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Multi-clonal Pseudo-colony Formation in the Calcareous Tube Worm *Salmacina dysteri* (Huxley) (Serpulidae, Polychaeta)

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Abstract On Okinawan coral reefs, individuals of the tubicolous polychaete *Salmacina dysteri* (Huxley) (Annelida: Serpulidae) aggregate and form an arborescent "pseudo-colony" on various substrates. This species is hermaphroditic, reproduces sexually and asexually, and broods embryos within its tubes until the third setigerous stage. Frequent asexual reproduction contributes greatly to pseudo-colony formation, since asexually-reproduced buds do not disperse but remain on the parent pseudo-colony by attaching to the tubes. Sexually-produced larvae which are capable of dispersal settled gregariously on colonies of the same species. Although not frequent, union of colonies occurred in the field. This evidence strongly suggests that pseudo-colony formation occurs by multi-clonal aggregation. Rapid colony growth promoted by joining of hetero-clonal mates seems beneficial, because survival rate of pseudo-colonies and the proportion of sexually-reproducing worms increased with pseudo-colony size. The pseudo-colony formation process is discussed in comparison with other colonial organisms.

Key words: clonal organism, colony, tubicolous polychaete, Serpulidae.

Serpulid polychaetes dwell in calcareous tubes usually attached to hard substrates. They are distributed from freshwater caves through brackish water to deep sea or hydrothermal vents all over the world. Many species live in aggregations or form colonies, and a few species even form serpulid reefs (ten Hove, 1979; ten Hove & van der Hurk, 1993). Aggregating species frequently have a lecithotrophic larval stage and settle close to conspecific tubes (Crisp, 1977). As a cause of mass occurence of serpulids, ten Hove (1979) suggested the following factors: scissiparity (budding), larval incubation, gregariousness or positive response to light during the larval stage, and biotic factors (competition, presence of specific substratum, tolerance to various environmental factors).

Salmacina dysteri seems to be the best studied species among more than 100 known serpulid species. It broods embryos in the tube, is capable of asexual reproduction, and forms a plate-like mass. Colony formation starts with incubated larvae settling in an aggregation (Simon-Papyn, 1959); thereafter, asexually-reproduced buds contribute to "colony" formation (Hanson, 1948). Detailed study is lacking with regards to colony formation, although the life history of *S. dysteri* has been elucidated (Nishi, 1992, 1993a, b; Nishi & Yamasu, 1992; Nishi & Nishihira, 1992, 1993, 1994).

Technically, serpulid species do not form "colonies" per se (ten Hove, 1979). Boardman *et al.* (1973) defined the term "colony" and restricted it to those species which have physiological connections among colony members and a common ancestrula. According to this definition, serpulid polychaetes do not form colonies because they lack physiological connections. However, the term "colony" has been used in the broader sense to include dense aggregations of individuals, such as echinoderm colonies, sea-bird colonies, and insect colonies, *etc.* (see Larwood & Rosen, 1979). Knight-Jones and Moyse (1961) called aggregations of *Filograna* (*Salmacina*) *implexa* a "pseudo-colony". In the present paper,

we use the term "pseudo-colony" for *Salmacina*'s arborescent or plate-like "colonies", which include both clonal and non-clonal worms, and the term "aggregation" for other polychaetes' simple aggregations of conspecific individuals, and the term "eu-colony" for colonies in the sense of Boardman *et al.* (1973), such as colonies of corals, bryozoans, and compound ascidians, *etc.*

In a pseudo-colony of *Salmacina* the colony should accept other clonal members to settle on the "colony" as there are no restrictions imposed by the lack of physiological connections (Nishi & Nishihira, 1993, 1994), and apparently such acceptance readily occurs (Nishi *et al.*, 1996a). The behaviour of individual worms of a pseudo-colony is very similar to that of individual modules in eu-colonial scleractinian corals, bryozoans and compound ascidians (Nishi, 1994). Understanding of multi-clonal colony formation is important in evaluating the benefits of monospecific aggregations and pseudo-colonies. In this paper, we describe the colony-forming process of *Salmacina* in both the field and laboratory, and discuss this strategy from the viewpoint of cost and benefit of aggregation of sessile organisms.

Materials and Methods

Salmacina pseudo-colonies were collected at Sesoko Beach, coral reef of Sesoko Island from 1–10 m depth, during June to July, 1992. Larvae of the 3rd setiger stage were gathered from 15 pseudo-colonies by breaking or open the tubes of brooding females, and released into 6 petri dishes (9 cm diameter, 120 m*l* capacity) to study larval settling behavior. In the petri dish, fragments of dead *Acropora* coral skeleton (about 5 cm length) and adult *Salmacina* tubes with and without worms (5 cm long fragments of about 50 tubes) were set together. After one week, almost all of the larvae had settled either gregariously or solitarily on tubes, coral skeleton fragments or glass dish bottoms. When the tubes of settled worms touched other tubes, they were categorized as an aggregation.

To determine if juveniles were present in pseudo-colonies, ten pseudo-colonies were placed in individual plastic containers for 3 to 5 weeks without exchanging seawater, and later fixed in Bouin's solution. Paraffin blocks were then prepared and sectioned in 10 μm thick slices. Adult worms are usually 100 to 150 μm in body width, and juveniles, 50–80 μm. Juveniles, newly metamorphosed from planktonic larvae (sexually-reproduced) had 3 pairs of branchial filaments and a thin semi-transparent tube. Their thoracic and abdominal segments were shorter and had a lower number of segments (4 to 8) than adults (10 to 25). In contrast, the asexually-reproduced juveniles, just after they are expulsed from the adult, had 4 to 5 thoracic and 7 to 10 abdominal segments (Nishi, 1994). Therefore, it was possible to discriminate between sexually-reproduced juveniles and asexually-reproduced ones from the body size and morphology of the anterior part of the body. For the estimation of larval settlement in the field, 14 colonies were collected, fixed in Bouin's solution and prepared as above.

For monitoring the colony-forming process in the field, 5 colonies containing about 10 worms each were collected, roughly sketched to show the position of all worms, and then stained with Alizaline Red S. For staining, pseudo-colonies were incubated for one day in a 5% Alizaline Red S filtered sea water solution under the ambient light conditions with sufficient aeration. Colonies were not fed. After staining, the pseudo-colonies were returned to the collection site in the field and loosely tied to large dead corals with string. Two weeks later, the pseudo-colonies were collected, roughly sketched, stained again, and then returned to the field for further observation. This procedure was repeated every 2 weeks for 2 to 5 months. This method is useful for the determination of asexual budding in each worm and recruitment of planktonic larvae, but does not allow assessment of sexual reprodution.

Results

Gregariousness of larvae during settlement to metamorphosis

In total, 182 larvae (226 larvae released) settled either solitarily (57 larvae on glass surface; 61 on serpulid tubes, 14 on dead coral skeleton) or in aggregations (35 on the

Table 1. Settlement of *Salmacina dysteri* larvae in petri-dishes. Number of juveniles which settled on tubes of the parent pseudo-colony are shown in parentheses. The surface areas of tubes and coral skeletons were not measured and probably not equal.

Replicate	No. of larvae		Serpulid tubes		Coral skeleton	On dish bottom		Number of aggregates
	added	settled	empty*	live**		solitary	aggregation	
1	50	43	5(3)	11(5)	10	7	10	2
2	40	32	2(0)	6(2)	8	8	8	2
3	35	30	7(5)	5(2)	2	12	4	2
4	25	21	0(0)	3(1)	4	9	5	1
5	49	30	5(3)	9(4)	2	11	3	1
6	27	26	2(0)	6(3)	3	10	5	2
Total	226	182	21(11)	40(17)	29	57	35	

* tubes without serpulid worms; ** tubes with living worms

glass surfaces, 15 on dead coral skeleton) containing varying numbers of individuals (Table 1). Aggregations contained 3 to 10 individuals with an average of 3.57 (S.D.= 1.63, N=10).

Nearly 1/3 of the larvae settled on the parent pseudo-colonies, about 1/3 larvae settled on the tubes without adult worms. The differences between the number of larvae which settled on tubes with living worms and those that settled on empty tubes was not significant (Chi-square test, $p>0.05$). The difference between the number of larvae that settled on the parent pseudo-colony and those that settled on another substrate was also not significant (Chi-square test, $p>0.05$). About 1/4 of the larvae settled with their tubes touching the tubes of other individuals, but whether the larvae settled solitarily or simultaneously in agregations is not clear from this experiment and was not determined either in the larval settlement experiment conducted by Nishi & Nishihira (1994).

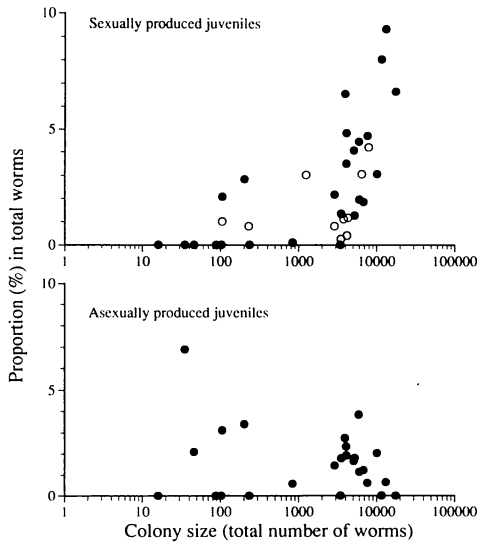

Fig. 1. Relationship between size of the pseudo-colony (expressed by log scale) and proportion of recruits in *Salmacina dysteri*.

Top graph: sexually-produced juveniles. ○: sexually-produced worms occurred in the separately-reared colonies after one month in the laboratory; ●: recently-settled, sexually-produced juveniles in the colonies in the field; bottom graph: recently-settled, asexually-produced juveniles in the field.

Recruitment of sexually- and asexually-reproduced juveniles

The pseudo-colonies were composed of both sexually- and asexually-reproduced worms in various proportions (Fig. 1). Smaller pseudo-colonies showed a tendency towards more asexually-reproduced juveniles than larger ones. An opposite tendency was seen in the proportion of sexually-reproduced juveniles. However, the relationships between proportion of sexually- or asexually-produced juveniles and colony size were not significant ($r=0.323$, $p>0.05$ and $r=0.493$. $p>0.05$, respectively). In the pseudo-colonies separately reared in the laboratory, a smaller proportion of sexually-reproduced juveniles was found than same-sized colonies in the field (Fig. 1).

Fecundity of pseudo-colony

The numbers of eggs and larvae were positively correlated to the size of the pseudo-

colony (Fig. 2) as expected from the result of size-dependent increase of sexually-reproducing worms (Nishi & Nishihira, 1994; Nishi, 1994). The relationships between colony size and the total number of embryos and larvae, number of larvae, number of eggs, number of oocytes, were all significant; colony size vs. total number of embryos and larvae, $r^2=0.724$, $p<0.01$: colony size vs. number of larvae, $r^2=0.826$, $p<0.01$: colony size vs. number of eggs, $r^2=0.629$, $p<0.01$: colony size vs. number of oocytes, $r^2=0.809$, $p<0.01$.

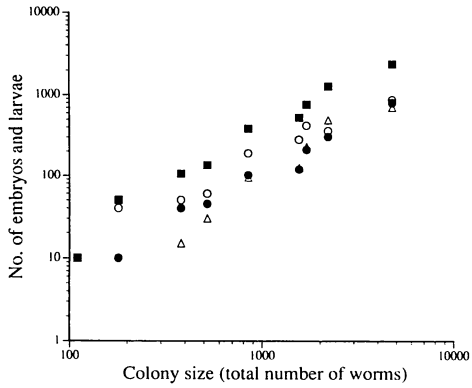

Fig. 2. Relationship between the size of the pseudo-colonies, expressed as the total number of worms, and the number of eggs and larvae of *Salmacina dysteri*. The total represents the number of oocytes in the coelom+eggs in tubes+brooded larvae. ○, oocytes; ●, eggs; ▲, larvae; ■, total.

Pseudo-colony formation in the field

Five pseudo-colonies were monitored in the field over 2 months, 3 (Fig. 3, A, B, C) of which were studied just after the recruitment of juvenile worms. Although the pseudo-colony was formed first by asexually-reproduced worms originating from the ancestral worm(s), asexually-reproduced worms from the recruits were proportionately larger in later stages of colony formation (B and D in Fig. 3). Fig. 3 shows that lower numbers of recruits occurred in the field than in the laboratory.

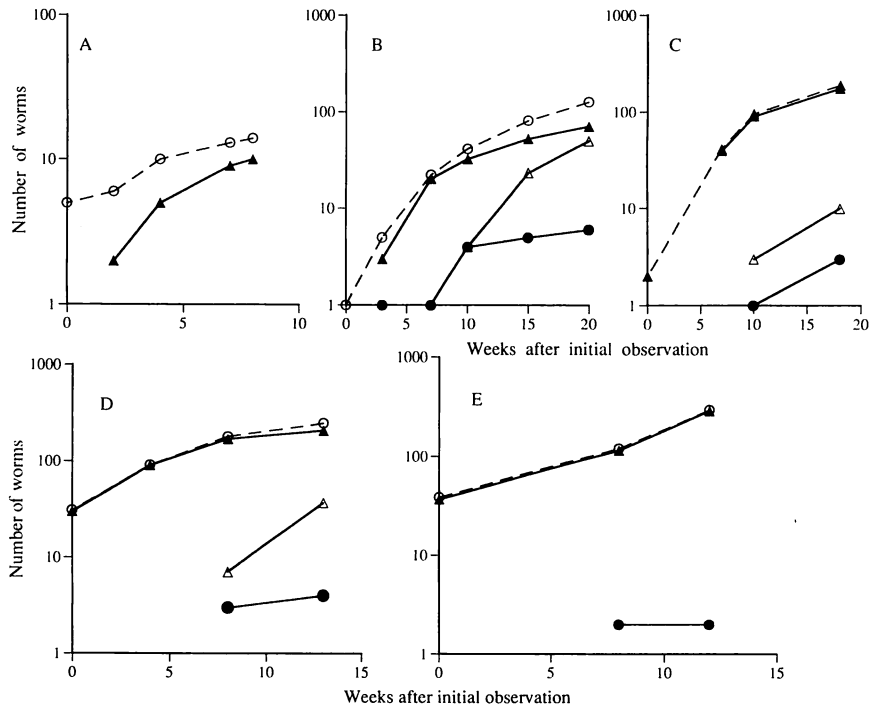

Fig. 3. Sequential change in the composition of worms of different life stages in a pseudo-colony of *Salmacina dysteri*. A–E show different colonies. --○--, total number of worms; —▲—, asexually-reproduced worms; -△-, newly recruited worms from planktonic larvae; -●-, asexually-reproduced worms from newly recruited worms.

Discussion

This study and earlier works (Nishi & Nishihira, 1993, 1994; Nishi *et al.*, 1996) suggested that *Salmacina dysteri* pseudo-colonies are composed of different genets. This speculation was based on the following findings: 1) larvae showed a weak gregariousness at settlement (Nishi & Nishihira, 1994, and this study): an aggregation of juveniles was observed in the congener, *Salmacina tribranchiata* (Jensen & Morse, 1984), which might also form multi-clonal colonies; 2) a batch of juveniles produced from a single parent formed some aggregations when they settled, and those produced from different parents formed one aggregation (Nishi, 1994, and this study); 3) at settlement, the larvae did not show any preference for colonies from which they originated (Nishi, 1994, and this study); 4) union among two or more colonies was observed (Nishi, 1994); and 5) an intra-colonial allozyme variation was found among the worms within one colony (Nishi, 1994; Nishi *et al.*, 1996).

From the electrophoretical analysis, the frequency of multi-clonal pseudo-colonies in the field is estimated at 50% or more in local populations (Nishi *et al.*, 1996). In that study, only a limited number of worms were used. Therefore, the electrophoretical analysis provided a minimum estimation of frequency of multi-clonal pseudo-colonies, such that most pseudo-colonies probably include aggregations of different genets. The union of pseudo-colonies did occur in the field, but is rare (<5% out of 200 colonies observed over 4 years; Nishi, 1994). In the field, most larvae settled solitarily and larval aggregations were rare (Nishi, 1994). The larval recruitment on the pseudo-colony is common both in the laboratory and field, then the larval habitat selection seems important in multi-clonal pseudo-colony formation among some factors concerning to colony formation.

Serpulid polychaetes secrete individual calcareous tubes. Colony union and aggregated settlement of larvae do not result in physiological connections among worms; therefore only multi-clonal pseudo-colony formation is expected (Nishi, 1994). However, *Salmacina dysteri* showed a pseudo-colony formation process and reproductive ecology similar to eu-colonial organisms, as found in previous studies (Nishi & Nishihira, 1992, 1993, 1994). Corals and other cnidarian colonies are rarely formed by larval aggregation (Duerden, 1902; Edmondson, 1946; Williams, 1976), or by tissue fusion in the adult stage (Grosberg, 1988) in the field. If a cnidarian colony started by larval aggregation, but fusion of polyps did not occur, the structure of the colonies is likely to be similar to the pseudo-colony of *Salmacina dysteri*.

The intertidal sea-anemone *Anthopleura elegantissima* is well studied and may be comparable to *Salmacina dysteri*. The sea anemone is solitary and can reproduce asexually, resulting in aggregation of clone-mates which lack any tissue connections. Clones are territorial; non-clone mates did not appear other clones' territories. Sexual reproduction is high in the central part of the aggregation of clone-mates (Francis, 1975). Similar trend of reproductive activity, such as reproductive modes, sexual and asexual, varied according to the position of the worms in *Salmacina* pseudo-colonies (Nishi & Nishihira, 1994) and has been observed in coral eu-colonies of *Pocillopora* (Harrigan, 1972; Rinkevich & Roya, 1985).

Salmacina dysteri pseudo-colonies grow fast and attain 5 to 8 cm in diameter within 6 months of larval settlement (Nishi, 1994). Rapid colony growth of *S. dysteri* seems to be achieved by frequent asexual reproduction, gregariousness and preferential settlement on the pseudo-colony, and colony union. This high growth rate is beneficial when reproductive ability of the colony is size-dependent, as in many eu-colonial species (Jackson, 1985). If some beneficial factors (*e.g.*, size-dependent reproductive capacity and survival rate of the colony; Nishi, 1994), multi-clonal pseudo-colony formation is beneficial for rapid colony growth, because large numbers of larvae can settle on the colony. It has been argued that formation of multi-clonal colonies is not always beneficial in eu-colonial species because some individuals are present as intra-specific somatic cell parasites, since body-fusion causes physiological connections (Buss, 1982). Individual worms in serpulid pseudo-colonies lack physiologi-

cal connections, and the only contact is with their calcareous tubes; thus, the union of colonies occurs easily when they meet in the field. In addition, recruitment of planktonic larvae on the colony does not apear to be inhibited in any way.

Furthermore, multi-clonal colonies probably obtain benefits by enhancing cross fertilization and by reducing the possibility of self-fertilization. The sperm of *S. dysteri* has a long, cone-like head and a long flagellum (Nishi, 1992), and fertilization occurs internally (Nishi & Yamasu, 1992). This type of sperm is not usually released in the water column (Jamieson & Rouse, 1987; Rouse & Jamieson, 1987). Therefore, if colonies are mono-clonal, and if sperm are not released, successful fertilization is probably difficult when the colonies are distant from each other (Pennington, 1985; Yund, 1990). Pseudo-colonies of *S. dysteri* usually occur at low densities (<1 colony m^{-2}), and are distributed solitarily (Nishi, 1994). Multi-clonal pseudo-colony formation may facilitate the avoidance of self-fertilization. Eu-colonial organisms, such as *Acropora,* usually avoid self-fertilization by self-incompatibility (*e.g.*, Heyward & Babcock, 1986).

Salmacina and other serpulid polychaetes form clonal or non-clonal colonies; thus, the structure of the aggregation is comparable to the crowdings of the mussel *Mytilus* or barnacles. However, pseudo-colony members behave as eu-colonial ones particularly with regards to reproduction as shown in the present study and Nishi & Nishihira (1994). *Salmacina* forms a well-defined arborescent colony, quite different from other serpulid aggregations of *Hydroides, Pomatoleios* and *Mercierella.* Therefore, *Salmacina* seems likely to be an ecologically intermediate form between clonal eu-colonial organisms (such as corals with physiological connections) and non-clonal aggregating solitary organisms (such as the polychaete *Mercierella,* the mussel *Mytilus,* and barnacles).

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管棲多毛類シライトゴカイのマルチクローナルな群体形成

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沖縄本島のサンゴ礁域において，カンザシゴカイ科の多毛類シライトゴカイの群体形成を調べた．この種は雌雄同体で，無性生殖を行い，幼生を棲管の中で保育する習性を示す．無性生殖によってできた幼稚体は分散することなく，親群体に留まる．有性生殖によっ

て生み出された幼稚体もまた同種の群体上に定着する．群体同士の合体も稀ではあるが，野外で観察された．これらの結果から，この種の群体は，単一のクローンからできる場合と，幾つかのクローンが含まれるマルチクローナルな群体である可能性がある．群体が大きくなると，群体の生存率が増加し，放出される幼生の数も増加するため，急激に群体の大きさを増加させる可能性のあるマルチクローナルな群体形成を行っていると考えられる．群体形成に関わる生態的要因を他の群体性の生物と比較しながら考察した．