

Direct Growth Measurements of Two Deep-sea Scalpellid Barnacles, *Scalpellum stearnsii* and *Graviscalpellum pedunculatum*

Yoichi Yusa^{1,*}, Natsumi Yasuda¹, Tomoko Yamamoto², Hiromi Kayama Watanabe³, Takuo Higashiji⁴, Atsushi Kaneko⁴, Kazuki Nishida⁵, and Jens T. Høeg⁶

¹Nara Women's University, Kitaouya-nishi, Nara 630-8506, Japan

²Kagoshima University, Kohrimoto 1-21-24, Kagoshima 890-8580, Japan

³Japan Agency for Marine-Earth Science and Technology, Natsushima 2-15, Yokosuka 237-0061, Japan

⁴Okinawa Churaumi Aquarium, Motobu-cho, Okinawa 905-0206, Japan

⁵Kagoshima City Aquarium, Kagoshima 892-0814, Japan

⁶University of Copenhagen, Universitetsparken 4, Copenhagen DK-2100, Denmark

(Received 5 March 2018; Accepted 4 May 2018; Published xx June 2018; Communicated by Benny K.K. Chan)

Citation: Yusa Y, Yasuda N, Yamamoto T, Watanabe HK, Higashiji T, Kaneko A, Nishida K, Høeg JT. 2018. Direct growth measurements of two deep-sea scalpellid barnacles, *Scalpellum stearnsii* and *Graviscalpellum pedunculatum*. Zool Stud 57:29. doi:10.6620/ZS.2018.57-29.

Yoichi Yusa, Natsumi Yasuda, Tomoko Yamamoto, Hiromi Kayama Watanabe, Takuo Higashiji, Atsushi Kaneko, Kazuki Nishida, and Jens T. Høeg (2018) Little is known about the growth rates of invertebrates living in ordinary deep-sea habitats such as continental slopes. Thus, the growth rates of two species of the deep-sea scalpellid barnacles, *Scalpellum stearnsii* and *Graviscalpellum pedunculatum*, were studied in two aquaria (at Nara and Okinawa Churaumi, Japan). In addition, growth of an *S. stearnsii* individual after 1 year of deployment was measured in the field. Overall, adult individuals of both species showed slow growths over 8 months (at Nara) and 2 years (at Okinawa) of rearing (e.g., at Nara: $2.0 \pm 3.6 \mu\text{m d}^{-1}$ for *S. stearnsii* and $5.9 \pm 2.7 \mu\text{m d}^{-1}$ for *G. pedunculatum*; mean \pm SD). In contrast, growth rates of juvenile *S. stearnsii* at Nara were greater ($15 \pm 7.7 \mu\text{m d}^{-1}$). The *in situ* growth rate of the adult *S. stearnsii* ($3.4 \mu\text{m d}^{-1}$) was greater than the average, but within the range of the rates of similar-sized individuals recorded in aquaria. Compared with other pedunculate barnacles, both species show small growth rates typical for deep-sea animals.

Key words: Cirripedia, Field measurement, Growth rate, Pedunculata, Rearing.

BACKGROUND

Life histories including growths of several deep-sea invertebrates living in hydrothermal vent fields, methane seeps, and on whale carcasses have recently become known (e.g., Britayev et al. 2007; Van Dover and Lutz 2004; Arellano and Young 2009; Miyamoto et al. 2013; Arellano et al. 2014). However, except for some species with fishery importance, very little is known about the growths of invertebrates living in ordinary deep-

sea habitats such as continental slopes, ridges, or ocean floor (Lampitt 1990; Herring 2001).

Barnacles (Crustacea: Thoracica) distribute widely from the intertidal to > 6,000 m depth (Newman and Ross 1971; Zevina 1981). Their sedentary nature makes their location and recapture relatively easy, even in the deep sea (Lampitt 1990). In addition, they normally have calcareous shell plates that record their growths, which can be traced even in fixed specimens (Blomsterberg et al. 2004) and fossils (Gale 2016).

*Correspondence: E-mail: yusa@cc.nara-wu.ac.jp

Some species of deep-sea scalpellid barnacles live in hydrothermal vent fields (e.g., *Leucolepas longa* Southward & Jones, 2003; Tunnicliffe and Southward 2004), others on rocks or dead shells (e.g., *Scalpellum stearnsii* Pilsbry, 1890; Ozaki et al. 2008), and still others are epibionts that utilize a diverse array of animals depending on species (e.g., *S. scalpellum* (Linnaeus, 1767) on hydroids or sea urchins and *Weltnerium nymphocola* (Hoek, 1883) on pycnogonids; Buhl-Mortensen and Høeg 2006 2013). Deep-sea scalpellids even use artificial substrata such as telegraph cables as attachment sites, and many museum specimens are recorded from this substrate (Nilsson-Cantell 1928). Therefore, barnacles are ideal animals for studying growth rates and other life history parameters, and such information is useful for inferring time passed, or even life histories of other species in the case of epibiotic barnacles (Gili et al. 1993). Yet, most studies on the life history of barnacles deal with shallow water species, and direct measurements of deep-sea species' growth patterns have been rare, conducted only in the small pedunculate barnacles *Poecilasma kaempferi* Darwin, 1852 (Lampitt 1990) and *Heteralepas canci* Chan, Tsang & Shih, 2012 (Yasuda et al. 2016). The growths of both species are fairly rapid: $61 \mu\text{m d}^{-1}$ for the former and $14\text{--}33 \mu\text{m d}^{-1}$ (depending on food availability) for the latter. However, growth rates of larger species living in the deep sea, including scalpellids, are virtually unknown.

We conducted direct measurements of growth patterns for two deep-sea scalpellid barnacle species, *Scalpellum stearnsii* and *Graviscalpellum pedunculatum* (Hoek, 1883) (sensu Gale 2016; sometimes referred to as *Anguloscalpellum pedunculatum*), under controlled rearing conditions in aquaria (Fig. 1). Moreover, we determined the *in situ* growth of an *S. stearnsii* individual. Here we report their growth rates and compare them with those of other pedunculates.

MATERIALS AND METHODS

Aquarium rearing

We reared *Scalpellum stearnsii* and *Graviscalpellum pedunculatum* individuals at Nara Women's University, Nara Prefecture, Japan (34.69°N , 135.83°E) and Okinawa Churaumi Aquarium, Okinawa Prefecture, Japan (26.69°N , 127.88°E).

The rearing at Nara Women's University was conducted for ca. 8 months (253 days) at $11\text{--}12^{\circ}\text{C}$ under constant dark except for observation and feeding. Initially, four small individuals of *S. stearnsii* were obtained from Suruga Bay (c. 35.0°N , 138.7°E) in April 2016 and were reared in an aquarium with 50-l sea water from 5th April to 14th December 2016. Then, five larger *S. stearnsii* individuals and five *G. pedunculatum* individuals were obtained from a depth of c. 400 m near Koshiki Islands (c. 31.9°N , 129.8°E) in April and May 2016 and were kept at Kagoshima City Aquarium. All these individuals were found either solitary or in small groups of 2 - 3 individuals; they were either attached to dead shells or pebbles or had no attachment substratum at capture. Such situations were usual based on our *in situ* observations using the remotely operated vehicle (ROV) *Hyper-Dolphin*, during the cruise of the R/V *Natsushima* (NT12-07) belonging to Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (see below). The specimens were brought to Nara in June 2016 and reared together with the smaller *S. stearnsii*. They were fed with newly hatched larvae of *Artemia salina* (Linnaeus, 1758) and a mixture of minced small sardines (*Engraulis japonicus* Temminck & Schlegel, 1846) and shrimp purchased at a local market. The amount of both *Artemia* (as dry eggs) and the mixture of sardines and shrimp (wet weight) was increased with the growth of individuals. The

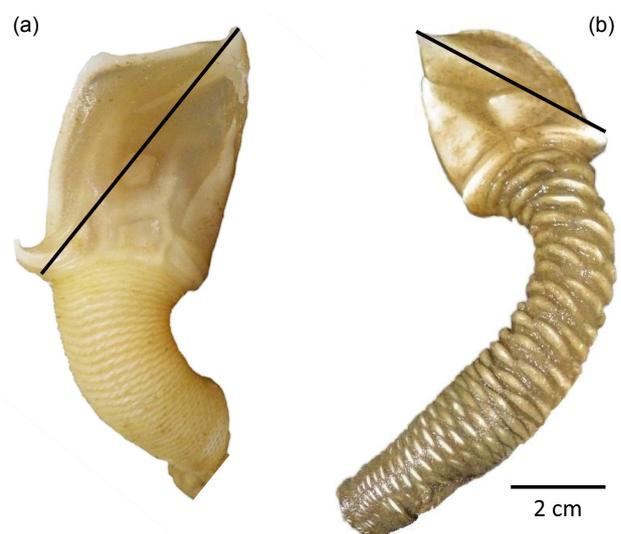


Fig. 1. Scalpellid barnacles *Scalpellum stearnsii* (a) and *Graviscalpellum pedunculatum* (b). The *S. stearnsii* individual showed maximum absolute increments at Okinawa, with small shell plates. Capitulum length measured is shown as a black line.

equation was:

Amount of each food item put in the aquarium per week (g) = sum of [capitulum lengths in mm]²*0.05,

with the maximum amount of 1.5 g each per week to avoid water fouling. The water was circulated using two water pumps, and about 1/3 of the water was exchanged monthly. Individuals were identified by a plastic tie wrapped at the base of the peduncle if needed, which had no apparent effects on growth and survival. The maximum length (from the apex to the base) of the capitulum was measured monthly (Fig. 1). There are good correlations among capitulum length, total length, and wet weight in *S. stearnsii* (Ozaki et al. 2008). Capitulum length is a good index of size because the capitulum does not shrink or extend like the peduncle or the total length and is measurable for any individual, unlike weight (which cannot be measured for individuals attached in groups on boulders).

The rearing at Okinawa Churaumi Aquarium was conducted using individuals collected from off Boso Peninsula (c. 35.1°N, 139.8°E). They were reared mainly in a 500-l aquarium (sometimes 80-l or 180-l aquaria were also used for some individuals for demonstration) from March 2014 at 9 - 14°C with dim light. A total of 24 *S. stearnsii* and 3 *G. pedunculatum* individuals were initially reared, and 14 *S. stearnsii* individuals were added in June 2015. Most were found attached to boulders, forming groups of 2 - 10 individuals. Minced frozen copepods, krill, and fish were given four times a day as food. Water was circulated using a pump and a small amount of filtered fresh sea water was always flown into the aquarium.

The measurements were made four times over c. 2 years (706 days), on 25th November 2014, 8th June 2015, 28th March and 31st October 2016. The individuals were photographed and identified by the position on the boulders to which they were attached and, in some cases, by a plastic tie wrapped at the base of the peduncle. Each time, the maximum length of the capitulum was measured. Survival rates were not quantified because several individuals were detached and their individual identification was not feasible.

***in situ* study**

We collected 24 individuals of *Scalpellum stearnsii* off Cape Nomamisaki, Kagoshima, Japan (c. 31.5°N, 129.9°E) in April 2011. After the capitulum lengths were measured, they were

stained using calcein (0.4 g l⁻¹) for 1 day before deployment to detect the shell increment (Fujikura et al. 2003). The bases of their peduncles were attached to the empty shells of *Crassostrea gigas* (Thunberg, 1793) with cyanoacrylate glue and plastic ties, which were tied onto a device made with a stainless steel frame ('Namekujira 11'; see Yasuda et al. 2016 for the photo of the device). The device was deployed on 13th April 2011 off Cape Nomamisaki, Kagoshima, Japan (31.34°N, 129.98°E) using the training vessel *Nansei-maru* of Kagoshima University. Cow and pig bones were also tied onto the frames, at least 20 cm apart from *S. stearnsii*, to collect *Osedax japonicus* Fujikura, Fujiwara & Kawato, 2006 (Miyamoto et al. 2013). The device was re-collected on 28th March 2012 at a depth of 229 m using the ROV *Hyper-Dolphin* during the cruise of the R/V *Natsushima* (NT12-07). Only one *S. stearnsii* was found; the other individuals disappeared due to detachment of the glue/ties and death after deployment. The water temperature at the site varies from c. 11 to 15°C (Yasuda et al. 2016).

The shell plate (scutum) of the individual was dissected out and sectioned across the growth lines. It was observed under a fluorescence scanning electric microscope with the UV wavelength (Fujikura et al. 2003).

Growth analyses

In this study, both absolute and relative growth indices were calculated. The absolute growth (in mm or μm) is the difference in the capitulum lengths (CL) of the same individual measured at two occasions: CL_f - CL_i, where CL_f is the final length and CL_i is the initial. The relative growth is the relative increase in capitulum length, calculated as: CL_f/CL_i. Both indices are also expressed in daily increments, where the absolute daily increment is (CL_f - CL_i) d⁻¹ and the relative daily increment is (CL_f/CL_i - 1) d⁻¹. These indices can be calculated from the initial and final lengths and number of days, which are often reported in barnacle literature (e.g., Evans 1958; Dalley and Crisp 1981; Inatsuchi et al. 2010; Yasuda et al. 2016) and hence allows species comparisons.

Pearson's correlation was used to investigate the relationship between initial capitulum length and daily growth rates. Normality of residuals was checked by Shapiro-Wilk's W test. All statistical analyses were conducted on the software JMP version 11 (SAS Institute, Cary, North Carolina).

RESULTS

Aquarium rearing at Nara

All scalpellid individuals survived 6-month (larger *Scalpellum stearnsii* or *Graviscalpellum pedunculatum*) or 8-month (smaller *S. stearnsii*) rearing periods at Nara and showed positive growth rates (Fig. 2a). The four small (17.6 - 27.9 mm initial capitulum lengths) individuals became 1.16 ± 0.116 (mean \pm SD) times larger after 8 months, or 1.13 ± 0.089 times after the initial 6 months. Their daily increment during the 6-month period was $0.067 \pm 0.047\%$ d⁻¹, or $15 \pm 7.7 \mu\text{m d}^{-1}$. The five larger *S. stearnsii* individuals showed slower growth, with the daily increment being $0.0032 \pm 0.014\%$ d⁻¹, or $2.0 \pm 3.6 \mu\text{m d}^{-1}$. There was a negative relationship between initial capitulum length and both indices of daily increments (relative: $n = 9$, $r = -0.823$, $P = 0.006$; absolute: $r = -0.860$, $P = 0.003$).

The growth rate of *G. pedunculatum* was between small and large *S. stearnsii*, with the daily increment of $0.014 \pm 0.007\%$ d⁻¹, or $5.9 \pm 2.7 \mu\text{m d}^{-1}$. The relationships between initial capitulum length and both indices of daily increments were not

significant (relative: $n = 5$, $r = -0.246$, $P = 0.69$; absolute: $r = -0.028$, $P = 0.96$).

Aquarium rearing at Okinawa

Rearing at Okinawa Churaumi Aquarium generally resulted in lower growth rates than at Nara, and many showed apparently negative growth rates due to abrasion of the shell plates (Fig. 2b). The *Scalpellum stearnsii* individuals became 1.015 ± 0.076 , 1.000 ± 0.033 , and 1.003 ± 0.020 (mean \pm SD) times larger during the periods between the measurements conducted on November 2014, June 2015, March and October 2016, respectively. These correspond to the daily increments of 0.0075 ± 0.039 , 0.00008 ± 0.011 , $0.0014 \pm 0.009\%$ d⁻¹, or -0.70 ± 13 , 0.05 ± 6.5 , $1.3 \pm 4.8 \mu\text{m d}^{-1}$. The maximum relative daily increment (0.116% d⁻¹) was recorded for the smallest individual (initial capitulum length = 8.70 mm), whereas the maximum absolute increment ($29 \mu\text{m d}^{-1}$) was recorded for the individual with the initial capitulum length of 41.30 mm. The shell plates of the latter individual were less well developed after the rapid growth (Fig. 1).

The growth rate of *Graviscalpellum*

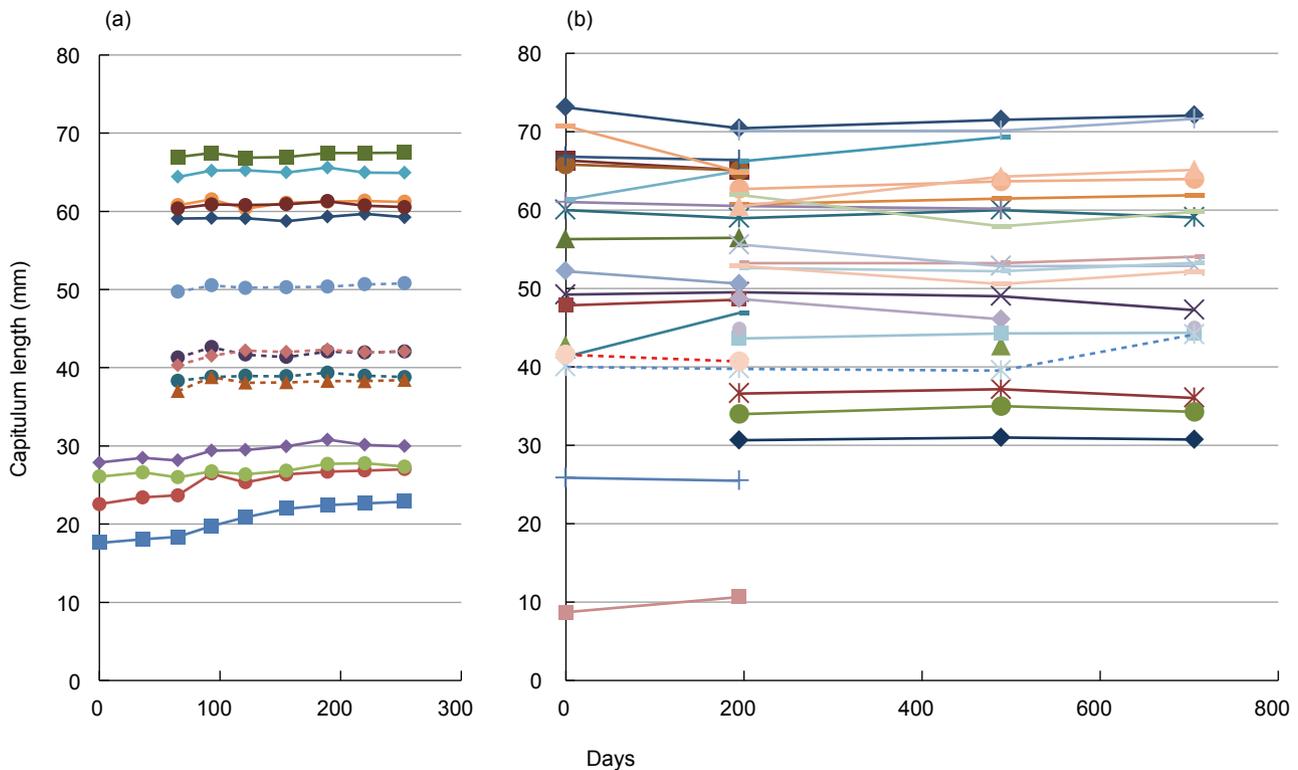


Fig. 2. Changes in capitulum lengths of *Scalpellum stearnsii* (solid lines) and *Graviscalpellum pedunculatum* (broken lines between 35 - 55 mm) over 8-month rearing at Nara (a) and 2-year rearing at Okinawa (b). Different colors indicate different individuals.

pedunculatum was obtained for only two individuals. Depending on the individual and period, their daily increments ranged from -0.003 to 0.054%, or -4.4 to 21 $\mu\text{m d}^{-1}$.

in situ study

We re-collected only one individual of *Scalpellum stearnsii*. This individual grew from 57.65 mm to 58.85 mm in capitulum length within almost 1 year (350 d). It became 1.02 times larger, with a 1.20 mm increment in capitulum length. The daily increment was 0.0059% d^{-1} of the initial length, or 3.4 $\mu\text{m d}^{-1}$.

Under the fluorescence microscope, a calcein-stained band was seen on the sectioned scutum of the re-collected individual (Fig. 3). A clear increment was observed on the shell.

DISCUSSION

This study obtained accurate growth rates for the first time in deep-sea scalpellid barnacles. The growth rate of *Scalpellum stearnsii* depended on body size and, presumably, age, such that small individuals tended to show higher growth rates, both as the absolute and relative values, than larger ones. Similar size-dependent growth rates have been reported widely in other barnacles (Batham 1945; Lampitt 1990; Inatsuchi et al. 2010). In *Graviscaepellum pedunculatum*; however, the relationship between size and growth rate was not significant, likely because a narrower size range of individuals was used for the experiment at Nara and only two individuals were successfully recorded at Okinawa.

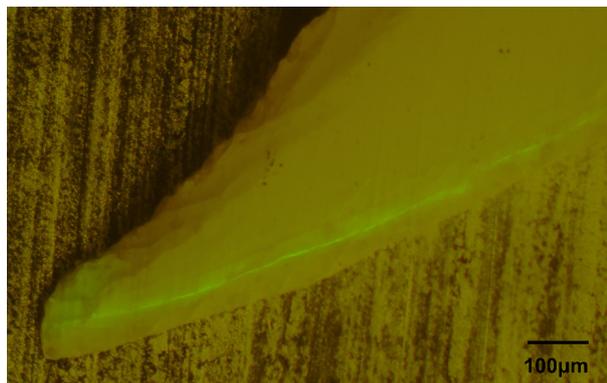


Fig. 3. *in situ* shell increment after 350-d deployment of *Scalpellum stearnsii* (narrow strip below the light calcein-stained band). Pictures under fluorescent and normal light were overlaid.

The growth rate of *S. stearnsii* also depended on rearing conditions. Rearing at Nara led to higher growth rates than at Okinawa, even among similar-sized individuals. In other pedunculate barnacles, temperature and food are among the most important factors relevant to growth (Inatsuchi et al. 2010; Yasuda et al. 2016). In this study, temperature was unlikely to be responsible, as the rearing temperatures greatly overlapped between the two experiments (11 - 12°C at Nara vs. 9 - 14°C at Okinawa). Food availability is more likely to be responsible for the difference, as the closed rearing system and living *Artemia* as a food source at Nara would have made food items suspended in the water for a longer time.

The *S. stearnsii* individuals that showed rapid growths tended to have less well-developed shell plates. Such specimens with small shell plates have been known in the field and their taxonomic treatment has been discussed. Annandale (1905) first described such specimens as a new species *S. inermis*, but later Annandale (1916) and Nilsson-Cantell (1928) found a variation in the degree of shell development in samples from the same localities and considered them to be intraspecific variations and called them *S. stearnsii* var. *inermis*. We agree with this interpretation and have shown that the degree of shell development depends on growth rate and hence environmental conditions.

We measured the *in situ* growth rate of an individual of *S. stearnsii* over nearly a year. It is rare to directly measure growth rate in a deep-sea barnacle, a second occasion following a measurement of an individual of *Poecilasma kaempferi* (Lampitt 1990). The growth rate of *S. stearnsii* (relative daily increment of 0.0059%, or 3.4 $\mu\text{m d}^{-1}$) was within the ranges observed in the aquaria. This result means that the rearing conditions in the aquaria were adequate for their growth. It should also be noted that the field growth rate was obtained near pig and cow bones, where densities of the bacterial mat and small animals might be higher than the average conditions in the area. Thus, the *in situ* growth rate might reflect somewhat food-rich conditions for *S. stearnsii*.

Nevertheless, the growth rates of *S. stearnsii* recorded both in the aquaria and the field, and those of *G. pedunculatum*, are among the lowest values recorded in pedunculate barnacles (Table 1). From the growth rates obtained in this study, both of the studied deep-sea scalpellid species would require at least several years to attain the size of sexual maturity (40 mm in *S. stearnsii* and 30 mm in *G. pedunculatum*; Ozaki et al. 2008;

personal observations). As temperature and food availability are known to affect growth rates in pedunculates (Inatsuchi et al. 2010; Yasuda et al. 2016), it is inferred that low temperature and low food availability in the deep sea do not allow high growth rates in these species. The fact that the vent species *Leucolepas longa* apparently grows rapidly (Tunncliff and Southward 2004) supports the importance of temperature and/or food on growth rate. In addition, in evolutionary terms, survival rate is another important factor affecting growth rate. Neustonic species such as *Lepas* spp. are well known for their rapid growths due to the need to attain sexual maturity before their substrata sink (Macintyre 1966; Inatsuchi et al. 2010), although they can survive at least for

some time in the deep sea (Wada et al. 2013). Epibiotic species such as *Conchoderma* and *Octolasmis* also need to grow rapidly before their host sheds its skin or dies (Dalley and Crisp 1981; Jeffries et al. 1985). The epibiotic species *P. kaempferi* also shows a rapid growth as a deep-sea species (Lampitt 1990). In contrast, relatively stable microhabitats (rocks or shell debris for both species), together with low temperatures and low food availability, may be evolutionary forces that have allowed *S. stearnsii* and *G. pedunculatum* to be slow growing. In addition, specimens of both species were often found attached on small shells or pebbles, or even without any attachment substrata, and our *in situ* observations using ROV *Hyper-Dolphin* indicated that these species can

Table 1. Examples of growth rates of pedunculate barnacles

Name	No. of days	Initial CL (mm)	Final CL (mm)	Absolute growth rate ($\mu\text{m d}^{-1}$)	Relative growth rate (% d^{-1})	Depth (m)
Lepadomorpha						
<i>Conchoderma auritum</i>	14	1	9.0	571.4	57.1	0
<i>Conchoderma virgatum</i>	14	1	12.0	785.7	78.6	0
<i>Lepas anatifera</i>	63	1	32.0	492.1	49.2	0
<i>Lepas australis</i>	56	1	28.0	482.1	48.2	0
<i>Lepas anserifera</i>	42	3.1	16.3	313.6	10.1	0
<i>Poecilasma kaempferi</i>	228	1	15.0	61.4	6.14	1526
<i>Octolasmis cor</i>	14.5	1	4.72	256.6	25.7	<10
Heteralepadomorpha						
<i>Heteralepas canci</i>	73	2.8	5.9	42.5	1.52	229
Scalpellomorpha						
<i>Smilium spinosa</i>	1871	11.4	15.5	2.18	0.019	0
<i>Pollicipes pollicipes</i>	270	4.6	15.7	41.1	0.89	0
<i>Scalpellum stearnsii</i>	188	45.29	46.73	7.65	0.032	229
<i>Graviscalpellum pedunculatum</i>	188	41.32	42.44	5.96	0.014	229

Name	Substratum	Note	Reference
Lepadomorpha			
<i>Conchoderma auritum</i>	animals/floats	Initial size inferred from cyprid size	Dalley and Crisp 1981
<i>Conchoderma virgatum</i>	animals/floats	Initial size inferred from cyprid size	Dalley and Crisp 1981
<i>Lepas anatifera</i>	floats	Initial size inferred from cyprid size	Skerman 1958
<i>Lepas australis</i>	floats	Initial size inferred from cyprid size	Skerman 1958
<i>Lepas anserifera</i>	floats		Inatsuchi et al. 2010
<i>Poecilasma kaempferi</i>	crustaceans	Initial size inferred from cyprid size	Lampitt 1990
<i>Octolasmis cor</i>	crustaceans	Initial size inferred from cyprid size	Jeffries et al. 1985
Heteralepadomorpha			
<i>Heteralepas canci</i>	rock	High food level	Yasuda et al. 2016
Scalpellomorpha			
<i>Smilium spinosa</i>	rock	Individuals with longest records	Batham 1945
<i>Pollicipes pollicipes</i>	rock	Approximate no. of days	Cruz et al. 2010
<i>Scalpellum stearnsii</i>	rock	Rearing at Nara	This study
<i>Graviscalpellum pedunculatum</i>	rock	Rearing at Nara	This study

survive without being buried on the silt bottom. Thus, their survival rates would be fairly high. Furthermore, phylogenetic effects, especially through the constraint on shell morphology, may be responsible for the difference in growth rates among species. This was exemplified in species with thin-shelled lepadomorphans and shell-less heteralepadomorphans, which generally attained higher growth rates than thick-shelled scalpellomorphans (Table 1). However, more data are needed to test such phylogenetic effects.

CONCLUSIONS

Barnacles have ideal features for measuring time. These include ubiquity, variable growth rates among species, the epibiotic nature of many species, and records of growth in the shells (Lampitt 1990; Blomsterberg et al. 2004; Inatsuchi et al. 2010). Variable growth rates within species according to environmental conditions may be a confounding factor, but age can be estimated once environmental conditions are known. Or alternatively, once growth rates under various conditions or ages are known, such information can be used to infer environmental conditions. In addition, clear growth lines are found both in the cuticle and in the shell plates (see Blomsterberg et al. 2004 and references therein). The cuticular lines are related to the molt cycle of the individual, but how these and the shell plate lines depend on parameters such as food availability and other environmental factors is completely unknown for deep-sea barnacles. Nevertheless, these deep-sea species are of special interest because their large size and slow growth suggests that they can achieve a high age and therefore represent a long time record of environmental conditions. Further study is needed to utilize barnacles as such 'biological clocks' or 'environmental indicators' in inferring present and past ecosystems.

Acknowledgments: We thank Drs. Norio Miyamoto, Katsunori Fujikura, and Yoshihisa Fujiwara, Ms. Yu Hirokane, Dr. Noriko Yasuoka, and staff at Kagoshima University, JAMSTEC, Okinawa Churaumi Aquarium, and Numazu Aquarium for their help. Drs. Keiji Wada and Hiroaki Sato gave valuable comments on an earlier version of this manuscript. This work was an achievement of the cruise of the R/V Natsushima (NT12-07), JAMSTEC. This work was funded by JSPS Kakenhi 15H04416.

Authors' contributions: YY, TY, HKW, and AK designed the study. YY, NY, HKW, TY, KN, TH, and AK performed the field work and experiments. YY, HKW, and JTH prepared the manuscript. All authors approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: The supporting data will be provided by the corresponding author on request.

Consent for publication: Not applicable.

Ethics approval consent to participate: This study complies with current Japanese laws.

REFERENCES

- Annandale N. 1905. Malaysian barnacles in the Indian Museum, with a list of the Indian Pedunculata. Mem Asiatic Soc Bengal 1:73-84 + 1 plate.
- Annandale N. 1916. Barnacles from deep-sea telegraph cables in the Malay Archipelago. J Straits Branch Roy Asiatic Soc 74:281-302.
- Arellano SM, Van Gaest AL, Johnson SB, Vrijenhoek RC, Young CM. 2014. Larvae from deep-sea methane seeps disperse in surface waters. Proc Roy Soc Lond B: Biol Sci 281:20133276. doi:10.1098/rspb.2013.3276.
- Arellano SM, Young CM. 2009. Spawning, development, and the duration of larval life in a deep-sea cold-seep mussel. Biol Bull 216:149-162. doi:10.1086/BBLv216n2p149.
- Batham EJ. 1945. *Pollicipes spinosus* Quoy and Gaimard. I: Notes on biology and anatomy of adult barnacle. Trans Roy Soc N Z 74:359-374.
- Blomsterberg M, Glenner H, Høeg JT. 2004. Growth and molting in epizoic pedunculate barnacles genus *Octolasmis* (Crustacea: Thecostraca: Cirripedia: Thoracica). J Morph 260:154-164. doi:10.1002/jmor.10132.
- Britayev TA, Martin D, Krylova EM, von Cosel R, Aksiuk TS. 2007. Life-history traits of the symbiotic scale-worm *Branchipolynoe seepensis* and its relationships with host mussels of the genus *Bathymodiolus* from hydrothermal vents. Mar Ecol 28:36-48. doi:10.1111/j.1439-0485.2007.00152.x.
- Buhl-Mortensen L, Høeg JT. 2006. Reproduction and larval development in three scalpellid barnacles, *Scalpellum scalpellum* (Linnaeus 1767), *Ornatoscalpellum stroemii* (M. Sars 1859) and *Arcoscalpellum michelottianum* (Seguenza 1876), Crustacea: Cirripedia: Thoracica): implications for reproduction and dispersal in the deep sea. Mar Biol 149:829-844.
- Buhl-Mortensen L, Høeg JT. 2013. Reproductive strategy of two deep-sea scalpellid barnacles (Crustacea: Cirripedia: Thoracica) associated with decapods and pycnogonids and the first description of a penis in scalpellid dwarf males. Org Divers Evol 13:545-557.
- Cruz T, Castro JJ, Hawkins SJ. 2010. Recruitment, growth and

- population size structure of *Pollicipes pollicipes* in SW Portugal. *J Exp Mar Biol Ecol* **392**:200-209. doi:10.1016/j.jembe.2010.04.020.
- Dalley R, Crisp DJ. 1981. *Conchoderma*: a fowling hazard to ships underway. *Mar Biol Lett* **2**:141-152.
- Evans F. 1958. Growth and maturity of the barnacles *Lepas hillii* and *Lepas anatifera*. *Nature* **182**:1245. doi:10.1038/1821245b0.
- Fujikura K, Okoshi K, Naganuma T. 2003. Strontium as a marker for estimation of microscopic growth rates in a bivalve. *Mar Ecol Prog Ser* **257**:295-301.
- Gale AS. 2016. Phylogeny of the deep-sea cirripede family Scalpellidae (Crustacea, Thoracica) based on shell capitular plate morphology. *Zool J Linn Soc* **176**:266-304. doi:10.1111/zoj.12321.
- Gili JM, Abellò P, Villanueva R. 1993. Epibionts and intermolt duration in the crab *Bathynectes piperitus*. *Mar Ecol Prog Ser* **98**:107-113.
- Herring P. 2001. *The biology of the deep ocean*. Oxford University Press, Oxford.
- Inatsuchi A, Yamato S, Yusa Y. 2010. Effects of temperature and food availability on growth and reproduction in the neustonic pedunculate barnacle *Lepas anserifera*. *Mar Biol* **157**:899-905.
- Jeffries WB, Voris HK, Yang CM. 1985. Growth of *Octolasmis cor* (Aurivillius, 1892) on the gills of *Scylla serrata* (Forsk., 1755). *Biol Bull* **169**:291-296.
- Lampitt RS. 1990. Directly measured rapid growth of a deep-sea barnacle. *Nature* **345**:805-807.
- Macintyre RJ. 1966. Rapid growth in stalked barnacles. *Nature* **212**:637-638.
- Miyamoto N, Yamamoto T, Yusa Y, Fujiwara Y. 2013. Postembryonic development of the bone-eating worm *Osedax japonicus*. *Naturwissenschaften* **100**:285-289. doi:10.1007/s00114-013-1024-7.
- Newman WA, Ross A. 1971. Antarctic Cirripedia: monographic account based on specimens collected chiefly under the United States Antarctic Research Program, 1962-1965 (Vol. 14). American Geophysical Union, Washington DC.
- Nilsson-Cantell CA. 1928. Studies on cirripeds in the British Museum (Nat. Hist.). *Ann Mag Nat Hist* **2**:1-39.
- Ozaki Y, Yusa Y, Yamato S, Imaoka T. 2008. Reproductive ecology of the pedunculate barnacle *Scalpellum stearnsii* (Cirripedia: Lepadomorpha: Scalpellidae). *J Mar Biol Ass U K* **88**:77-83.
- Skerman TM. 1958. Rates of growth in two species of *Lepas* (Cirripedia). *N Z J Sci* **1**:402-411.
- Tunncliffe V, Southward AJ. 2004. Growth and breeding of a primitive stalked barnacle *Leucolepas longa* (Cirripedia: Scalpellomorpha: Eolepadidae: Neolepadinae) inhabiting a volcanic seamount off Papua New Guinea. *J Mar Biol Ass U K* **84**:121-132.
- Van Dover CL, Lutz RA. 2004. Experimental ecology at deep-sea hydrothermal vents: a perspective. *J Exp Mar Biol Ecol* **300**:273-307.
- Wada Y, Miura Y, Fujiwara Y, Yamamoto T, Okoshi K, Yusa Y. 2013. First finding of the neustonic barnacle *Lepas pectinata* and nudibranch *Fiona pinnata* in the deep sea. *Cah Biol Mar* **54**:437-440.
- Yasuda N, Miyamoto N, Fujiwara Y, Yamamoto T, Yusa Y. 2016. Effects of food availability on growth and reproduction of the deep-sea pedunculate barnacle *Heteralepas canci*. *Deep Sea Res I: Oceanogr Res Pap* **108**:53-57. doi:10.1016/j.dsr.2015.12.008.
- Zevina GB. 1981. Barnacles of the suborder Lepadomorpha (Cirripedia, Thoracica) of the world ocean. Part 1: Family Scalpellidae. Zoological Institute of the Academy of Science, St. Petersburg. (in Russian)