Spacing Pattern of Two Serpulid Polychaetes, *Pomatoleios kraussii* and *Hydroides elegans* Revealed by the Nearest-neighbor Distance Method

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Abstract   Spacing patterns of *Pomatoleios kraussii* and *Hydroides elegans* (Polychaeta, Serpulidae) were studied using the nearest-neighbour distance method. *Pomatoleios kraussii* tended to show a uniform distribution at low or moderate densities, but an aggregated distribution at high densities. *Hydroides elegans* usually showed a uniform distribution.   The nearest-neighbour distances between the tube openings were analyzed sequentially to determine the ontogenetic change in their spatial relationship.   The estimated positions of tube openings between the nearest-neighbours in both species were >2 mm apart throughout their growth, probably to avoid contact with the branchial crowns of other worms.   Solitary *H. elegans* appears to be a very exclusive species, since contact of branchial crowns was never observed in the field.   Artificially induced contact of the branchial crowns of two adjacent worms made both worms grow faster than usual.   Such enhanced growth enabled the two adjacent worms to avoid branchial crown contact at the expense of tube wall thickness. The branchial crowns of the aggregative *P. kraussii* also did not make contact with each other, but this was because the crowns were not fully extended.   Their tubes were frequently twisted around each other, resulting in higher densities.

Key words: tubicolous polychaete, dispersion, aggregation, Serpulidae.

Serpulid polychaetes live in calcareous tubes, and are fundamentally solitary, but commonly show aggregated distributions (ten Hove, 1979). For example, *Serpula vermicularis* and *Filogranella elatensis* form serpulid reefs (Bosence, 1979; Ben-Eliahu & Dafni, 1979), and *Pomatoleios kraussii* and *Galeolaria caespitosa* frequently construct intertidal mono-specific belts (O'Donnell, 1984; Nishi, 1993).

The serpulid polychaetes have been studied intensively for their distribution patterns and larval ecology, probably because larval settlement behaviour seems to delimit the potential range of adult distribution (Doyle, 1975; Scheltema *et al.*, 1981). Despite their importance, the resulting spacing patterns of the adult worms have not been studied previously. This paper is the first to analyze the

spacing pattern of tubicolous polychaetes in their adult stages.

Previous studies of the colony-forming processes of the serpulid *Salmacina dysteri* (Nishi & Yamasu, 1992; Nishi & Nishihira, 1992, 1993, 1994) suggested that its spacing ability is highly limited and that exclusiveness is an important factor in its colony formation. For example, if the worms are very exclusive in avoiding contact between their tubes, they can not form colonies or dense aggregations.   Furthermore, even when highly exclusive worms form a mono-specific aggregation, their tube openings will be spaced apart.

We selected two species of serpulid polychaetes for the present study, *Pomatoleios kraussii* (Baird) and *Hydroides elegans* (Haswell), because they are abundant in intertidal
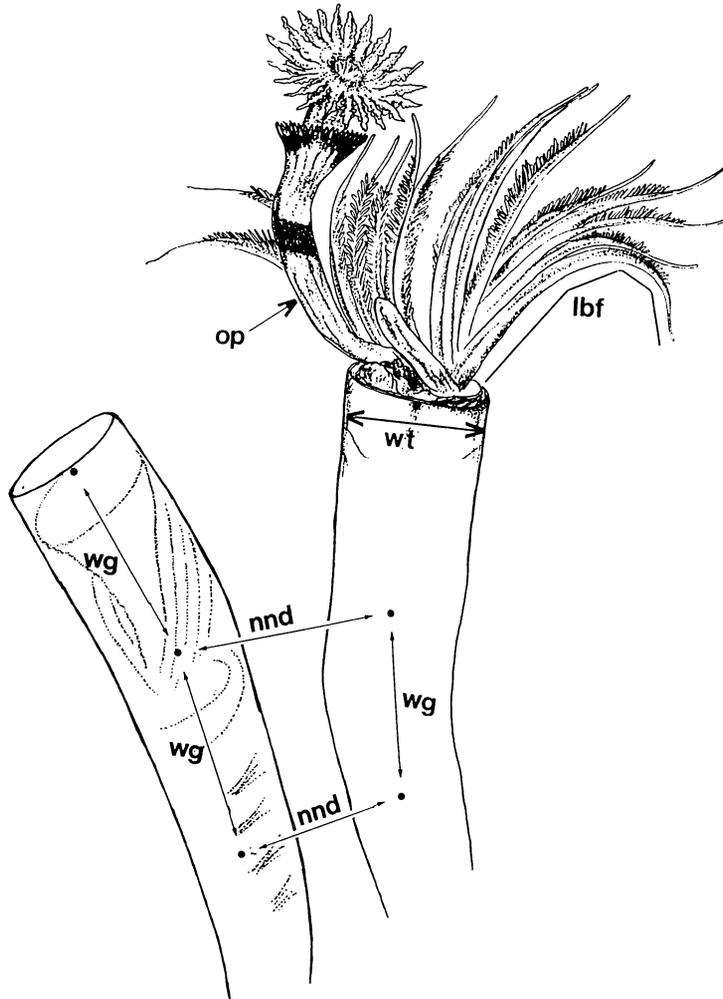
Fig. 1. Head, branchial crown, and tubes of *Hydroides elegans*; lbf and wt show the measurements used as an index of feeding territory and tube growth, respectively (lbf: length of branchial filament; op: operculum; wt: width of tube), wg and nnd represents weekly tube growth and nearest-neighbour distance.

zones and in aquaria. They are easy to handle because their calcareous tubes can withstand rough treatment, and their tube growth can easily be traced back to the time of settlement, allowing reconstion of this growth history from settlement to the current stage(s).

Materials and Methods

Collection site

Pomatoleios kraussii individuals were collected from Haneji Inlet, Motobu Peninsula, Okinawa Island, and *Hydroides elegans* from the walls of concrete aquaria at Sesoko Sta-tion, Tropical Biosphere Research Center, University of the Ryukyus, Sesoko Island, between October 1990 and October 1991. Live specimens were transferred to aquaria in the laboratory at the University of the Ryukyus, Nishihara. The lengths of the tubes and branchial crowns, and the diameters of the tube openings were measured (Fig. 1).

Analysis of spacing pattern

Pomatoleios kraussii; For analysis of the spacing pattern of *Pomatoleios* worms, the upper surface of two cement blocks (30 cm
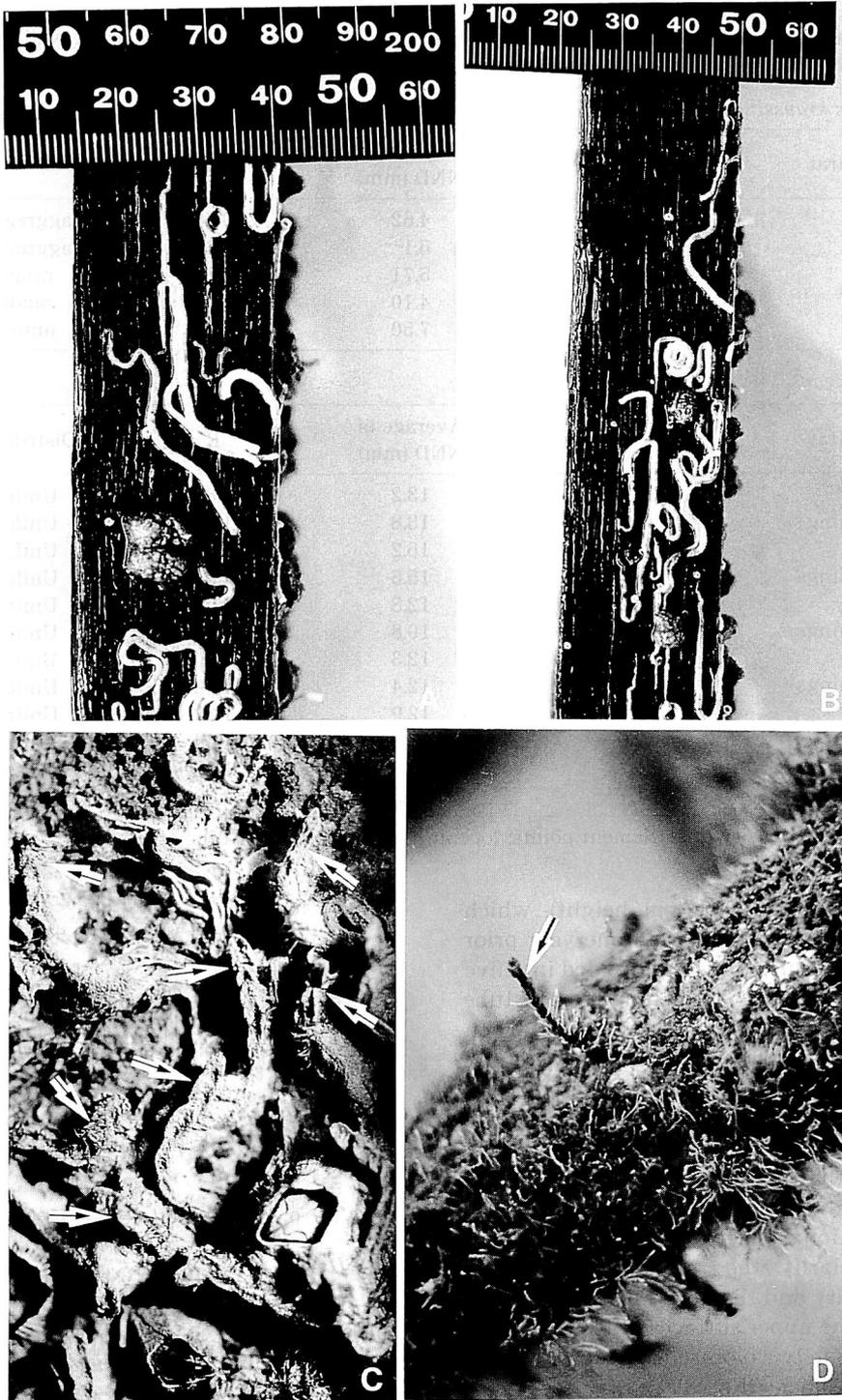
Fig. 2. Tubes of *Hydroides elegans* and *Pomatoleios kraussii*.
A & B, *Hydroides* tubes on wooden planks; C, *Pomatoleios* tube (arrow) on cement block; D, *Hydroides* (arrow) and other small serpulid tubes on a PVC tube.

Table 1. Nearest-neighbour distances of two species of serpulid polychaetes. *Pomatoleios kraussii* (n=50) was measured on concrete blocks, and *Hydroides elegans* (n=88) on aquarium wall at Sesoko Station. NND shows nearest-neighbour distance.

Pomatoleios kraussii

Quadrat	Density (N·cm^{-2})	Average of NND (mm)	R	Distribution
1	1.68	4.62	0.68	aggregated
2	1.73	5.1	0.79	aggregated
3	1.14	5.71	1.09	random
4	0.68	4.10	0.99	random
5	0.58	7.50	1.97	uniform

Hydroides elegans

Quadrat		Density (N·cm^{-2})	Average of NND (mm)	R	Distribution
1	base*	2.1	13.2	1.82	Uniform
	opening*	2.1	13.8	1.90	Uniform
2	base	1.8	15.2	2.27	Uniform
	openings	1.8	15.5	2.31	Uniform
3	base	2.2	12.8	1.73	Uniform
	openings	2.2	10.8	1.45	Uniform
4	base	2.7	12.3	1.50	Uniform
	openings	2.7	12.4	1.52	Uniform
5	base	2.6	12.9	1.33	Unifrom
	openings	2.6	15.9	1.65	Uniform
6	base	1.7	12.3	1.88	Uniform
	openings	1.7	16.3	2.50	Uniform

* "base" is the density of settlement points; "opening" is the density of tube openings.

length, 20 cm width, 10 cm height), which had been placed in the ocean one year prior to the start of this work, was divided into five 10 cm² areas, and the position of each tube opening was plotted on tracing paper. Then the nearest-neighbour distance method (Clark & Evans,1954; R<1, aggregated; R=1, random; R>1, uniform) was applied (Table 1). We were unable to analyze the spacing pattern of the tube attachment site, because of damage during collection.

Six additional 10 cm² sections were analysed to clarify the relationship between worm density and the nearest-neighbour distances on the upper surfaces of two (sparsely and aggregately colonised) randomly selected cement blocks (Fig. 3).

Hydroides elegans; On one side of an aquarium, six sections (25 cm×25 cm) were marked and photographed for analysis of the dispersal pattern of *Hydroides elegans*. The position of the attachment site and the open-
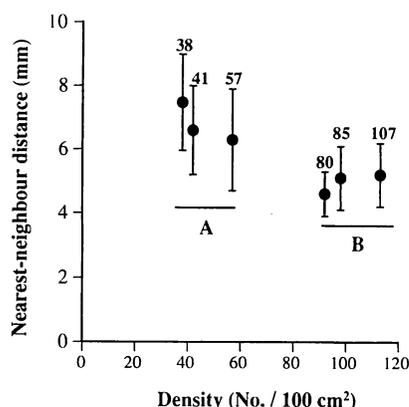
Fig. 3. Relationship between densities (A: low densities; B: high densities) and nearest-neighbour distances for *Pomatoleios kraussii*.

ing of each tube were plotted for each individual on tracing paper. Then the nearest-neighbour distance method (Clark & Evans, 1954) was applied (Table 1).

Six PVC plates (30 cm×20 cm) and four

wooden planks (10 cm × 30 cm, 10 cm height) were immersed at 1–2 m depth in an outdoor tank at Sesoko Station for two to four months to obtain adult worms of *Hydroides elegans*.

Measurement of worm size and nearest-neighbour distance

Nearest-neighbour distances were measured for the worms that colonized the surfaces. Tube length was 8–40 mm for *H. elegans,* and 4–15 mm for *P. kraussii.* Worms with a tube length of 10–25 mm (*H. elegans*) or 6–15 mm (*P. kraussii*) were selected and used in the following experiments.

Worms of both species with complete tubes were photographed (see Fig. 2), and the ontogenetic changes in the nearest-neighbour distances were analyzed. Based on the result of previous growth experiments in the field (Nishi, 1993), and estimation of the tube growth rates, the locations of tube openings at previous weekly intervals were estimated, and their positions were marked on the tubes. The distances between the corresponding tube openings were then measured.

Changes in nearest-neighbour distance for *Hydroides elegans*

The nearest-neighbour distance of *Hydroides elegans* was measured on whole tubes that were detached from the substratum using forceps and glued to a microscope slide (76 × 26 mm). Growth of the tube length and the nearest-neighbour distances between tube openings were measured for various competing worms in a rearing experiment under artificial contact of half of the branchial crowns. Rearing experiments were carried out in the laboratory using seawater at 24–28°C under ambient light conditions. The original tubes were dyed with a 5% solution of Alizarine Red S in seawater for the tube growth study. Measurements were taken every two or three days.

A pair of worms were kept on each wooden plank for about ten months from settlement, and their growth rates, tube opening diameters, and branchial crown length were measured using Vernier calipers at weekly intervals.

Measurement of tube wall growth

After two to three months of the growth experiment, tubes of *Hydroides elegans* were separated into several fragments, and the tube wall thickness was measured using SEM micrographs in order to study the relationship between growth rate and tube wall thickness.

Results

Pomatoleios kraussii

From the cement block experiment, worms of 5–35 mm in tube length (N = 50) were sampled. Larger worms have a tougher tube with a plate-like keel and become entangled with other tubes, particularly at high densities. Smaller worms (< 5 mm in tube length) lack an obvious keel, and about half of these worms were attached to larger tubes of living or dead worms.

On the cement blocks, the worms showed a random or uniform distribution (R = 0.99–1.97) at lower densities (around or below 1 worm per cm^2), and an aggregated distribution (R = 0.68 and 0.79) at higher densities (over 1.5 worms per cm^2) (Table 1).

Nearest-neighbour distances were plotted against tube densities (Fig. 3). At higher densities (B), distances were shorter (about 5 mm) than at lower densities (A) on both blocks, and there was a significant difference between distances at higher (A; average 6.52, S.D. 4.23) and lower (B; average, 4.68; S.D., 3.95) densities (size-blocked t-test, p < 0.05).

Four living pairs of worms with complete tubes were randomly selected. The nearest-
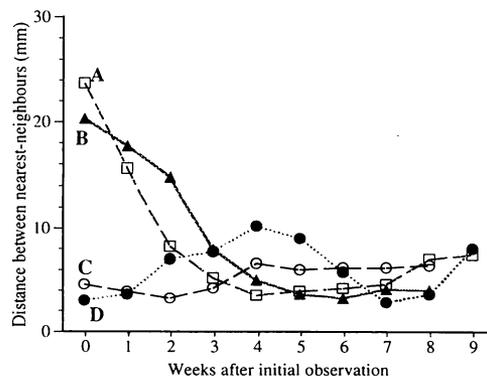
Fig. 4. Weekly change in the nearest-neighbour distances of four pairs (A, B, C, and D) of *Pomatoleios kraussii* on cement blocks.
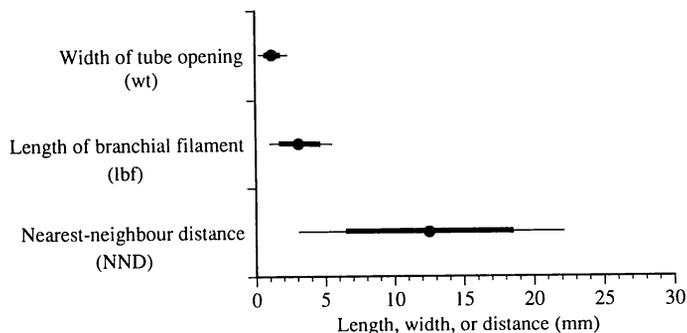
Fig. 5. Nearest-neighbour distance (NND), length of branchial filaments (LBF in Fig. 1) and tube width (TW in Fig. 1) of *Hydroides elegans* on wooden planks (N=20). ●, average, ▬, S.D., —, range.

neighbour distances between tube openings varied with time and were usually more than 2 mm (Fig. 4). When the tubes became closer than 2–3 mm, the worms rapidly changed their growth direction to maintain the distance at more than 2 mm. Some pairs (C and D) remained closer than 5 mm for 3 to 5 weeks. Branchial crowns did not touch either in nature or in the laboratory, even at high densities, because a spacing of over 2 mm allowed no contact between the crowns whose average tube opening diameter (= length of branchial filament×2, see Fig. 1) was 1.2 mm (S.D. 0.23, N=20), although the crowns were not extended fully.

Hydroides elegans

The tubes of this species are usually linear or slightly meandering, and rarely coiled in a spirorbid manner. They are frequently erect from the substratum.

In total, >400 worms on the vertical concrete walls of the aquarium and >100 worms on the wooden planks and two fouling plates were sampled. The average density on the vertical wall of the aquarium was 2.4/10 cm². This species showed a uniform distribution of settlement points and tube openings on the concrete wall (Table 1). Contact between the branchial crowns was very rare: only 3 out of over 500 cases were found.

The length of the branchial filaments (e.g., the radius of the branchial crown as shown in Fig. 1) was rarely less than the nearest-neighbour distance. Thus, the extended branchial crown was able to come into contact with the branchial filaments of other worms. However, almost all distances be-
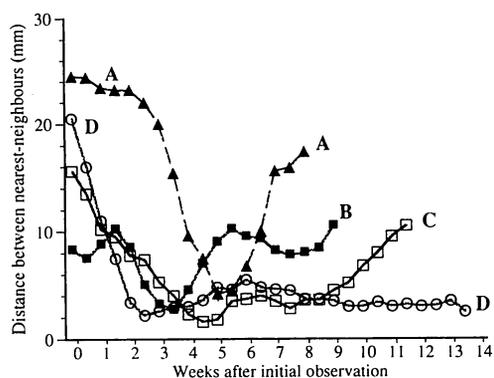
Fig. 6. Changes in nearest-neighbour distance with growth of *Hydroides elegans* on the concrete wall of the aquarium. Different symbols represent different pairs of worms.

tween tube openings (N=120) exceeded 2 mm (Fig. 5), except for two that were less than 1 mm.

Among the worms attached to wooden planks, four (designated A to D) living pairs with complete tubes were selected. When selected pairs of worms became closer than 2–3 mm, they rapidly changed their growth direction and the distance became wider (Fig. 6). Only a single pair, C, remained close at approximately 3 mm for 3 to 4 weeks. The branchial crowns of this pair did not make contact with each other because the tube openings were oriented in opposite directions. On the vertical wall of the aquarium, worms grew facing various directions, and crossing of the tubes was common. The mouth openings were always separate from each other, so that contact between branchial crowns was avoided, as seen in the laboratory (Fig. 7).
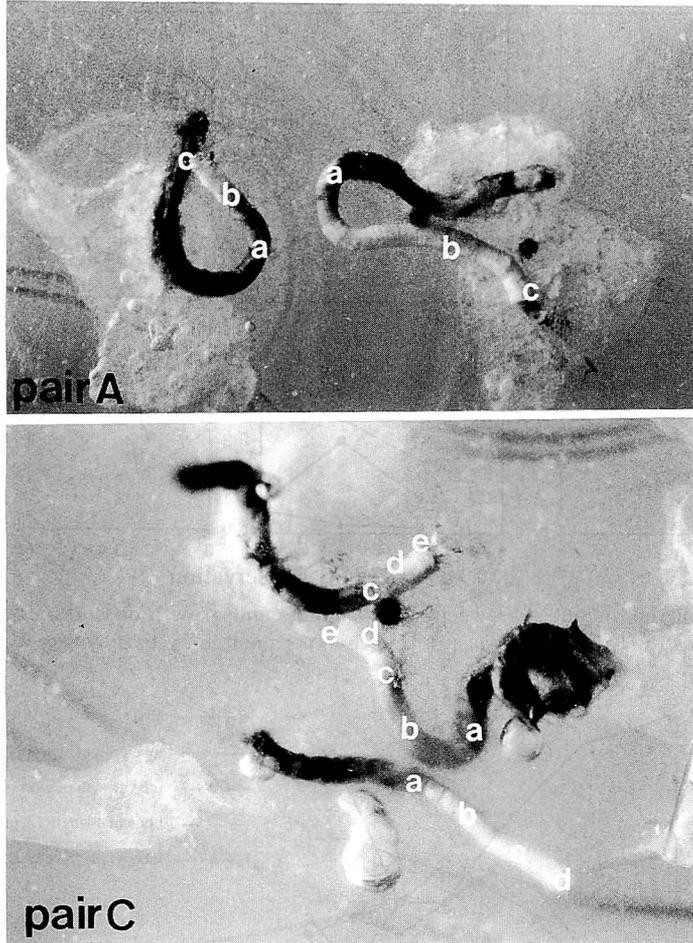
Fig. 7. Changes in growth direction and nearest-neighbour distances after artificial contact of branchial crowns in *Hydroides elegans*. Pairs A, and C of Fig. 8 are shown. Points of the tube opening marked at the same time are represented by the same letters on different individuals.

Changes in nearest-neighbour distance for Hydroides elegans

After artificially inducing contact of the branchial crowns of a pair of worms, the worms grew in different directions, often within one week, to avoid continued crown contact (Figs. 7 & 8). In pair A, both worms extended their tubes rapidly; the worm on the left changed its growth direction toward the left at a right angle to the other worm (Fig. 7, upper photo, and Fig. 8). In pair B, one worm had a linear tube and the other a coiled one; both worms grew rapidly to avoid the other, and coiling was reversed after contact. In pair C, both worms grew rapidly, so that the distance between their tube openings was widened. When a new worm was added,

the central worm changed its growth direction to avoid the newcomer (Fig. 7, lower photo). In pairs D and E, branchial crown contact was not present after two weeks. In pair F, one of the worms died leaving only the tube; the other extended its tube linearly to cross that of the dead worm (Fig. 8, F). Pair C comprised one small (tube length, 6 mm) and one large (28 mm) worm, which extended their tubes equally (Fig. 8, C). All other pairs were of about the same size (10–25 mm in tube length).

The changes in the nearest-neighbour distances were analysed for each growth stage from settlement to maturity in a fixed pair (Fig. 9). Because only one pair survived for over 2 months during the observation period
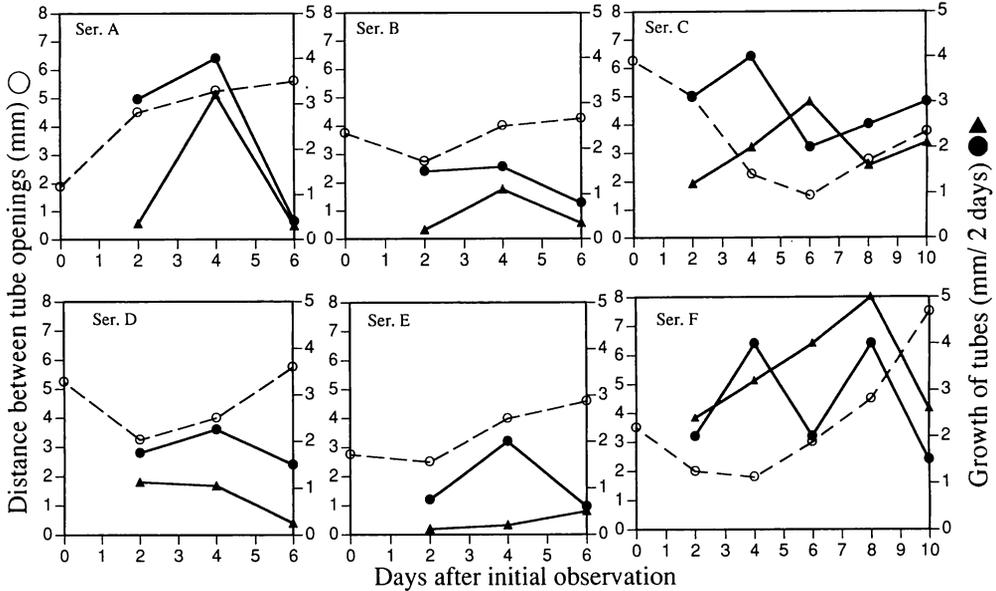
Fig. 8. Changes in the distances between tube openings and growth of tubes after artificial contact of branchial crowns in *Hydroides elegans*. For each experiment, only two worms were measured.
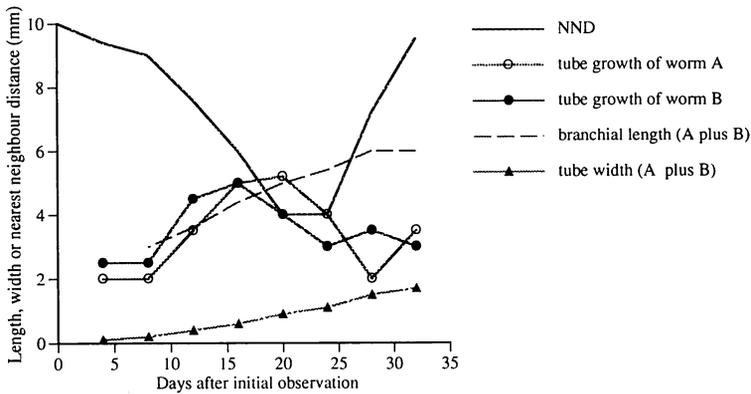
Fig. 9. Changes in the nearest neighbour distance (NND) during growth of a pair in *Hydroides elegans* from settlement to maturity on a wooden plank. Growth of tubes was measured every four days for each worm.

after settlement, we analysed this pair. The length of the branchial filament multiplied by two approximates the diameter of the extended branchial crown. A nearest-neighbour distances less than this value indicates possible contact of the branchial crowns (when both worms are nearly equal in size). However, the branchial crowns extended horizontally and usually bent downward, and as a result the branchial crowns made contact very rarely. Therefore, about 80–90% of the diameter (length of branchial filaments×2) seems to represent the actual

range of possible contact.

Tube wall growth

Rapidly growing worms had thinner tube walls than slower growing ones (Fig. 10). There was a significant negative correlation between tube wall thickness and growth rate ($r=0.57$, $p<0.05$), suggesting proportionate deposition of calcium carbonate.

Discussion

Serpulid polychaetes are suspension feeders (Fauchald & Jumars, 1979). The mini-
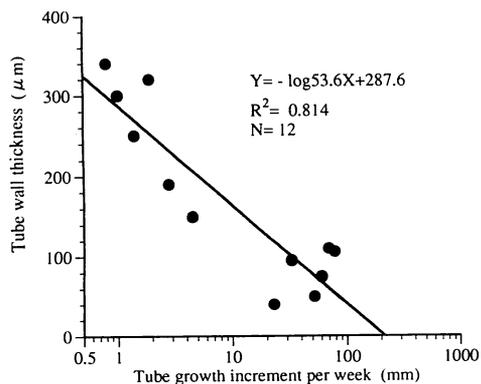
Fig. 10. Relationship between tube wall thickness and tube growth rate for *Hydroides elegans*.

mum space they require for feeding probably does not exceed the range covered by their branchial crowns. The space for feeding, therefore, is approximated by a circle, whose diameter is equal to the length of the branchial crown multiplied by 2. *Hydroides elegans* thus requires a feeding territory of about 2 mm in diameter to extend its branchial crown. Such feeding territories have been found in other suspension feeders: *Phoronopsis viridis* which shows a uniform distribution related to the extension of its branchial crown (Johnson, 1959); *Polydora* sp. and a tubicolous amphipod determine their territories by fighting using palps or appendages, respectively (Levin, 1981; Connell, 1963). The ranges of their territories might change with density (Crisp, 1961; Roe, 1975), but those of some spionid polychaetes are not affected by their own density (Levin, 1981). *Pomatoleios kraussii* and *Hydroides elegans* have a fixed feeding range represented by the circle formed by their branchial crown, and their distribution pattern is apparently related to the density. *P. kraussii* had a tendency to show an aggregated distribution under crowded conditions, and a uniform distribution at low densities (Table 1). In contrast, *Hydroides elegans* tended to show a uniform distribution irrespective of density. This difference is probably caused by the ability of the worm to change its direction of growth. *P. kraussii* appears to lack this flexibility of tube growth pattern.

Nearest-neighbour distances of *Pomatoleios*

kraussii tended to be smaller under crowded conditions, as reported for other spirorbids (Wisely, 1960; Knight-Jones & Moyse, 1961). Worm size also seems to affect the nearest-neighbour distance. Smalley (1984) showed that, in vermetid gastropods, colonies or aggregations comprise larger individuals at low densities, whereas only small worms are seen under crowded conditions. In the present study, however, no definite relationship between worm size and density was observed.

In studies of the spacing patterns of tube dwellers, the ontogenetic change in the nearest-neighbour distance is very useful for tracing the positions of previous tube openings. The comparison of nearest-neighbour distances between settlement sites and tube openings at a given time is a very simple and clear-cut method. The comparisons between the two distances seem to be suitable for tentative analysis of intra-specific interactions.

Solitary animals with a calcareous exoskeleton or tunic are not affected by fouling unless their feeding apertures are blocked (Jackson, 1977). Therefore, smaller tube worms and vermetid gastropods overgrown by encrusting animals are able to survive by changing their growth pattern from a sessile to an erect form (Hadfield *et al.*, 1972; Stebbing, 1973; Wilson, 1968; Jackson, 1977). *Pomatoleios* and *Hydroides* changed their growth direction in a competitive environment, but they did not change to an erect form in the present experiment. However, in aquaria at Sesoko Station, where small serpulid polychaetes were abundant (*Salmacina dysteri, Rhodopsis pusilla,* and *Josephella maenzelleri*; Nishi, 1993), substratum colonized by *Hydroides* was frequently covered by these small serpulids and the tubes of *Hydroides* exhibited an erect growth form (Fig. 2D; note also that the tube of *Hydroides* is covered by small serpulid polychaetes).

An alternative interpretation is that a decrease in the thickness of the calcareous tube is an effective way of quickly extending tube length to escape interaction among branchial crowns. *Hydroides elegans* employed this strategy. The tube wall thickness was negatively correlated with its growth rate, the worm growing faster at the expense of tube

wall thickness. A similar pattern of tube growth rate to tube wall thickness has also been demonstrated in the serpulids, *Josephella marenzelleri* (Nishi, 1992), *Rhodopsis pusilla* and *Salmacina dysteri* (Nishi, manuscript in preparation).

Acknowledgement

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管棲多毛類ヤッコカンザシとカサネカンザシの近接個体間距離と分散パターン

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管棲多毛類の2種, ヤッコカンザシとカサネカンザシ (カンザシゴカイ科) の分散パターンを近接個体間距離法を用いて解析した. ヤッコカンザシは密度が低い場合は一様分布をする傾向があるが, 高密度では集中分布をする傾向があった. カサネカンザシは一様分布をする傾向にあった. 近接個体間の口間距離を棲管の成長に伴いどのように変化するかを調べた. まず, 現在の棲管の口を基とし, そこから1週間ごとの成長量を引いたところをマークし, 近接個体間距離の変化を時間をおって推定した. 両種ともに口間距離は常に2mm以上であり, これはお互いのえらの接触を避けた結果だと考えられる. カサネカンザシにおいてはえらの接触は野外で観察されなかった. カサネカンザシにおいて, 実験下でえらの接触をおこさせると, 2個体ともに急激に棲管を伸長し, えらの接触を避けることが確かめられた. 急激に成長する際の棲管の壁は, 棲管の伸長が遅いときに比べて薄かった. ヤッコカンザシも野外でのえらの接触は見られなかったが, 彼らはえらを最大限にひろげることはなかった. また棲管は様々な角度に伸長し, 高密度時でもお互いのえらが接触することを避けていると考えられる.