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TRENDS IN HYDROZOAN BIOLOGY - IV. *C.E. MILLS, F. BOERO, A. MIGOTTO and J.M. GILI (eds.)*

Life in tidepools: distribution and abundance of two crawling hydromedusae, *Staurocladia oahuensis* and *S. bilateralis*, on a rocky intertidal shore in Kominato, central Japan*

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SUMMARY: Two crawling medusae, *Staurocladia oahuensis* (Edmondson, 1930) and *S. bilateralis* (Edmondson, 1930) were found to be abundant in intertidal rock pools in Kominato from late summer until early winter. The two species were found to rarely share the same individual alga, and sometimes showed exclusive occupancy of pools at higher intertidal levels. The abundance of the two species of medusae fluctuated widely over time with both species showing similar population structures during their period of occurrence. The asexual reproduction of the medusae was considered to be a cause of the distributional pattern and the fluctuation in abundance. An experiment was conducted to evaluate the rate of asexual reproduction under different conditions. At 12°C neither species performed asexual reproduction, while at 17°C and higher temperatures both species reproduced asexually at a high rate. The number of each population was found to nearly double in about a week. The coexistence of the two species of medusae in tidepools is discussed in relation to the habitat characteristics. *S. oahuensis* and *S. bilateralis* were not known previously from Japan; this constitutes a new record of both species from Japanese waters. We also found both species in several other warm water locations in Japan.

Key words: crawling medusae, new record, asexual reproduction, tidepools, distribution and abundance, coexistence.

INTRODUCTION

Crawling medusae are small benthic medusae that live on algae and seagrasses. Most of them are known to reproduce asexually either by budding or fission including schizogony (Bouillon, 1978); all are hydrozoans. They are primarily non-swimmers and move by crawling or creeping on the substrate by means of walking tentacles, although swimming behavior has also been observed in a few species (Browne, 1910; Brinckmann, 1964). Because of this they are confined to coastal waters, and are sometimes common along shorelines (Gilchrist, 1919; Edmondson, 1930; Millard, 1975). However, with an exception of the European species, *Eleutheria dichotoma* Quatrefages, 1842, they have been rather neglected animals, and little is known about their life in natural habitats.

We found that two species of crawling medusae were common in Kominato and they often occurred in abundance in intertidal rock pools from late summer to early winter. The two species were identified as *Staurocladia oahuensis* (Edmondson, 1930) and *S. bilateralis* (Edmond-

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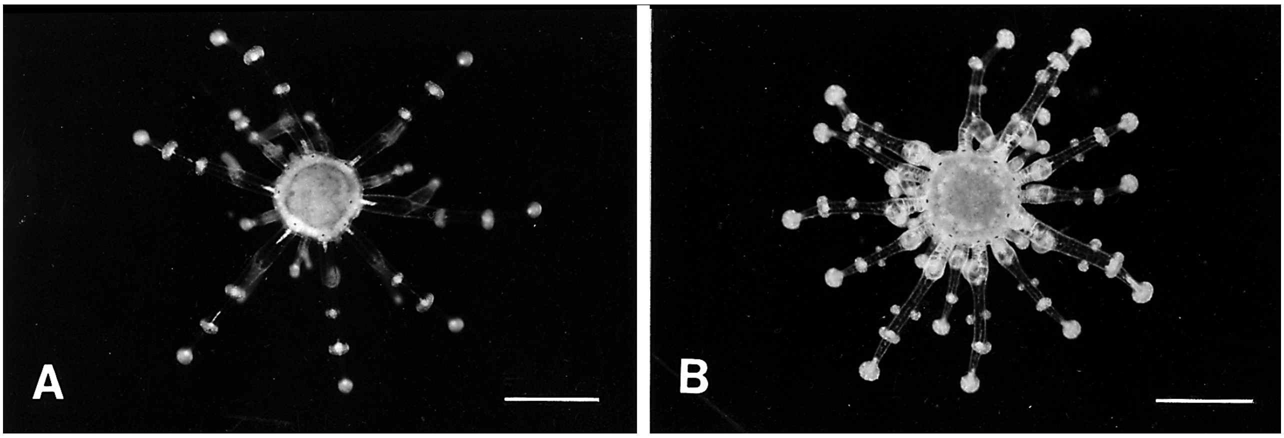

FIG. 1. – A: *Staurocladia oahuensis*. B: *Staurocladia bilateralis*. Scale bars, 0.5 mm.

son, 1930), based on extensive morphological comparisons. This is the first record of both species from Japanese waters. There has been only one other published report on each species since they were described from Hawaii in 1930. *S. oahuensis* is also known from Chile (Kramp, 1952) and *S. bilateralis* is also reported from the Seychelles (Bouillon, 1978). These species are thus still poorly known.

The abundance of the two medusae allowed us to redescribe both species based on many specimens, and to investigate some aspects of their biology. As they were often abundant in tidepools, we focused on their life history in relation to the habitat. Tidepools are considered to be unique habitats in marine environments, and a number of ecological studies have been made on the community structure and organization of their inhabitants (see Metaxas and Scheibling, 1993, for references). Crawling medusae are distinctive, with supposedly high population growth rates by asexual reproduction and limited dispersal ability. It is of special interest to see how such organisms are distributed in tidepools and how their abundance fluctuates over time. In this study we describe patterns of distribution and abundance of the two crawling medusae in the habitat, and discuss it in light of their biology.

MATERIALS AND METHODS

Identification of the species of *Staurocladia*

The characters described and illustrated by Edmondson (1930) were used to differentiate *Staurocladia oahuensis* and *S. bilateralis*. In *S. oahuensis*, the upper or dorsal branch of each tentacle is provided with two aboral clusters of nematocysts in addition to the capitate terminal cluster (Fig. 1A), whereas *S. bilateralis* bears one aboral and two lateral clusters besides the terminal cluster (Fig. 1B). The bell diameter and number of radial canals, which seem to be helpful for identification of some other species of *Staurocladia* (Kramp, 1961; Bouillon, 1978), cannot discriminate these two species, because they are similar in size (about 0.5 mm in bell diameter on average), and the number of radial canals varies from about five to more than 15 among individuals in both species. The number of tentacles is also a variable character for both species. Some specimens are provided with only about five fully-grown and five newly-developing tentacles whereas others have more than 20 fully-grown and several young tentacles. The bell of both species is provided with a number of red eye-spots along the margin on its aboral surface and has a marginal nematocyst ring on its oral side. The velum is very thin and broad, reaching the manubrium.

Study site

Samples for the field investigations and the experiment of this study were made on a rocky intertidal shore in Kominato, Boso Peninsula (35°07'N, 140°11'E). It is in a small bay (about 1.5 km wide and 1.5 km deep) at about 0.5 km from the entrance. The bay opens directly to the Pacific Ocean, facing south with most of the coast quite exposed to ocean surges. The tidal amplitude in Kominato is about 150 cm (mean high water spring tide, mean tide level and mean low water spring tide are respectively 153 cm, 94 cm and 0 cm above sea level), and the surface seawater temperature ranges annually from about 10°C to 25°C.

Field investigations

In order to see how abundance of the two medusae fluctuated over time, density of the medusae on *Sargassum thunbergii* (Mertens) and *Ulva conglobata* Kjellman, which are among the most common algae in the intertidal zone in Kominato, was investigated from the end of August, 1995, until late February, 1996, at about one-month intervals. The two algae were haphazardly collected from three adjacent tidepools (T-2, T-3 and T-4 in Table 1) and separately put in 500 ml plastic containers. Formalin was added to the two containers (to a concentration of about 5%) to fix the medusae. Each container was emptied into a plastic bowl where the collected algae were shaken vigorously to detach crawling medusae; the algae were then removed to measure wet weight. Crawling medusae were sorted out from the residue, identified under a Nikon stereomicroscope (model SMZ-U), and the number of specimens was counted for each *Staurocladia* species. Bell diameter of the specimens was measured with an ocular micrometer calibrated to 0.033 mm to see how population structure of the two medusan populations changed during their seasonal occurrence. As some medusae were oblong in bell shape, length of the bell was measured at two perpendicular axes, and the mean of the two values was regarded as a representative diameter.

The distribution between tidepools of the two species was investigated twice, on November 3 to 4, and November 30 to December 1, 1998. Small pieces of algae were picked up haphazardly from eight tidepools (T-1 to T-8 in Table 1), and a "Lower" site, which consisted of six shallow pools at the lower mid intertidal fringe. The tidepools T-1 to T-8 are scattered almost along a line in the order with a distance of about one to several meters between one another. The height of the pools above sea level is shown in Table 1. Most of the algae taken for both investigations were *Sargassum* spp. (87.5% and 80.0% of the first and second investigation respectively), as they were the most common algae in the study area, but a number of *Ulva conglobata* (11.7% and 16.3%) and a few other algae (0.8% and 3.7%) were also examined where found. The weights of algal pieces were 2-34 g for *Sargassum* spp., 1-6 g for *Ulva* and 4-7 g for other species. Each algal piece was put in a separate plastic bag and brought back to the laboratory, where each was carefully searched for living crawling medusae. Medusae collected from the pieces were identified under the stereomicroscope, and the number of each species was counted.

Culture experiment

Medusae of moderate to large size were collected on November 5 and 6, 1998, kept at 15°C without food for a day or two, and were then separated into groups of ten specimens which were put in the same plastic container (6 cm in diameter and 3 cm in depth) to be reared together during a nine-day experiment. Sixteen and 12 groups were obtained for *Staurocladia oahuensis* and *S. bilateralis* respectively. Eight groups of *S. oahuensis* and four of *S. bilateralis* were given no food throughout the experiment, while the other eight sets of both species were fed newly hatched *Artemia* sp. nauplii in saturation every other day. The starved groups and those given food were both evenly divided into four subgroups, each of which were cultured at four different temperatures, 27°C, 22°C, 17°C and 12°C. Thus eight experimental groups, shown in Table 2, were set up for each species

TABLE 1. – The number of *Staurocladia oahuensis* and *S. bilateralis* collected from different tidepools on November 3 to 4, 1998 (1) and on November 30 to December 1, 1998 (2). "The number of algal pieces found with medusae / the number of pieces examined" at each pool is also shown as "inhabited". Height is in cm above sea level (mean low water at spring tide).

Pool	Height (cm)	1			2		
		inhabited	*S. oahuensis*	*S. bilateralis*	inhabited	*S. oahuensis*	*S. bilateralis*
T-1	95	4/10	86	0	3/20	1	2
T-2	118	3/20	5	0	0/20	0	0
T-3	117	15/20	0	35	15/20	0	61
T-4	99	2/10	0	2	2/10	6	1
T-5	79	5/10	3	12	7/10	41	6
T-6	80	5/15	6	10	12/20	33	17
T-7	114	0/5	0	0	0/5	0	0
T-8	120	0/10	0	0	1/10	2	0
"lower"	ca. 60	6/20	3	8	11/20	88	26
Total		40/120	103	67	51/135	171	108

TABLE 2. – The bell diameter in mm (mean±SD) of *Staurocladia oahuensis* and *S. bilateralis* before and after experiment under different conditions. The numeral of the group shows the temperature (°C) at which the experimental group was cultured, with "s" or "f" standing for "starved" or "fed" respectively. The difference of the size before and after the experiment is given as positive (+) or negative (-) growth. All differences shown were found to be significant (P<0.05 for all) based on the t-test (t-test with Welch's correction was applied for 22f of *S. oahuensis*, and for 27f, 22f, 17f of *S. bilateralis*).

Species	Group	Before	After	Growth
S. oahuensis	27s	0.559±0.062 (20)	0.321±0.059 (27)	-
	27f	0.570±0.063 (20)	no data	
	22s	0.587±0.067 (20)	0.349±0.048 (35)	-
	22f	0.563±0.044 (20)	0.402±0.128 (48)	-
	17s	0.587±0.047 (20)	0.426±0.058 (31)	-
	17f	0.582±0.071 (20)	0.451±0.091 (40)	-
	12s	0.573±0.051 (20)	0.499±0.069 (20)	-
	12f	0.589±0.057 (20)	0.473±0.152 (14)	-
S. bilateralis	27s	0.531±0.048 (10)	0.291±0.041 (14)	-
	27f	0.538±0.052 (20)	0.451±0.098 (13)	-
	22s	0.538±0.070 (10)	0.347±0.065 (9)	-
	22f	0.549±0.053 (20)	0.606±0.153 (37)	+
	17s	0.535±0.065 (10)	0.306±0.065 (9)	-
	17f	0.560±0.068 (20)	0.631±0.131 (39)	+
	12s	0.528±0.067 (10)	0.434±0.032 (10)	-
	12f	0.563±0.060 (20)	0.489±0.094 (20)	-

by nutritional condition and temperature. During the experiment the number of individuals in each vessel was counted every day. After counting the number, individual medusae were transferred by a pipette to a new vessel with fresh filtered seawater of adjusted temperature. Bell diameters of all specimens in each experimental group were measured at the beginning and end of the experiment. The same method as described above for the investigation of the size distribution of field populations was applied for the bell diameter measurements.

RESULTS

Temporal fluctuation of abundance

Abundance of the two species fluctuated considerably during the six months of the field study (Fig. 2). *Stauroclaclia bilateralis* was very abundant in late August, 1995, when nearly 500 medusae were collected from about 40g of *Ulva conglobata*, and 150 medusae from about 100 g of *Sargassum thunbergii*. In early October, however, this rich population was virtually gone and no specimens of *S. bilateralis* were collected. In November the population showed some recovery, and it grew further from then into December. On the other hand, *S. oahuensis* was similarly rare in August and October. It became

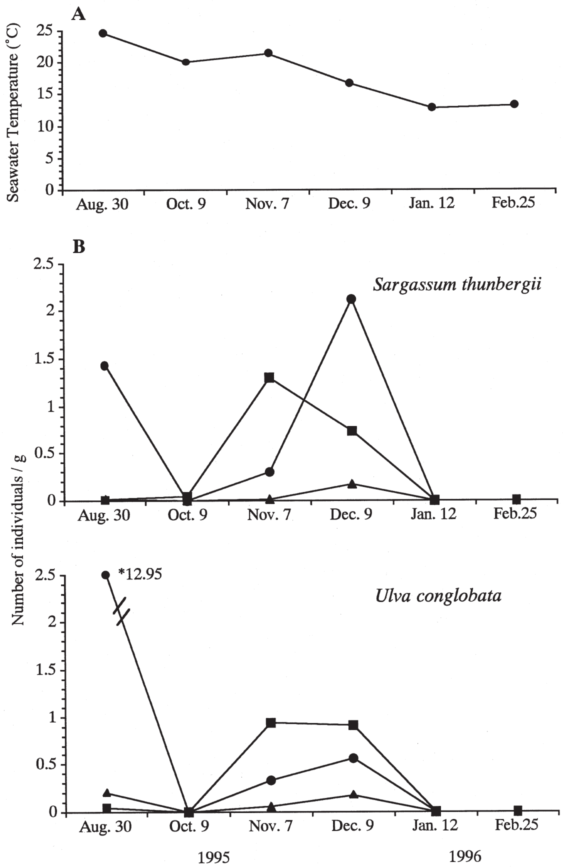

FIG. 2. – A: Seawater temperature in Kominato during the investigation. B: The density of *Staurocladia oahuensis* (n), *S. bilateralis* (l) and unidentified medusae (s) on *Sargassum thunbergii* (upper) and *Ulva conglobata* (lower).

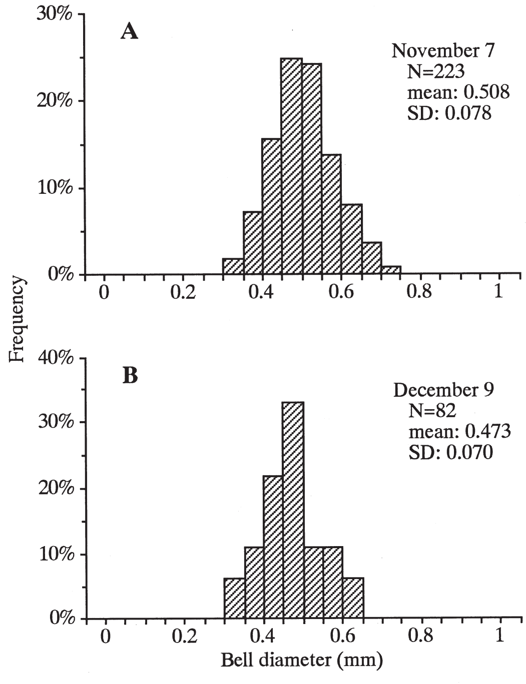

FIG. 3. – Size distribution of *Staurocladia oahuensis* on November 7, 1995 (A) and on December 9, 1995 (B).

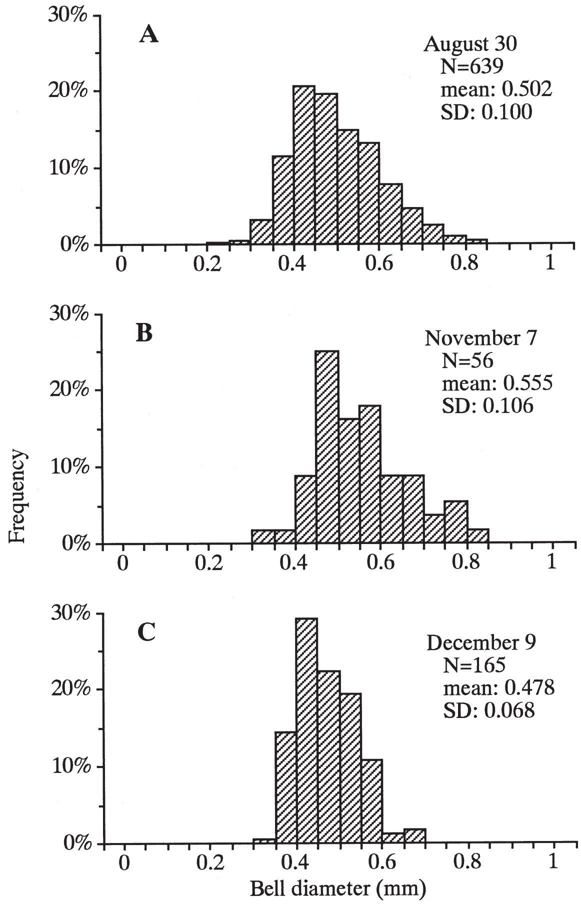

FIG. 4. – Size distribution of *Staurocladia bilateralis* on August 30, 1995 (A), on November 7, 1995 (B) and on December 9, 1995 (C).

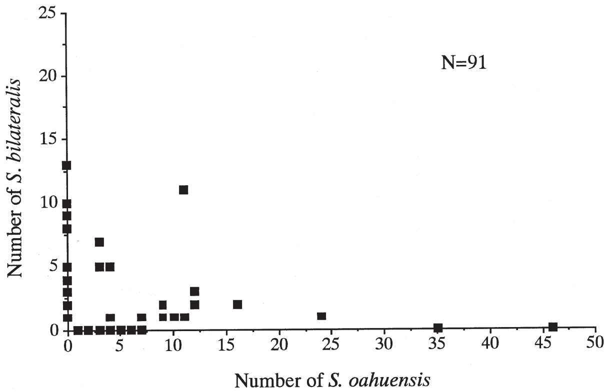

FIG. 5. – Relative abundance of *Staurocladia bilateralis* (vertical) to *S. oahuensis* (horizontal) on each algal piece.

quite abundant by early November, and was still common in early December. However, by mid-January both species had totally disappeared and the populations had not started to recover yet by late February.

Population structure

Size distribution of the tidepool populations was similarily unimodal for both species with the mode at 0.4 to 0.6 mm in bell diameter, and did not change much during the investigation (Figs. 3 and 4). The mean ± SD of the bell diameter of *S. oahuensis* in August and October was 0.507±0.206 mm, and 0.501±0.037 mm, respectively. A slight difference was found in the average size of the *S. oahuensis* population between November and December (t-test, P<0.001). The bell diameter of *S. bilateralis* was larger in November than in August (t-test, P<0.001), and then slightly decreased from November to December (t-test with Welch's correction, P<0.001).

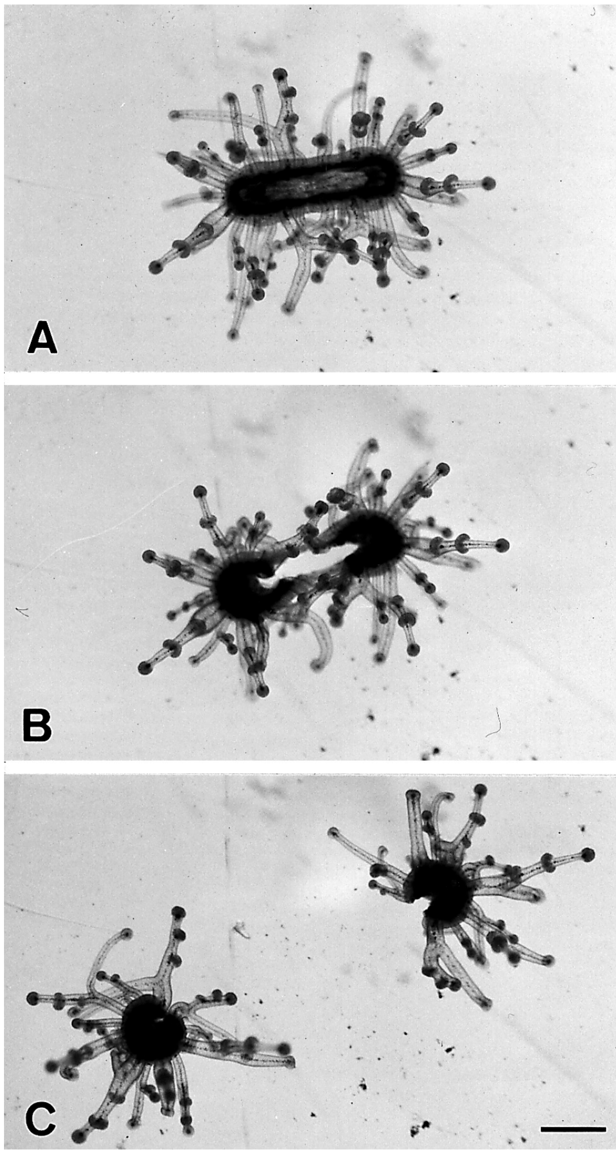

FIG. 6. – Three stages (A, B, C in series of time) of asexual reproduction, illustrated by *Staurocladia oahuensis*. Scale bar, 0.5 mm.

Distribution of two medusae among tidepools and algae

Six out of the eight upper tidepools were found to be harboring crawling medusae on both occasions, as were the “Lower” pools (Table 1). The two species were found together in lower pools such as T-5, T-6 and those grouped together as “Lower”, while higher pools were often found to be occupied by a single species alone.

More than half of the investigated algal pieces were found to be devoid of medusae (Table 1), and the majority of the algae inhabited by medusae was occupied by only a single species (Fig. 5) in both investigations. The number of the algal pieces with two species in a mixture was only 2 and 13 in the first and second investigations, respectively. No correlation was detected between the abundances of the two species of medusae ($r=-0.103$, $P=0.329$)

Asexual reproduction

Both medusae reproduced asexually by fission. A medusa elongated and the bell became very thin, especially in the central part (Fig. 6A). In the course of this bell elongation, a hole appeared at the center, and it gradually enlarged leaving only narrow marginal parts to be barely connected (Fig. 6B). Finally the medusa pulled completely apart, dividing into two daughter medusae each with an indentation on one side (Fig. 6C). The indentation was filled in and the bell became rounded within one day.

Rate of asexual reproduction

The rate of asexual reproduction was affected by temperature and also by the nutritional state of medusae. Both species were able to perform asexual reproduction at 17°C and higher temperatures, but not at all at 12°C (Fig. 7). Reproduction rate, however, did not show a clear temperature-dependent increase at temperatures higher than 17°C in either species. When starved, medusae reproduced only for a few days in most cases, and reproduction virtually ceased thereafter in both species (Fig. 7, A and C). A decrease in numbers by death of some specimens occurred on several occasions, although death was a rather rare event during the nine days of starvation for both species.

On the other hand, when fed, all specimens of *S. oahuensis* and half of *S. bilateralis* died at 27°C (Fig. 7, B and D) within three days. *S. bilateralis*,

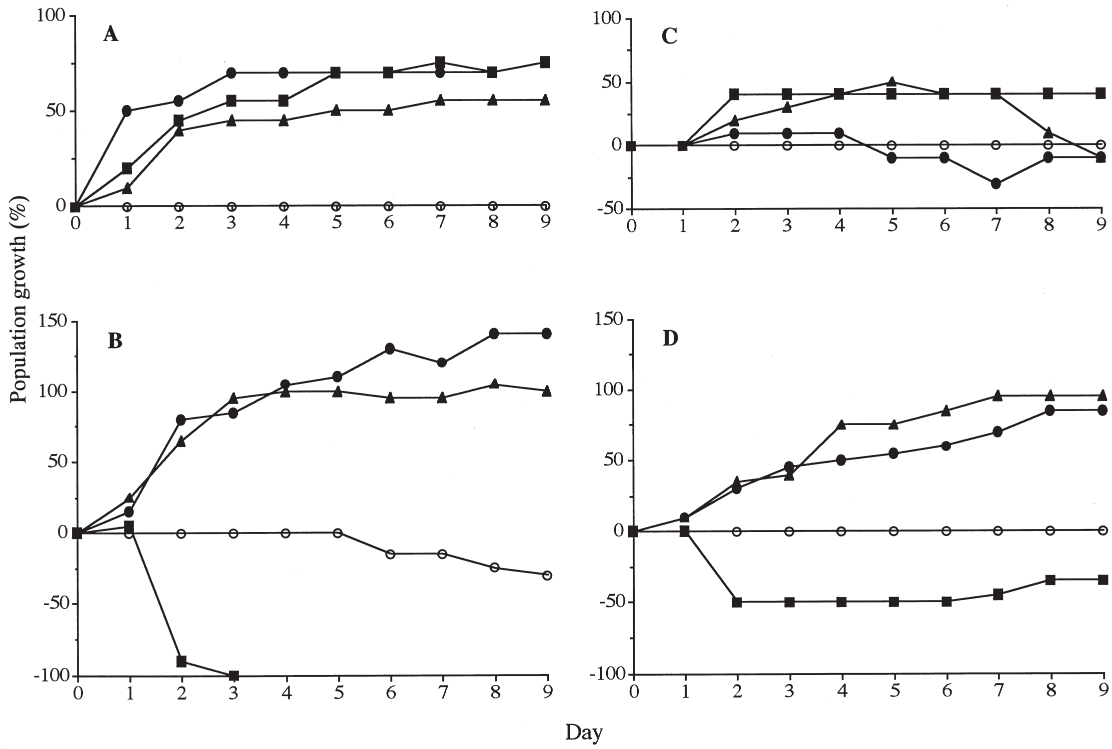

FIG. 7. – The rate of population growth under different experimental conditions. A: *Staurocladia oahuensis* under starvation. B: *S. oahuensis* given food. C: *S. bilateralis* under starvation. D: *S. bilateralis* given food. The experiment was done at four different temperatures, 27°C (n), 22°C (s), 17°C (l) and 12°C (m) for each group.

however, did not decrease further in number, and the survivors showed some population growth afterward at the same temperature. At the lower temperatures *S. bilateralis* given food did not die at all, whereas some of *S. oahuensis* died at lower temperatures as well. Both species continuously reproduced asexually when given food at 22°C and 17°C, where in nine days the experimental populations grew on average by 90% in *S. bilateralis* and by 120% in *S. oahuensis*.

At the beginning of the experiment, the size distribution of individuals was not different among all experimental groups both in *S. oahuensis* (ANOVA, P=0.584) and *S. bilateralis* (ANOVA, P=0.647). After nine days both species showed significant size decrease at all temperatures when starved (Table 2). Even when given food every other day, *S. oahuensis* medusae significantly decreased in size at all temperatures, and *S. bilateralis* decreased in size at 27°C and 12°C. At 22°C and 17°C, however, *S. bilateralis* grew significantly during the nine days of experiment. The bell diameter of medusae did not differ between starved and fed groups in *S. oahuensis* at any temperature, while it was significantly larger in groups given food than in starved medusae in *S. bilateralis* at all temperatures (t-test with Welch's correction for all, P<0.001 for 27°C to 17°C and P<0.05 for 12°C).

DISCUSSION

Being the smallest members of the genus, *Staurocladia oahuensis* and *S. bilateralis* would be easily overlooked in the field, and might be mistaken for a juvenile form of some larger species even when found. We discovered some *S. bilateralis* specimens in a collection of *S. vallentini* deposited in the Showa Memorial Institute, National Science Museum, Tsukuba. The *S. bilateralis* specimens were collected in Misaki, Sagami Bay, in 1936. We visited the place on July 9, 1998, and confirmed the occurrence of *S. bilateralis*, and there we also found *S. oahuensis*. A medusa assignable to *S. oahuensis* has been found in a filtration tank in a fish farm in Hota, Tokyo Bay (Oikawa, 1995), and we have collected *S. bilateralis* at Yobuko, Kyushu, too. *S. oahuensis* and *S. bilateralis* seem to be widely distributed in warm waters in Japan.

We have also looked for polyps of *S. oahuensis* and *S. bilateralis* in the field, but with no success. Polyps of the genus *Staurocladia*, where known, have oral capitate tentacles and some filiform tentacles in the middle, are up to a few millimeters in height, and form stolonal colonies (Gilchrist, 1919; Lengerich, 1923; Prévot, 1959; Kakinuma, 1963; Brinckmann, 1964; Hirohito, 1988; Schuchert, 1996). It should be very difficult to find them in the field. We have also not been successful in obtaining planulae of the two species to raise them to polyps in the laboratory. Thus polyps of the two species are still unknown. B. Schierwater similarly did not locate any polyps of *Eleutheria dichotoma* during field collections of that species of crawling medusa in the Mediterranean Sea (personal communication, Bodega Bay, CA, 1998).

Staurocladia oahuensis and *S. bilateralis* in Kominato were observed to reproduce asexually by fission as described by Edmondson (1930) for Hawaiian specimens. In Hawaiian specimens, however, division into two daughter medusae was initiated by a constriction on the central part of the mother medusa (Edmondson, 1930). There may be slight differences in the details of asexual reproduction between localities, but Edmondson (1930) seems to have inappropriately used the word "budding" for the mode of asexual reproduction. This is probably why budding has been known as the mode of asexual reproduction for *S. bilateralis* (Bouillon, 1978).

A high rate of population growth by asexual reproduction in both species was demonstrated by the experiment; the rate is comparable to that of *Eleutheria dichotoma* by budding (Schierwater and Hauenschild, 1990). Low temperature proved to be a critical inhibitory factor for asexual reproduction for both species of *Staurocladia* (Fig. 7), and probably plays an important role in the mid-winter disappearance of the two species (Fig. 1). The lowest tides in Kominato occur at night during winter so that medusae living in tidepools may often be subjected to lower air temperatures than the ambient sea water low temperatures of 12°C.

Low temperature not only inhibits asexual reproduction but also seems to have a bad effect on the medusae themselves. At 12°C several medusae of *S. oahuensis* died during the last few days of the experiment (Fig. 7). *S. bilateralis* specimens decreased in size even when fed at 12°C, despite no dividing event, whereas at 17°C and 22°C specimens grew while performing fission (Table 2). Harada (1954) reported that medusae of *Staurocladia acuminata* (Edmondson, 1930) became inactive with tentacles shrinking at about 10°C. Such low temperatures may produce great stress in species also capable of living in the tropical waters in Hawaii. The decrease of bell size in the field population in December (Figs. 3 and 4) may also be attributable to the effect of low temperature on these crawling medusae.

High temperature may also provide great stress for both species, as suggested by the mass mortality of both medusae at 27°C when they were fed. The seawater temperature in Kominato often reaches this value in shallow water from summer to early autumn, when temperatures can attain even higher values in tidepools that are well separated from the sea for long daytime periods under high radiation. Crawling medusae living in such pools may often experience temperatures higher than 27°C. In fact we have found many medusae in tidepool water as warm as 35°C. This implies that both species of medusae can tolerate temperatures higher than 27°C; death in the experiment may have been caused by deterioration of the culture water in the small containers under an oversupply of food.

As mentioned above, the mid-winter disappearance of the two medusae seems to be a seasonal event, although the brief disappearance in early October, 1995, cannot be similarly explained. It is impossible to specify its cause by this study, but one possibility is a big typhoon (940 hPa) that hit Kominato on September 17 of that year. The coast of Kominato is very susceptible to high waves generated by typhoons. Typhoons are often accompanied by heavy rain, as the September 1995 typhoon was. Wave action and precipitation are among the main disturbances for shoreline animals, and they may cause large temporary damage to populations of crawling medusae in Kominato.

Tidepools are subjected to various disturbances, and both species of crawling *Staurocladia* medusae often occur in abundance in such pools. The crawling medusae are also found on algae growing subtidally, but not in such abundance as in tidepools. These medusae are both small in size, and can achieve rapid population growth by asexual reproduction. These features show that the medusae are suited to living in tidepools (Emson, 1985). Furthermore, pool-dwelling might provide an advantage to the medusae. Hadrys *et al*. (1990) suggested an increase in the risk of the crawling medusa *Eleutheria dichotoma* becoming detached by water currents during feeding. Crawling medusae are able to firmly adhere to the substrate with their tentacles, but when walking and feeding, some tentacles leave the substrate and they become less resistant to water currents. When well separated from the sea, tidepools provide much less turbulent water where the crawling medusae can feed and probably perform fission more easily. Higher population growth may thus be achieved in tidepools than in the subtidal zone.

S. oahuensis and *S. bilateralis* occur sympatrically in Kominato, but looking at the distribution on smaller scales, the two medusae are rarely close neighbors (Fig. 5). This is especially true at higher intertidal levels where tidepools are often occupied by a single species of *Staurocladia* (Table 2). Because of a longer time of separation from the sea, these upper pools probably receive fewer immigrants, which may facilitate such exclusive occupancy. In contrast, crawling medusae should meet more frequent dispersal events at lower intertidal levels, where well-mixed populations of the two medusae are formed. But even in lower pools, the two species do not share the same algal blade very often.

As there is no negative correlation between the numbers of the two species living on a same algal piece, competitive interaction is unlikely to be the determinant of this spatial segregation. Even when they are directly touching, two individuals of different species or of the same species showed no aggressive behavior, and they remained fairly immobile even in crowded containers in the laboratory. The possibility of interference between the two medusae seems very low. As the two species both prey mainly upon harpacticoid copepods (Y.M. Hirano, unpublished data) they may compete over food on some crowded algae. However, the population density of medusae seems to be not very high on most algal pieces, and a number of algae are left uncolonized. Exploitative competition between the two species of crawling medusae is also unlikely in such environment.

Many forces of disturbance in tidepools might prevent either species from constantly competing with the other, and would permit *Staurocladia oahuensis* and *S. bilateralis* to live together even without significant niche differentiation. In fact, the two species are similar in ecological requirements such as habitat algae, seasonal occurrence and prey, although they may differ in life history strategies. The experiment suggested that *S. oahuensis* may reproduce at a higher rate than *S. bilateralis* with the bell diameter decreasing even when given food. In contrast, *S. bilateralis* increased in size while performing fission at a moderate rate, and seemed to have higher tolerance to temperature extremes. These differences may play some role in further facilitating the coexistence of the two crawling medusae. Tidepools experience wide fluctuations of physical variables such as temperature and dissolved oxgen (Huggett and Griffiths, 1986). In such habitats *S. oahuensis* may predominate over *S. bilateralis*, thanks to its high rate of reproduction, under favorable conditions, while *S. bilateralis* may be more competitive because of its robustness under less favorable conditions.

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REFERENCES

Brinckmann A. – 1964. Observations on the structure and development of *Staurocladia portmanni* sp. n. (Anthomedusae, Eleutheridae). *Can. J. Zool.*, 42: 693-705.

Browne, E.T. – 1910. Coelenterata V. Medusae. *Nat. Antarct. Exped., 1901-1904. Nat. Hist.*, 5, *Zool. Bot*: 1-62.

Bouillon, J. – 1978. Hydroméduses de l'archipel des Seychelles et du Mozambique. *Rev. Zool. Afr.*, 92: 117-172.

Edmondson C.H. – 1930. New Hawaiian Medusae. *Occ. Pap. Bishop Mus.*, 9: 1-16.

Emson, R.H. – 1985. Life history patterns in rock pool animals. In: P.G. Moore and R. Seed (eds.), *The Ecology of Rocky Coasts*, pp. 220-222. Hodder and Stoughton, London.

Gilchrist, J.D.F. – 1919. On a species of the crawling medusa *Eleutheria*, from the Cape of Good Hope (*Cnidonema capensis*, g. et sp. n.) and the southern Eleuthriae. *Quart. J. Micro. Sci.*, 63: 509-529.

Hadrys, H., B. Schierwater and W. Mrowka. – 1990. The feeding behaviour of a semi-sessile hydromedusa and how it is affected by the mode of reproduction. *Anim. Behav.*, 40: 935-944.

Harada, I. – 1954. On the discovery and breeding of *Eleutheria* (Anthomedusae) in the Shimoda Marine Biological Laboratory. (In Japanese) *Collecting and Breeding*, 16: 105-107.

Hirohito, Showa Emperor. – 1988. *The Hydroids of Sagami Bay I.* Biological Laboratory Imperial Household, Tokyo.

Huggett, J. and C.L. Griffiths. – 1986. Some relationships between elevation, physico-chemical variables and biota of intertidal rock pools. *Mar. Ecol. Prog. Ser.*, 29: 189-197.

Kakinuma, Y. – 1963. On the hydroid of a hydrozoan, *Staurocladia* sp. *Bull. mar. biol. Stat. Asamushi,* 11: 171-174.

Kramp, P.L. – 1952. Reports on the Lund University Chile Expedition 1948-1949. 2. Medusae collected by the L.U. Exp. 1948-1949. *Acta Univ. Lund*, NF. 2, Bd. 47: 1-19.

Kramp, P.L. – 1961. Synopsis of the Medusae of the World. *J. Mar. Biol. Ass. U.K.*, 40: 7-469.

Lengerich, H. – 1923. Vergleichende Morphologie der Eleutheriiden II. *Zool. Jb. Abt. Anat.*, 44: 311-388.

Metaxas, A. and R.E. Scheibling. – 1993. Community structure and organization of tidepools. *Mar. Ecol. Prog. Ser.*, 98: 187-198.

Millard, N.A.H - 1975. Monograph on the Hydroida of South Africa. *Ann. S. Afr. Mus.*, 68: 1-513.

Oikawa, K. – 1995. On a crawling medusa of the genus *Staurocladia* obtained from a fish farm at Hota, Chiba Prefecture (In Japanese). *Bull. Chiba Pref. Fish. Exp. Sta.*, 53: 47-50.

Prévot, E. – 1959. Morphologie et évolution des structures tentaclaires chez les Hydraires Gymnoblastes Capitata. *Rec. Trav. Stat. Mar. Endoume*, 29: 91-126.

Schierwater, B. and C. Hauenschild. – 1990. The position and consequences of a vegetative mode of reproduction in the life cycle of a hydromedusa and an oligochaete worm. In: M. Hoshi and O. Yamashita (eds.), *Advances in Invertebrate Reproduction 5*, pp. 37-42. Elsevier Science Publishers, Amsterdam.

Schuchert, P. – 1996. The marine fauna of New Zealand: Athecate hydroids and their medusae (Cnidaria: Hydrozoa). NIWA, *New Zealand Oceanogr. Inst. Memo.* 106.