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Differences in Larval Settlement Site between Generalist and Specialist of Aeolid Nudibranchs

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ABSTRACT—The preys of three flabellinid nudibranchs and the distribution of their pediveliger larvae were investigated to reveal the relation between the width of dietary spectrum and the larval recruitment site. Hundreds of pediveligers were found in total from the field. *Flabellina amabilis* and *Flabellina* sp. were specialists consuming exclusively one hydroid species, while *Flabellina athadona* was a generalist eating five hydroid species. Not only in the specialists but in the generalist, the pediveligers were associated with their adult diet hydroids, although there was a hydroid species on which the larvae of the generalist could hardly succeed to settle. As to microdistribution of pediveligers on the hydroids, there was a significant difference between the specialists and the generalist; pediveligers of *F. amabilis* and *F.* sp. were mostly found to directly adhere to the naked hydranths, while those of *F. athadona* were found away from the naked hydranths. The causes of these phenomena are discussed.

INTRODUCTION

It is important for ecological studies on the nudibranchs to know whether the veliger larvae settle directly on the adult preys, or they settle and metamorphose elsewhere and immigrate on to the preys as juveniles or adults. That the larvae may not settle on all the prey species is strongly suggested in a hydroid-consuming dendronotid of which the adult exploits several prey species (Swennen, 1961; Lambert, 1991). In contrast, there is a dorid nudibranch which eats only one species of sponge although the metamorphosis of larvae is also induced by three other sponges (Hubbard, 1988). Although many laboratory studies have been done on the settling behaviour and metamorphosis of opisthobranch larvae (Hadfield and Swizer-Dunlap, 1984; Havenhand, 1991 for review), there have been very few attempts to find larvae in the field except for those of Tardy (1964, 1970). In the circumstances, the presence of the larvae on adult diets in nature needs to be studied in detail.

The present study investigated the preys of three sympatric aeolid nudibranchs, *Flabellina athadona* (Bergh, 1875), *Flabellina amabilis* Hirano and Kuzirian, 1991 and *Flabellina* sp., and the distribution of their larvae (pediveligers which have already lost the vela), in order to reveal the relation between the width of dietary spectrum and the larval recruitment site. To our knowledge, this study provides the first information from the field on the above mentioned relation, not by the deduction from laboratory works.

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MATERIALS AND METHODS

The present study was conducted at Oshoro Bay, Japan Sea coast of western Hokkaido (43° 14' N, 140° 51' E) in the winters of 1991 and 1992. The three nudibranchs all appear there during winter. The width of dietary spectrum of the three nudibranch species was determined by two of the criteria of Swennen (1961): constant association of the nudibranch and its suspected hydroids in the field, and actual feeding of the suspected hydroids during laboratory observation. Observations of nematocysts in the cnidosac were also made to determine the dietary history of the individuals.

Many colonies of hydroids determined as diet on the basis of the above criteria were collected to investigate the distribution of the pediveligers on them. Hydroids growing on algae and those on small sized stones or boulders were collected with the substrata. The species growing on the bedrock were torn off from the hydrorhizas which are firmly attached to the bedrock. The hydrorhizas of such species were not available for examination. The collected hydroid colonies were sorted by species and gently put into plastic bottles or bags to bring back to the laboratory. The pediveligers were searched for on the hydroids under a stereomicroscope, and the adhering sites of the pediveligers were recorded. They were very inactive not moving around. Species identification of the pediveligers was made based on the specific patterns of pigmentation on their soft part (Hirano Y. J., unpublished data).

RESULTS

Dietary spectrum

As shown in Table 1, *Flabellina amabilis* and *Flabellina* sp. were specialists consuming exclusively one hydroid species, while *Flabellina athadona* was a generalist eating five hydroid species. Adults of the three nudibranchs were observed to eat the hydranths of their prey hydroids. The nematocyst composition in the cnidosac of specialists was always identical to that of the associated hydroid, while in generalist it usually varied with individuals, even among

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Table 1. Prey hydroid species of *Flabellina athadona, Flabellina amabilis,* and *Flabellina* sp. + marks represent the predation confirmed.

Hydroids		Nudibranch species		
		F. athadona	*F. amabilis*	*F.* sp.
Campanularia platicarpa	(Thecata)	+		
Abietinaria costata	(Thecata)	+		
Coryne uchidai	(Athecata)	+		
Hataia parva	(Athecata)	+		+
Eudendrium boreale	(Athecata)	+	+	

Table 2. Number of pediveligers which were found from different sites of different hydroid species. The boldface is the total number on each hydroid species. The 'others' represents tiny algal fronds and/or unidentified campanularids associated with the hydroids in question. The observations conducted in 1991 and 1992 are separately shown. In 1991, only two hydroid species were examined.

	F. athadona		*F. amabilis*		*F.* sp.
	91	92	91	92	92
Campanularia platicarpa	**40**	**74**	0	0	0
hydrotheca	7	14	0	0	0
hydrocaulus	11	12	0	0	0
hydrorhiza	9	34	0	0	0
others	13	14	0	0	0
Abietinaria costata	—	**50**	—	0	0
hydrotheca	—	32	—	0	0
hydrocaulus	—	15	—	0	0
others	—	3	—	0	0
Coryne uchidai	—	**120**	—	0	0
hydranth	—	0	—	0	0
hydrocaulus	—	89	—	0	0
hydrorhiza	—	15	—	0	0
others	—	16	—	0	0
Hataia parva	—	**43**	—	0	**18**
hydranth	—	2	—	0	18
stone surface	—	33	—	0	0
others	—	8	—	0	0
Eudendrium boreale	**10**	**2**	**42**	**83**	0
hydranth	0	0	23	66	0
hydrocaulus	0	2	18	17	0
others	10	0	1	0	0

those collected from the same hydroid species. Nematocysts from two or more hydroid species were often mixed in the cnidosac of *F. athadona,* which shows that this generalist can shift its habitat and food from one hydroid species to another.

Distribution of pediveligers

Hundreds of pediveligers were found by two surveys. The pediveligers were observed to adhere to various sites of the hydroids. Table 2 shows distribution of the pediveligers on the hydroid species listed in Table 1 (schematically illustrated in Fig. 1). Pediveligers of *Flabellina amabilis* were found only on *Eudendrium boreale* Yamada, mainly adhering directly to the lower part of naked hydranths. Although pediveligers of *Flabellina* sp. found were comparatively few, all of them were obtained from the naked hydranths of *Hataia parva* Hirai and Yamada (entire body of this solitary hydroid is called as hydranth, see Hirai and Yamada, 1965). One of the pediveligers was adhering to the tentacle densely packed with nematocysts. Not a single larva of these two specialist nudibranchs were found on any hydroid species other than the adult prey.

Pediveligers of *Flabellina athadona* were more or less associated with all five hydroid species confirmed as its adult

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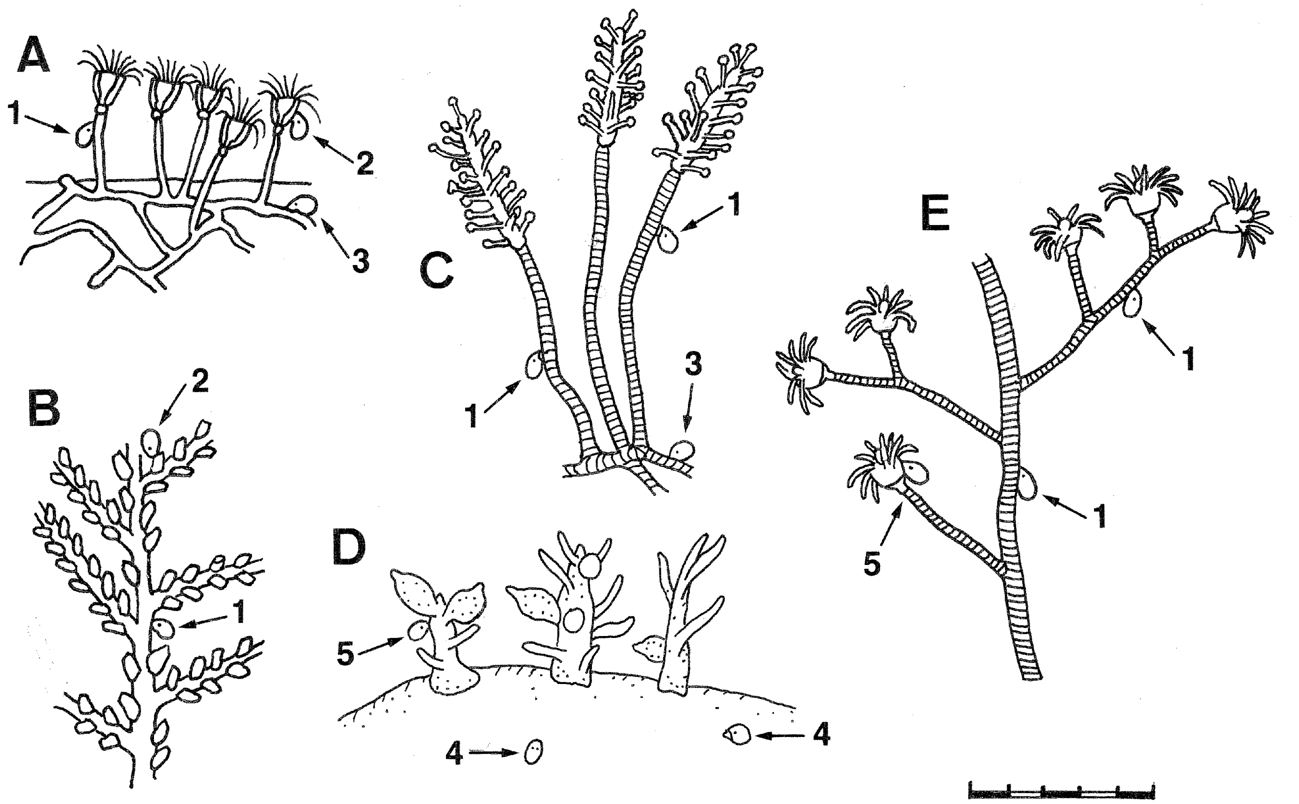

Fig. 1. Schematic illustrations of adhering sites of pediveligers of three nudibranch species on five hydroid species. A, *Campanularia platicarpa*; B, *Abietinaria costata*; C, *Coryne uchidai*; D, *Hataia parva*; E, *Eudendrium boreale.* Numerals with arrows indicate the parts of hydroids on which the pediveligers were found: 1, hydrocaulus; 2, hydrotheca; 3, hydrorhiza; 4, stone surface; 5, hydranth. All the pediveligers in A-C, those with numeral 4 in D, and those with numeral 1 in E are of *Flabellina athadona.* The pediveliger with numeral 5 in D and that with numeral 5 in E are of *Flabellina* sp. and *Flabellina amabilis*, respectively. Bar represents 5 mm.

diet. On *Campanularia platicarpa* (Bale), *Abietinaria costata* (Nutting) and *Coryne uchidai* Stechow, they were found on all parts of the hydroids but the naked hydranth. Most of the pediveligers of *F. athadona* were also away from the naked hydranth of *Hataia parva,* and were found on the boulder surface near attaching sites of the hydroids. Two individuals exceptionally obtained from the hydranths of *H. parva* were lightly adhering to the base of hydroid. Although pediveligers of *F. athadona* were also obtained from the colonies of *E. boreale,* they were very few; in total only 12 were found. Two of them were observed to adhere to the hydroid itself, however the others were attached to tiny algal fronds or small unidentified campanularid hydroids growing on *E. boreale.* Compared to *F. amabilis* the number of the pediveligers of *F. athadona* on *E. boreale* is strikingly small.

DISCUSSION

First of all, it was clearly shown that the specialists, *Flabellina amabilis* and *Flabellina* sp., started their benthic life on the only prey hydroid at the stage of the pediveliger. The direct adhesion of the larvae to the naked hydranth appears to show that the specialist larvae are already capable to eat the adult prey. In contrast, the larvae of the generalist, *Flabellina athadona* were seldom found from the naked hydranths. Why don't they adhere there? Possible explanations are that the larvae of the generalist might be less tolerant against the naked part of hydroids, or that they might be removed by reverse predation of adult prey hydroids. The reverse predation was actually observed by Hadfield (1963) and Rivest (1978). However, the possibility of the reverse predation will be excluded because the pediveliger of *F. athadona* is the largest among the three species (Hirano Y. J., unpublished data). The former explanation seems more supportable; the specialized character of being immune to the naked hydranths, may be given only to the larvae of the specialists.

There is another possible interpretation, that is the larvae of the generalist may not avoid the naked hydranth but may rather prefer the perisarc covering the soft hydroid body. The perisarc and also the stone surface are usually covered with sessile diatoms, often very densely. As Lambert (1991) supposes, microalgal diet would allow meiofaunal-sized juveniles to increase in size before shifting to the adult diet. Many pediveligers of *F. athadona* were in fact found on the dense mat of such diatoms on the perisarc

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of hydroids. If there is a similarity of the associated diatom species among the prey hydroids for the generalist, it is considered to be highly adaptive for its larvae to use the diatom as a cue for the settlement. Because the period of the pelagic life of *F. athadona* is supposed to be quite long judging from the size difference of the newly hatched veliger (ca. 100 μm in shell length) and the pediveliger (ca. 400 μm) (Hirano, Y. J., unpublished data), the larvae will most likely perish if they do not have any cues for settlement. Ability to find the suitable benthic habitat should be necessary for generalist larvae as well.

Although the pediveligers of *F. athadona* were found associated with all of the five adult diet species, their rare occurrence on *E. boreale* is noteworthy. It is hard to determine the cause of this rare occurrence. There seems several possibilities to consider. *E. boreale* may have bigger mouths than the other hydroids, it may be better "armed", or it may be less attractive to the larvae of *F. athadona.* The first possibility could be ruled out, because the smaller larvae of *F. amabilis* can settle on the hydroid. It is very unlikely that the hydroid selectively eats the larvae of *F. athadona.* The second possibility also seems to be ruled out. The pediveligers of *F. athadona* were mostly found adhering to the perisarc of hydroids. How could the nematocysts of *E. boreale* prevent the larvae from adhering to the perisarc? The third reasoning has no objection at present, but it raises another question. What is responsible for being less attractive? It might be the chemical substance from the hydroid itself; however, the existence of the possible mediator, namely sessile diatoms is also recalled here. *E. boreale* might differ from the other hydroids in the associated diatom species, or it might collect too few diatoms to attract the larvae of the nudibranch. *E. boreale* grows on the rocky walls where strong waves generated by the seasonal wind sweep over the shrubby colonies of the hydroid during winter when both the hydroid and the nudibranchs appear. Actually the hydrocauli of *E. boreale* are "cleaner" than those of the other hydroids. The role of sessile diatoms should be studied as a possible intermediate diet from the phytoplanktivore to the carnivore.

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