Use of Annual Density Banding to Estimate Longevity of Infauna of Massive Corals

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Key words: coral growth ring, infauna, age estimation, polychaete, Okinawa

A major problem arising during the demographic analysis of marine organisms is the choice of parameters to be measured and analyzed. These parameters must represent a minimum variability for a given age. The best known parameter for a demographic study is a set of size frequency histograms. The growth parameters most often used are dry or fresh weight and body length or width. In tube building organisms, tube weight and size are the best parameter. The calcareous hard shells of molluscs and corals are known to show growth lines in the hard materials depending on warm and cold seasons, tidal frequencies, one-day activities, etc. (see Rhods and Lutz1)). These parameters must be manipulated with extreme care and with expert techniques. Examination of populations in the field is a best way to study its growth, age and whole life span, but in long-live organisms, this is hard to do. The information remaining on the hard structure of marine organisms, particularly on soft-bodied worms such as polychaetes2-5) allows their life history data to be analyzed in a laboratory in some cases.

Coral growth bands have been known to show annual growth and the growth bands can be counted using Soft X-rays,6-8) fluorescent-microscope,9) and by laser densimetry.10) The information derived from coral growth bands applies to many areas of oceanography, paleontology, etc.8,11) Nishi and Nishihira12) demonstrated the method to estimate the age of a tropical tubicolous polychaete Spirobranchus corniculatus (Grube), a sand-tube sabellariid polychaete, Idanthyrsus sp., a vermetid gastropod Dendropoma maxima Sowerby, a pecten bivalve Pedum spondyloideum Gmelin, and a coral barnacle Caniellius sp. The three tubicolous former species showed growth in various directions, and 15 to 20 years (S. corniculatus), 8 years (Idanthyrsus sp.), and 15 years (D. maxima) longevity were reliable estimates in this study. In contrast, the pecten bivalve and the coral barnacle showed lesser longevities, usually less than 7 years, and they grew vertically in almost the same direction as the host coral; thus, their growth rates can be estimated roughly by shell or slit-like hole length in relation to average host coral growth. We present here a new and practical method to estimate age and longevity of non-boring coral infauna, and we discuss marine organism growth and longevity with emphasis on polychaetes.

Growth bands of the colonies of the scleractinian coral Porites collected at Okinawan coral reefs were counted on Soft-X Ray micrographs, and age and growth rates of infaunal non-boring organisms were estimated indirectly from the annual coral-growth rings of the host coral. The organisms include a calcareous-tube polychaete Spirobranchus corniculatus (Grube), a sand-tube sabellariid polychaete, Idanthyrsus sp., a vermetid gastropod Dendropoma maxima Sowerby, a pecten bivalve Pedum spondyloideum Gmelin, and a coral barnacle Caniellius sp. The three tubicolous former species showed growth in various directions, and 15 to 20 years (S. corniculatus), 8 years (Idanthyrsus sp.), and 15 years (D. maxima) longevity were reliable estimates in this study. In contrast, the pecten bivalve and the coral barnacle showed lesser longevities, usually less than 7 years, and they grew vertically in almost the same direction as the host coral; thus, their growth rates can be estimated roughly by shell or slit-like hole length in relation to average host coral growth. We present here a new and practical method to estimate age and longevity of non-boring coral infauna, and we discuss marine organism growth and longevity with emphasis on polychaetes.

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A major problem arising during the demographic analysis of marine organisms is the choice of parameters to be measured and analyzed. These parameters must represent a minimum variability for a given age. The best known parameter for a demographic study is a set of size frequency histograms. The growth parameters most often used are dry or fresh weight and body length or width. In tube building organisms, tube weight and size are the best parameter. The calcareous hard shells of molluscs and corals are known to show growth lines in the hard materials depending on warm and cold seasons, tidal frequencies, one-day activities, etc. (see Rhods and Lutz1)). These parameters must be manipulated with extreme care and with expert techniques. Examination of populations in the field is a best way to study its growth, age and whole life span, but in long-live organisms, this is hard to do. The information remaining on the hard structure of marine organisms, particularly on soft-bodied worms such as polychaetes2-5) allows their life history data to be analyzed in a laboratory in some cases.

Coral growth bands have been known to show annual growth and the growth bands can be counted using Soft X-rays,6-8) fluorescent-microscope,9) and by laser densimetry.10) The information derived from coral growth bands applies to many areas of oceanography, paleontology, etc.8,11) Nishi and Nishihira12) demonstrated the method to estimate the age of a tropical tubicolous polychaete Spirobranchus corniculatus (described as S. giganteus, its taxonomy, see Nishi13) by counting the annual growth bands in the coral skeleton overlying calcareous tubes. Soft X-ray micrographs of slabs cut along the growth axis of many massive corals display alternating dark and light bands which outline the former positions of the outer surface of the colony (Fig. 1). These dark and light bands represent variations in the density at which the skeleton was deposited. A pair of bands—high density and low density (e.g., light plus dark bands)—represent one year's growth.7,14)

In the application of this method to coral infauna, there are 4 basic assumptions as follows: 1) organisms do not bore into the coral skeleton, 2) they do not extend their tubes or shells beyond the surface of the coral skeleton, 3) a single individual occupies one tube, shell or hole, and it does not move to other tubes, shells or holes, and 4) they are alive at the time of examination or only recently died. For the last assumption, for example, tubes of Spirobranchus and vermetids were used by crustaceans or small fish after the worms' death.5,10) The life span of those tubes occupied by hole users could be estimated with age of original worm plus years (times) utilized by hole-users. Although the user of the empty tube or hole does not secrete calcareous materials any more, the estimation of times used by the secondary space user is practically not always difficult. To know the age of the tube itself, not the worm, the tubes lacking original individual that had secreted the tube could be useful.

Materials and Methods

Over 40 massive coral colonies of Porites lutea with tube...
worns, pecten shells, or coral-barnacles were collected at Sesoko Island and Zampa Cape, Okinawa Island during 1994 to 1995. Only non-boring infauna species were studied. After collection, corals were dried after rinsing with synthetic detergent; thereafter, they were sliced into 2 to 5 mm thick slices (maximum 10 mm thickness) at the portion including the tubes or shells. The sliced plates were then radiographed under Soft X-Rays (Softex, Hitachi MB3). The exposure was 40 kVp, 3 mA, for 4 to 5 minutes (in a slice 3-4 mm thick). The source to subject distance was 50 cm. The areas of interest of the soft X-radiographs (generalized) is shown in Figs. 1 and 3 (partly drawn from photos of Nishi and Nishihira12)).

Usually we prepared one or two slices per worm, with a maximum of 10 per worm, and the slice included the whole or only a part of the tube (Figs. 1 and 3). If the slice included the whole tube or hole cut longitudinally as shown in Fig. 3A, the exact growth dates could be determined from the settlement to recent years. For pecten bivalves and barnacles, we can cut the slice including its entire hole. If the slice included two openings of the same tube as shown in Fig. 3B, the growth rate between the two openings could be determined accurately. Some slices of tube of tubicolous species, however, contained only one opening clearly cut horizontally, so we could only compare the size of recent tube openings on the coral surface with the opening that appeared in the slice.

Life Habits of Coral-Infauna Studied

1) Tube worms (Polychaetous Annelida) Spirobranchus corniculatus (Grube) is well known to be a coral inhabitant; it presently is in a taxonomically complicated state.13,17 Its life history and ecology have been studied by many researchers.14-20 The larvae settle on the exposed coral skeleton near the living part of the coral and extend their tubes toward living tissue, then the tube is covered by the living coral tissues and the tube entrance (aperture) appears on the surface of the living tissues of coral (Smith18; Figs. 1 and 2A, B).

Idanthrysus sp. (Sabellariidae) dwells in packed sand-tubes and appear on dead coral colonies and on living massive colonies17 (Nishi and Kirtley, unpublished data: Figs. 1 and 2C, D). We studied only those individuals on living massive Porites colonies in the present study.

2) A vermetid gastropod Dendropoma maxima Sowerby is a well known vermetid in coral reef area and frequently is found in dead and living corals in various regions24,25 (Figs. 1 and 2E, F). Vermetids feed by a combination of mucous nets and ctenidial cilia which collect detritus and other planktonic particles from the water.21 Dendropoma maxima is a solitary species and commonly appears on massive coral species.20 They are distributed on dead and living corals, but only those on living Porites were studied.

3) A scallop bivalve Bivalves living in scleractinian corals are also available as materials for age-estimation. Pedum spondyloideum Gmelin attaches to living massive corals at a very early growth stage and subsequently becomes completely enclosed within the coral except for its ventral region, which maintains an elliptical opening20 (Figs. 1 and 2G, H). The growth rates of the coral and the scallop are precisely balanced, and the form of the scallop is highly modified by its semi-enclosed existence to prevent overgrowth by the coral, its upward growth results in an extremely elongate shell.20

4) A coral barnacle Some species of coral-associated barnacle are buried in living colonies with a part of the shell apparent on the colony surface (Fig. 1 and Figs. 2K, L). Their growth is limited in vertical extent and their orifices usually appear on the surface. In Okinawan coral reefs, many species are known to live as coral associates.28-30 Among the barnacles, Cantellius sp., which was investigated in this study, is common in Porites colonies (Nishi pers. obs.). The species has different forms in re-
Fig. 2. Photos of coral infauna.

A-B, Spirobranchus corniculatus apertures (A) and tube (B); C-D, Idanthyrsus sp. aperture (C) and section of tube (D); E-F, Dendropoma maxima aperture (E) and internal plug (F); G-H, Pedum spondioidium; J, K, L, Cantellius sp., aperture (J) and section of empty shell (K, L).

lation to size; in large-sized forms the shell is depressed and the base is deep and cylindrical; in small-sized forms the shell is conical and the base is shallow and cup shaped (Fig. 1, right, and Fig. 2K and L) relative to the general shape of commensal cirripeds stated by Hiro.31,32) As stated by Hiro,33) in the initial stage of development, the associated cirriped has a somewhat conical shell and increases more in breadth than in length, probably to attain its full size before being surrounded by the host (Fig. 2K); however, in later stages, the lengthwise growth of the basal part becomes more pronounced, lest the cirriped should be completely embedded (Fig. 2L). In Cantellius sp. embedded in massive Porites colonies, the upper surface of the shell is always exposed, being at the same level as the surface of the coral (Figs. 1, right and 2J). Therefore, the age of each individual can be estimated by the annual growth rate of the host coral.

Results

Coral Growth

Growth of coral colonies of Porites lutea varied greatly
from 4 to 15 mm yr⁻¹ (average 9.5 mm, S.D. 2.65, N=50) among colonies and even within a colony. This variation is mainly by environmental condition around coral colonies which varied in individual colony and in years, and might partly be due to the cutting direction of the colony, because the colony might have had grown in various directions. Among 40 colonies examined, an ordinary annual growth was 6 to 12 mm (Fig. 3).

Polychaeta Spirobranchus corniculatus

Examples of growth estimation of *Spirobranchus* are shown in Fig. 4 which shows that the diameter of the opening and the number of growth bands between the recent tube opening and the opening in the slice. The growth rate was 0.1 to 0.8 mm yr⁻¹ in tube-orifice inner diameter (average 0.45 mm, S.D. 0.21, N=100 for 20 worms). Very little growth was detected in some worms, while others grew fast and attained 5 mm tube-orifice diameter within 6 years (Fig. 4). Tube orifice diameter is known to be correlated roughly with tube length, which ranged 3 to 20 cm and usually grew to various directions. Most tube apertures were directed upper-laterally (Fig. 2A), rarely vertically and completely upward in direction. Some worms grew with 3 to 5 mm tube opening diameter within 10 years from the settlement, and some larger worms which originally had 2 to 4 mm tube opening diameter at 1981 to 1982 grew to a stage with a 6 to 9 mm tube opening diameter within 12 or 13 years (Fig. 4). The largest worm had a 10 mm orifice diameter in this study, and the worm was estimated to had lived more than 15 or 20 years. In field, a maximum of 14 to 15 mm orifice diameter was observed, thus the longevity of the tropical tube worm is possibly about 30 years in Okinawa.

Polychaeta Idanthyrsus sp.

Sabellariid polychaete with sand tube (Fig. 2C, D) has an annual growth rate similar as or slightly faster than *Spirobranchus*, usually being 0 to 1.2 mm yr⁻¹, with an average of 0.61 mm (S.D. 0.36) in tube-orifice inner diameter (N=5: Fig. 5). The largest worm had a tube with 1.2 mm orifice diameter and over 20 cm length, suggesting an age of over 8 years.

A Vermetid Gastropod

Among coral infauna studied, *Dendropoma maxima* was largest, and it grew faster than the other species (0.2 to 2.5 mm in tube orifice inner diameter yr⁻¹, average 0.85 mm, S.D. 0.45) and attained an orifice diameter of >10
mm within 10 years and estimated longevity being 10 to 15 years (Fig. 6). Tubes frequently run on the coral colony surface with the anterior part not buried in living tissues (Fig. 2E) and the growth rate was inconsistent; this suggests a more rapid linear growth of individual tubes than of host coral growth in some cases.

Some vermetid worms have made internal plugs in tubes (Fig. 2F) and therefore the tube was frequently partly damaged. In such cases, we could not trace entire tubes.

A Scallop Pedum spondyloidium

Growth rate of the scallop, Pedum spondyloidium varied from 2 to 8 mm in shell length yr\(^{-1}\) (average 5.5 mm, S.D. 2.3) and 2 to 10 mm yr\(^{-1}\) in shell width (average 5.8 mm, S.D. 3.1, N=5; Fig. 7). In early stages, it grew rather quickly (3 to 8 mm in maximum shell width yr\(^{-1}\)), and the growth rate decreased to 3 to 6 mm in its later stages (over 20 mm width). Maximum shell width was 30 mm, possibly indicating over 6 years longevity.

A Coral Barnacle Cantellius sp.

The visible part of the cirriped on the coral surface was very small, although the maximum shell opening diameter >5 mm., and the growth rate yr\(^{-1}\) was 0.25 to 2.5 mm (average 0.96 mm, S.D. 0.53, N=7; Figs. 2K, L, and 8).

The growth rate was high in the first and second years; it has a somewhat conical shell and increased more in breadth than in length (Fig. 2K), about 1 to 2.5 mm in orifice diameter was attained in two years, and the growth rate decreased suddenly so that the lengthwise growth of the basal part became more pronounced and showed only 0.25 to 1.0 mm yr\(^{-1}\) (Fig. 8). The observed maximum shell diameter was 7 mm, and that particular barnacle was possibly older than 5 to 7 years.

In 10 coral colonies, 10 barnacle shells completely buried into coral skeleton were found, the sizes of which ranged from 30 to 60 mm in shell height, with a maximum shell diameter being 4 to 7 mm. Those individuals might have died in the 3rd to 7th year after settlement.

Relationship between Tube or Hole Length and Estimated Age

For five species studied here, hole depth or tube lengths were measured and compared to host coral growth. In tube-dwelling polychaetes and the vermetid, tube length va-
Age Estimation of Coral Infauna

ried in individual tubes and by species, their growth was clearly inconsistent (Fig. 9). In contrast, hole depths of pecten and coral barnacle were clearly correlated with estimated ages (Fig. 9) and thus with host coral growth rate. It seems that hole depths for the pecten and the coral barnacle show a value similar to that of the host coral growth, although the holes of Pedum were frequently depressed (Fig. 2G, H) and exact growth rate may be difficult to estimate only from growth of host coral.

Discussion

We estimated the average age of calcareous and sand-tube dwelling polychaetes of 5 to 8 mm tube orifice diameter to be 5 to 10 years old (Figs. 4 and 5). These worms had a body length 5 to 10 cm (for size distribution of S. corniculatus, see Nishi & Kikuchi33). In the present study, a maximum of 20 years in Spirobranchus, and 8 years in Idanthyrsus can be taken as the best estimate of life span; the estimated maximum longevity of *Spirobranchus* is one of the longest among marine annelids reported in the literature (Table 1). The longevity of *Sabellariidae* is 3–10 years,30 with the maximum known in *Sabellaria alveolata* as 10.5 years35,36 although Gruet37 estimated the age as 3–5 years in the same species. The values of life span of *Polyochaeta* ranged from 2 to 3 months in small worms such as *Spirorbis* and 8 to 12 years in larger worms such as terebellids, large serpulids, and others (Table 1). The body size of *Spirobranchus* and *Idanthyrsus* are smaller than that of other species with nearly the same age (Table 1). For example, *Terebellidae* showed a longevity of 5 to 7 years at over 10 cm body length,3 commensal scale worm also had a longevity of 4 to less than 10 years at over 10 cm body length.39 *Nephthyidae* and *Lumbrineridae* polychaetes are well known to show an exact correlation between growth ring on chitinous jaws and ages.3,19,30 *Nephys* with 5 to 8 years life cycle has a body with 5 to 10 cm length, as in *Spirobranchus* and *Idanthyrsus*. In this study. Up to now, the longest life span among marine annelids is known for *Spirobranchus polycerus* on West Indies coral reefs (probably 12 years estimated by host coral growth bands, Marsden42) except for our previous work and Smith’s work on *S. giganteus* (over 20 years) or *S. corniculatus* (over 20 years).12,19

In coral barnacles, Hiro32 suggested that the age of coral barnacles can be roughly estimated by the annual

### Table 1. Age of polychaetes studied by growth line on rigid structures, population dynamics and rearing experiments

<table>
<thead>
<tr>
<th>Species</th>
<th>Max. age</th>
<th>Size or weight of worms</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Spirobranchus polycerus</em></td>
<td>12</td>
<td>5–8 cm</td>
<td>coral growth ring</td>
<td>Marsden 42)</td>
</tr>
<tr>
<td><em>S. giganteus</em></td>
<td>20</td>
<td>5–10 cm</td>
<td>coral growth</td>
<td>Smith 19)</td>
</tr>
<tr>
<td><em>S. corniculatus</em></td>
<td>20</td>
<td>5–10 cm</td>
<td>coral growth ring</td>
<td>this study</td>
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<tr>
<td><em>S. corniculatus</em></td>
<td>40?</td>
<td>10 cm</td>
<td>coral growth ring</td>
<td>Nishi and Nishihara 12</td>
</tr>
<tr>
<td><em>Lumbrineris fragilis</em></td>
<td>12</td>
<td>0.36 cm head width</td>
<td>population, growth line</td>
<td>Valderhaug 41)</td>
</tr>
<tr>
<td><em>Sabellaria alveolata</em></td>
<td>10</td>
<td>5 cm body length</td>
<td>population</td>
<td>Wilson 35, 36)</td>
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<td><em>Pectinaria grunulata</em></td>
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<td>30 cm body length</td>
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<td>Curtis 2)</td>
</tr>
<tr>
<td><em>Arctone viatica</em></td>
<td>7–8</td>
<td>2.4 mm body width</td>
<td>growth rings</td>
<td>Britayev 54)</td>
</tr>
<tr>
<td><em>Arctone viatica</em></td>
<td>&gt;3</td>
<td>2.4 mm body width</td>
<td>population</td>
<td>Britayev 54)</td>
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<tr>
<td><em>Arctone viatica</em></td>
<td>10</td>
<td></td>
<td></td>
<td>Palmer 38)</td>
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<tr>
<td><em>Nephys caeca</em></td>
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<td>20 cm body length</td>
<td>growth ring</td>
<td>Olive 40)</td>
</tr>
<tr>
<td><em>Nephys ciliata</em></td>
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<td>12 cm body length</td>
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<td>Kirkegaard 39)</td>
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<tr>
<td><em>Thekepus setosus</em></td>
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<td>30 cm body length</td>
<td>population</td>
<td>Duchene 55)</td>
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<tr>
<td><em>Terebellides stromii</em></td>
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<td>4 cm body length</td>
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<td><em>Melina cristata</em></td>
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<td>35 mm body length</td>
<td>population</td>
<td>Hutchings 56)</td>
</tr>
<tr>
<td><em>Aglaphamus verrilli</em></td>
<td>5+</td>
<td>6 cm body length</td>
<td>population,</td>
<td>Estcourt 57)</td>
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<td></td>
<td></td>
<td></td>
<td>rings on jaw</td>
<td></td>
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<tr>
<td><em>Nephys hobergii</em></td>
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<td>population, growth</td>
<td>Kirkegaard 39)</td>
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<tr>
<td><em>Nephys hombergii</em></td>
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<td>population</td>
<td>Olive 40)</td>
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<tr>
<td><em>Eunoe oerstedii</em></td>
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<td>30 mm</td>
<td>population</td>
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<tr>
<td><em>Harmatohoe imbricata</em></td>
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<td>&gt;400 mg</td>
<td>population, aquarium</td>
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<td><em>Lagis koreni</em></td>
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<td></td>
<td>population</td>
<td>Daly 59)</td>
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<td><em>Harmatohoe imbricata</em></td>
<td>2</td>
<td></td>
<td>population</td>
<td>Kirkegaard 58)</td>
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<tr>
<td><em>Ophelia borealis</em></td>
<td>2</td>
<td>50 mg</td>
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<tr>
<td><em>Owenia fusiformis</em></td>
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<td>7 mg and 18 mm</td>
<td>population</td>
<td>Curtis 2)</td>
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<tr>
<td><em>Anthoestia sarsi</em></td>
<td>2</td>
<td></td>
<td>population</td>
<td>Curtis 2)</td>
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<tr>
<td><em>Pectinaria hyperboraea</em></td>
<td>2</td>
<td>Dry weight 150 mg</td>
<td>population</td>
<td>Peer 60)</td>
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<tr>
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<td></td>
<td>growth ring</td>
<td>Estcourt 57)</td>
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<td><em>Perinereis cultrifera</em></td>
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<td></td>
<td>population</td>
<td>Olive 3)</td>
</tr>
<tr>
<td><em>Gatvika cirrosa</em></td>
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<td>30 mm</td>
<td>population</td>
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<tr>
<td><em>Goniada maculata</em></td>
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<td>12 mm</td>
<td>population</td>
<td>Kirkegaard 58)</td>
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<tr>
<td><em>Hydroides hexagonis</em></td>
<td>2</td>
<td>12 mm length</td>
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<td>Grave 61)</td>
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<td><em>Chitonopoma occidentalis</em></td>
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<td>aquarium</td>
<td>Smith and Haderlie, 62)</td>
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<td><em>Pholoe minuta</em></td>
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<td>maximum 10 mm</td>
<td>growth ring</td>
<td>Olive 3)</td>
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<tr>
<td><em>Spirorbis sp.</em></td>
<td>2 mon.</td>
<td>3 mm in length</td>
<td>aquarium</td>
<td>Smith and Haderlie, 62)</td>
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</table>
growth rate of the coral (p. 410). He cited the growth data of Ma43 and estimated barnacle ages of at least 5 years in individuals associated with Favia speciosa in Tanabe Bay, Pacific side of central Honshu, Japan. This value is similar to that of our study although this value might vary according to host coral growth rate, as suggested by Hiro.51

In pecten shells, a less long life is attained on the coral colony in comparison with other Pecten shells.44 In this study, we analyzed small to middle sized Pedum shells because of the difficulty of collection, and maximum sizes of about 8 cm height and 5 cm width (Nishi, pers. obs. in 1995). Their maximum longevity might be about 10 years at Okinawa.

How can the coral associated polychaetes live so long? Marsden42 noted that the longer life span of S. giganteus than S. polycerus is probably due to the host coral stability; S. giganteus live on longer lived massive coral colonies, whereas S. polycerus lives on ephemeral plate-like coral colonies. The sedentary polychaetes living on coral colonies possibly cannot live longer than the host coral colonies. Massive Porites colonies sometimes reach over 5 m in diameter in Okinawan coral reef (Nishihira, pers. obs.) and Potts et al.45 estimated over 500 years age in large Porites colonies. Spirobranchus and Idanthyrsus probably attain a long life by colonizing the long-lived, stable coral colony.

Why do the coral-associated tube worms have a relatively small body even though they have long life cycles? One reasonable explanation is great cost for the construction of the thick calcareous or tough sand tubes among coral colonies. Spirobranchus tube-wall s are very thick (over 1 mm), with a rigid keel, and sometimes deposit a calcareous partition on the posterior part of the tube12; the tube construction is very tough as shown in Ficopomatus.46

Calcareous materials are produced anteriorly on the tube lip for growth and posteriorly to protect against organisms coming into tubes or to plug holes made by boring organisms. Spirobranchus and Dendropoma tubes rarely have posterior tabula or packing structures (in Dendropoma, see Fig. 2F; for Spirobranchus, Lommerzheim72; Nishi and Nishihira53). Producing large amount of calcareous materials on the posterior side and potential danger from invading organisms into tubes probably causes slower growth of the coral infauna, especially of tube-dwelling species.

Coral infauna probably preferentially select host corals that are stable and which therefore protect the infauna from predation. Scott46 confirmed that coral associates, including boring organisms, occur commonly in the common (abundant), less aggressive corals with smaller polyps; and the relative abundance of the corals appears to be stable over time. Some coral infauna are species specific on host coral species (e.g., for Spirobranchus, Dai and Yan62; Nishi and Kikuchi52; review of host and associates, Patton62; Scott46). Spirobranchus prefers living coral, and competitively subordinate species.46 We can add a new idea that Spirobranchus and Idanthyrsus probably select those host corals which have nearly the same growth rate as that of the polychaetes. If tubificid polychaete settle on rapidly growing species, tubes may not be so tough. In contrast, if they settle on slowly growing coral colonies, their tubes might remain small and short for some years. Although calcareous tube worms extend their tubes in various directions and in various amounts according to the environmental conditions, they can regulate the growth rate of their tubes by changing the tube wall thickness,51 and thus the tube construction work might require a high metabolic cost.

By counting annual growth bands, we can age and estimate the growth rate of coral infauna. However, we probably cannot estimate a reliable longevity only by this method. That is because empty holes or tubes on coral colonies are usually used by hole dwellers, including crustaceans and fishes. Nishi52 noted the occurrence of empty tubes of Spirobranchus fully buried in coral skeletons, the tube mouth being not apparent on the coral surface. Even for such a tube embedded in the coral skeleton, there is no reason to consider that the worm died and that the coral had overgrown the tube. To know the correct longevity of coral infauna, the desirable method may be rapid collection of the coral colony and preparation of cut slabs or fixation for further manipulation of age-estimation of corals and worms.

In contrast to the tube-dwelling species, organisms dwelling in the slit-like hole or simple tubes like coral barnacles have more easily estimated ages and growth, because their growth direction is nearly the same as that of the host coral, and growth amounts of the associates also nearly same as that of the host coral (see results). This shows that they are obligate coral-dwellers on living tissues. Obligate living coral-dwellers can regulate their growth to coincide with that of the host coral, but others need not do this. Tubicolous species may possibly regulate their growth direction and amount of tube growth.51 The tubes of Dendropoma and Idanthyrsus rarely or frequently appeared to surpass the host coral growth and are found partly uncovered by living coral tissues.

We applied the method given by Nishi and Nishihira52 to five marine animals in this study, and this method is suggested also to be applicable to other coral infauna. For a mollusca, Magilus antiquus Montfort, also living in coral mass, the method seems useful, as suggested by Nishi.59 We examined this species tentatively only for a single individual; although we cannot obtain fresh materials in living corals, its age is possibly in excess of 5 years in an individual with over 10 cm calcareous part length (calcareous siphon) deposited in nearly 8 cm depth below the coral surface.

Whether the organism concerned is a boring species or not is probably judged by the shape of the holes or tubes. Boring organisms usually make vertical straight or complex long tubes or holes, other tubes or holes usually taper posteriorly (Fig. 1, comparing Notaulax and other tubes or holes).

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