreased sharply before assuming a more gradual taper to the apical tip. The distance from the base tip to the point of maximum rod diameter increased with rod size. As a percent of total length, however, this distance was about 5–10% regardless of size group. Maximum rod diameter was similar among the four rods in each size group (Table 1). The average maximum thickness for small,

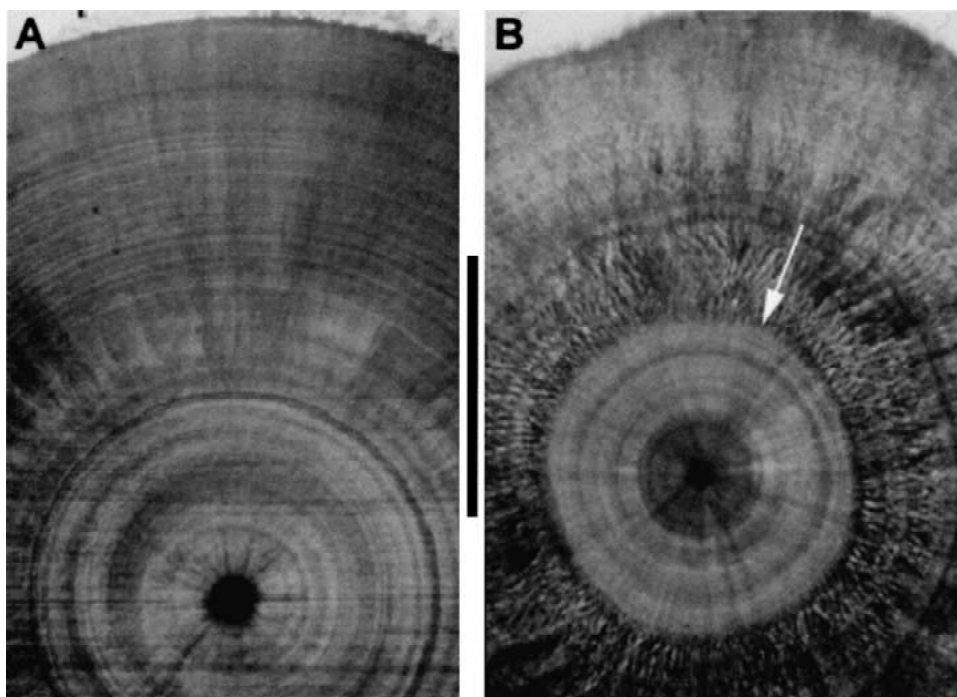


Figure 2. Photographs (32 \times) of transverse sections of an axial rod taken in the distal part at 25 cm from the basal tip (A), and in the basal part at 5 cm (B) from the basal tip. The axial rod, 167 cm total length, was from a *Halipterus willemoesi* colony collected in the Bering Sea. The arrow points to the interface within the rod base between the inner core of smooth, concentric increments, and the outer rough material (scale bar = 1 mm).

medium, and large rods was $1.01 \text{ mm} \pm 0.06$ (SE), $2.81 \text{ mm} \pm 0.10$, and $6.34 \text{ mm} \pm 0.19$, respectively.

The number of couplets per cross section changed with rod diameter (Fig. 4A, B). For each rod, maximum couplet count occurred at the maximum rod diameter. Among the rods examined, the average count at maximum diameter increased with rod size (Table 1): small, 7.1 ± 0.7 (SE); medium, 19.3 ± 0.5 ; and large, 44.3 ± 2.0 . These counts are assumed to indicate colony age in years; thus, the maximum estimated age for the largest colony, 167 cm total length, was 48.3 ± 1.5 SD yr.

Assuming an annual rate of couplet formation, the estimated annual growth rate in colony length varied with rod size, whereas change in diameter was near constant (Table 1). Total colony length divided by the average estimated age resulted in average annual growth rates of 3.9 ± 0.2 (SE), 6.1 ± 0.3 , and $3.6 \pm 0.1 \text{ cm yr}^{-1}$ for small, medium, and large-size colonies, respectively. Estimated growth rates calculated for change in size, from small to medium and medium to large, also varied as the rod increased in length. Growth estimates from small to medium colony size was 7.42 cm yr^{-1} and 1.68 cm yr^{-1} from medium

to large. Estimated annual increase in rod maximum diameter varied little among colonies (small, 0.145 ± 0.008 (SE); medium, 0.146 ± 0.002 ; and large, $0.144 \pm 0.004 \text{ mm yr}^{-1}$) reflecting low among-group variability in mean couplet width. The average annual increase in rod maximum diameter among all colonies was estimated to be 0.145 ± 0.003 SE mm yr^{-1} . This relationship was used to estimate an age prediction model using maximum rod diameter (estimated age (yr) = $7.0 * (\text{maximum rod diameter, mm}) - 0.2$; $R^2 = 0.99$). The average width of each couplet was somewhat variable along the rod for all sizes ($0.128 \pm 0.013 \text{ mm}$; Fig. 4C), particularly at the base and apex which reflects our observation that the innermost couplets tend to be relatively wide. At maximum diameter, the average increment width was near constant among the three colony sizes ($0.072 \pm 0.050 \text{ mm}$; Table 1).

The X-ray diffraction analysis of the axial rod indicated the carbonate structure is a high-magnesium calcite. Magnesium comprised 3–4 weight percent of the carbonate. Sodium was present at 1–1.5 weight percent.

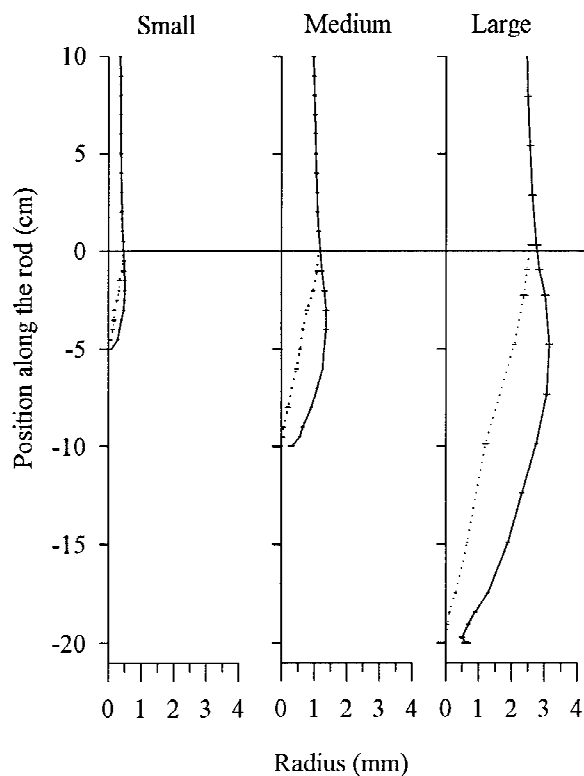


Figure 3. Measurements from cross sections taken throughout the base of twelve axial rods of *Halipterus willemoesi* were used to calculate the average (\pm SE) radius of the inner core (dotted line, Fig 2B) and the average (\pm SE) total rod radius (solid line) for each size group (four rods per group, Table 1). For each size group, superimposed plots of these two measurements versus cross section position along the rod (distance from the base tip) illustrate how core radius and thickness of the rough outer material varies longitudinally, and that the core extends to the basal tip regardless of rod size. Position along the rod is scaled so that zero (solid horizontal bar) corresponds with the probable relative position of the seafloor surface.

Radiometric results indicated that ^{210}Pb activities were relatively high and that exogenous ^{210}Pb was present in all samples except one (Table 2). Whole and cored samples had ^{210}Pb activities that exceeded the activity of ^{226}Ra in 7 out of 8 samples. The one sample that had a ^{210}Pb activity (0.0229 ± 0.0022 dpm/g) that was lower than ^{226}Ra activity (0.121 ± 0.0013 dpm/g) allowed for the calculation of an age from the disequilibrium of ^{210}Pb : ^{226}Ra . The result was 5.7 yr (1.7–10.2 yr range) for that colony. The next set of 5 samples from colonies 2 and 3, all of which were cores, had ^{210}Pb : ^{226}Ra ratios that exceeded 1.0. Therefore, the ageable sample was thought to be anomalous and the method of disequilibria dating was dropped.

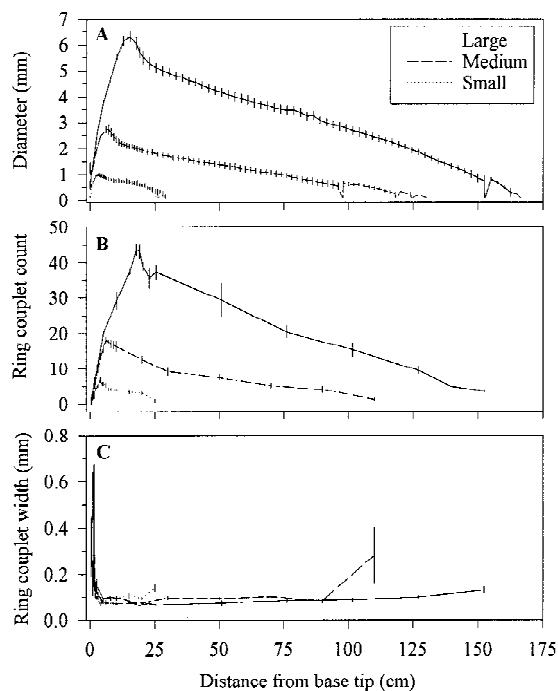


Figure 4. Average diameter (A) and growth increment count (B) from along the axial rods of small ($n=4$), medium ($n=4$), and large ($n=4$) *Halipterus willemoesi* colonies collected in the Bering Sea. Average increment width (C) was calculated as one-half diameter divided by increment count. Vertical bars indicate the standard error of the mean.

The alternate approach to determining a growth rate was to pursue the decay of ^{210}Pb over the length of the colony (Andrews et al., 2002). In general, ^{210}Pb activity in cores taken from near the basal and apical tips was high relative to activity in the middle of the rod. The range of activities for the 8 core samples taken from colony 3 ranged from 0.692 ± 0.036 to 2.76 ± 0.13 dpm/g. No growth rate or age was determined because the ^{210}Pb activities did not follow a consistent pattern over the length of the colony.

Discussion

Knowledge of structural and temporal growth are important factors in understanding the life history of organisms like coral whose structure provides habitat for other species (i.e., biogenic habitat), and in understanding how skeletal structures may record environmental variability. *In situ* observations indicate that *H. willemoesi*, or similar species, stand erect on the sea floor with the peduncle, which corresponds to the base of the axial rod (Fig. 1), embedded in sed-

Table 2. Results from the radiometric analysis of axial rod sections (whole or core) taken from three *H. willemoesi* colonies collected in the eastern Bering Sea.

Colony	Distance (cm) ^a	Sample type (whole/core)	Sample weight (g)	Activity of ²¹⁰ Pb (dpm/g)	Sigma (1 SE)	Activity of ²²⁶ Ra (dpm/g)	Sigma (1 SE)	²¹⁰ Pb: ²²⁶ Ra activity ratio
1	11.6	Whole	0.699 ^b	1.79	0.12	0.125	0.001	14.3
	11.6	Whole	0.699 ^b	1.92	0.10	0.125	0.001	15.4
	16.7	Whole ^c	0.7244	0.0229	0.0022	0.121	0.001	0.19
2 (PC-C)	13.1 ^d	Core	0.1543	0.875	0.033	0.147	0.002	5.95
	18.2 ^d	Core	0.1711	0.728	0.028	0.132	0.002	5.52
3 (PC-B)	11.6	Core	0.0691	0.917	0.050	0.157	0.001	5.84
	16.7	Core	0.0700	0.773	0.045	0.149	0.006	5.19
	24.4	Core	0.0313	0.715	0.055	0.178	0.044	4.02
	52.3	Core	0.0633	0.727	0.041	N.P.	–	–
	77.7	Core	0.0415	0.774	0.046	N.P.	–	–
	103.1	Core	0.0702	0.692	0.036	N.P.	–	–
	128.5	Core	0.0600	1.03	0.050	N.P.	–	–
	156.4	Core	0.0200	2.76	0.13	N.P.	–	–

N.P. Not processed

^aDistance from basal end to the center of each section.

^bSame sample for ²²⁶Ra analysis, split for ²¹⁰Pb analysis.

^cSmall amount of exterior removed by grinding.

^dSample length was 6 cm.

iments (Krieger, 1993). The rough part of the base corresponds to secure attachments between the rod and the surrounding soft tissue. In contrast, the upper part of the rod may be smooth so that the soft tissue better slides along it as the colony flexes in near-bottom currents. Based on cross sections through the base, the rough material overlays a core of well defined rings resembling the distal, above-sediment, part of the colony (Fig. 2).

As with *P. guernei* (Chia & Crawford, 1973), *H. willemoesi* probably begin to burrow into the sediment as newly settled planula larvae. The axial rod probably forms early after settlement (Chia & Crawford, 1977), but exactly when is unclear. With development, each colony probably burrows deeper to better anchor and support itself. We believe that depositions onto the rod above the seafloor surface result in smooth concentric rings and that lower depositions result in the rough material. Thus, the two layers of the base (Fig. 3) can be explained by rough material being deposited onto the rod as burrowing by the colony draws the rod farther into the sediment. The core of smooth rings at the base tip is difficult to explain unless the tip is the first-formed part of the rod. The relatively thin covering of rough material over this core at the tip probably results from relatively little material being deposited onto the tip during subsequent growth. Deposits onto the remaining parts of the rod must therefore cause

it to thicken and elongate. This is relevant to ring-count age estimates because our couplet counts at the maximum diameter of axial rods from large colonies (ca. 160 cm total length) probably did not include the youngest part of the rod, perhaps the first couple of growth rings were missed.

Average width of growth-ring couplets was nearly constant in cross sections of the axial rod. This was especially true for determinations made at the maximum diameter of the rod (Table 1). The calculated average width of the couplets (0.072 ± 0.005 mm) was similar to the result from a study on the axial rod of the sea pen *Ptilosarcus guernei* (0.1 mm), a shallow-water species (Birkland, 1974).

Age, estimated from counts of ring couplets, was similar within size groups and was used to determine growth rates (Table 1). The average growth rate for each colony indicated that growth was fastest for the medium sized colonies (97.8–130.3 cm), slower in the small size class (25.3–29.3 cm), and slowest for largest sizes (152.6–166.7 cm). Calculated interval growth, small to medium size and medium to large size, clearly indicated that growth was rapid (7.42 cm yr⁻¹) from an average length of 27.5 cm to 117.7 cm. Interval growth from 117.7 cm to 159.7 cm was slower at 1.68 cm yr⁻¹.

The growth pattern in length indicates slow initial growth followed by rapid growth at intermediate

rod size progressing towards an asymptotic length. This is similar to growth models used in other studies of octocoral growth. Velimirov (1975) used a sigmoidal function to describe the growth of the Mediterranean gorgonian *Eunicella cavolinii*, which approached asymptotic size at approximately 15 years. Cordes et al. (2001) used a Gompertz function to model the growth of the deep-sea alcyonacean *Anthomastus ritteri*, which reached an asymptotic size between 30 and 35 years. Although neither study formed conclusions about the maximum age for these colonies, the ages estimated for asymptotic size for *A. ritteri* were similar to the maximum ages reported in this study. No growth model was applied to the data for *H. willemoesi* because few length intervals were sampled.

In contrast to the rate of growth in length, the rate of growth in diameter was nearly constant despite differences in rod size. An age prediction equation was developed based on maximum rod diameter (estimated age (yr) = $7.0 * (\text{maximum rod diameter, mm}) - 0.2$, $R^2 = 0.99$). This relationship needs to be further reinforced, however, because of the low number of samples ($n = 12$). Assuming the age estimates are valid, this relationship could be used in age composition monitoring of trawl bycatch.

Radiometric age determination using the disequilibria of ^{210}Pb : ^{226}Ra and the decay of ^{210}Pb was unsuccessful in establishing a validation of age or growth rate estimates for *H. willemoesi*. In one sample, an age estimate of 5.7 yr (1.7–10.2 yr range) was determined for a colony (Table 2). This estimate, however, is suspect because subsequent samples had ^{210}Pb and ^{210}Pb : ^{226}Ra activity ratios that exceeded 1.0 (Table 2). These high activity ratios indicate an accumulation of ^{210}Pb from an exogenous source. Because all ^{210}Pb must result from the decay of ^{226}Ra for the technique to work (Burton et al. 1999), the presence of exogenous ^{210}Pb in these samples precluded the use of measured ^{210}Pb : ^{226}Ra activity ratios as an indicator of age.

An alternate approach using the decay of ^{210}Pb over the length of a coral colony was successfully applied to red tree coral (*Primnoa resedaeformis*; Andrews et al., 2002). The approach was successful for *P. resedaeformis* because the activities of ^{210}Pb in a series of core samples (material from the inner part of the skeleton when viewed in cross section) from near the apical tip to near the base followed the expected decay pattern and allowed for growth rate estimation and validation of annual growth rings. This approach

was applied to one sea pen colony (PC-B), but was unsuccessful because the activity of ^{210}Pb from near the apical tip to near the basal tip did not follow a consistent reduction in activity (Table 2). This may indicate that ^{210}Pb was taken up by the colony unequally throughout life, which may be a reflection of either environmental variability or a violation of the closed system assumption (Burton et al., 1999).

It is increasingly common to find that deep-sea organisms can attain ages that are on the order of decades to hundreds of years (Andrews et al., 1999a; Kastle et al., 2000; Andrews et al., 2001; Cailliet et al., 2001). The patterns of growth in their skeletal tissues may therefore reflect long histories of environmental variability such as the seasonal flux of particulate matter. This flux has been linked to reproductive cycles in some deep-sea organisms (Valiela, 1984), but not deep-sea pennatulids (Rice et al., 1992; Tyler et al., 1995; Eckelbarger, 1998). Furthermore, the longevity of these organisms and the biogenic habitat they may provide to other species makes it essential that fishing-related impacts be studied in detail (Krieger, 1993; Auster & Langton, 1999; Freese et al., 1999), particularly as fishing activities reach greater depths and fish stocks decline. This perspective on fishing-related impacts has been mandated in management practices in 1996 with the Sustainable Fisheries Act, where understanding and protection of essential fish habitat has become paramount (Rosenburg et al., 2000).

Future efforts using other methods, such as fluorochemical marking and linear extension rates may provide validated estimates of age and growth rates for *H. willemoesi*. It remains to be seen if the growth rates and age estimates determined in this study are accurate; however, in light of their importance as biogenic habitat, it is prudent to take heed of the high estimated longevity of *H. willemoesi*, which may approach or exceed 50 years.

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