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Life history of the Polychaete *Polydora variegata* that bores into the shells of Scallops in Northern Japan

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ABSTRACT

The genus *Polydora* (Polychaeta, Spionidae) is widely known for its boring activities in molluscan shells. Here we describe the life history of *Polydora variegata*, which causes considerable damage to scallops sown in the waters of Abashiri Bay, off the Okhotsk Sea coast of Hokkaido, Japan, by spreading blisters and penetrating the shells. The life span of *P. variegata* was 2.5 years after settlement, and the main spawning period of both 0- and 1-yr-olds was from August to October. Three-setiger larvae hatched from the egg capsule mainly from September through November. Settlement of 17-setiger larvae took place during the drift-ice period. There was a tendency for the earliest settlement of *P. variegata* to occur on a narrow band around the periphery of the left valve of the scallops. A large body size, high reproductive activity and a long life span seem to be characteristic of this species of boring polychaete.

RÉSUMÉ

Cycle de vie du Polychète *Polydora variegata*, espèce perforante des Coquilles Saint Jacques dans le nord du Japon

Le genre *Polydora* (Polychètes, Spionidae) est bien connu pour ses activités de perforation des coquilles de mollusques. Ce travail décrit le cycle de vie de *Polydora variegata*, espèce qui cause des dommages considérables aux coquilles Saint-Jacques de la baie d'Abashiri, au large des côtes d'Hokkaido, en mer d'Okhotsk, Japon, par l'étendue des boursouflures et la pénétration des vers dans l'épaisseur des coquilles. La durée de vie de *P. variegata* est de deux ans et demi après la fixation, et la principale période de reproduction pour les deux groupes d'individus d'âge 0 et d'âge 1 s'étend d'août à octobre. Les larves à trois sétigères sortent de la capsule de l'oeuf principalement de septembre à novembre. La fixation des larves à 17 sétigères se situe au moment de la débacle des glaces. On a noté une tendance des *P. variegata* à se fixer d'abord sur une bande étroite autour de la périphérie de la valve gauche des coquilles Saint-Jacques. Une grande taille corporelle, une activité reproductrice élevée et une longue durée de vie semble être les caractéristiques de cette espèce de polychète perforante.

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INTRODUCTION

The spionid genus *Polydora* is found in a wide variety of substrates that range from soft clays or mud to hard calcareous materials (BLAKE & EVANS, 1972). The life history and population dynamics of the genus have been discussed by DORSETT (1961), DARO & POLK (1973), GUDMUNDSSON (1985), and ZAJAC (1992). Nearly all the previous studies have dealt with *Polydora* that inhabit soft-bottom habitats, but there have been only few studies on dealing with those species which bore into shells.

Infestation by *Polydora* of commercially important molluscan shells is an important problem in aquaculture. *Polydora* not only reduces the value of molluscs but causes considerable damage to the shell, especially those in cultures. The species that bore into the shells of *Patinopecten yessoensis* do not feed on the host's tissue; the shell is used only as a refuge (SATO-OKOSHI & OKOSHI, 1992). Therefore, the polychaete is an inhabitant of the molluscan shell and not a parasite. Nonetheless, some worms do penetrate the inner surface of the shell and induce secretion by the shell of a thin layer of a dark or black organic material. Natural scallops with sufficiently thick shells suffer little damage even with heavy penetration by *Polydora*. However, cultured scallops have thin shells, a low growth rate and as a result, considerable damage when subjected to a heavy infestation by *Polydora*.

The Okhotsk Sea coast of Hokkaido is well known for its natural supply of scallops. Sowing of cultures was started in the waters of Abashiri Bay in 1977 in order to counteract the instability of the natural population. In these cultures, worms were observed to bore into the left valves, an average of 162 per shell; a maximum of 327 worms per shell have been counted (SATO, 1988). Very few worms bored into the right valve. The reproductive characteristics of *Polydora variegata* have been reported by SATO-OKOSHI *et al.* (1990). Details of its infestation and the nature of the burrows have been characterized for population in Abashiri Bay and elsewhere (MORI *et al.*, 1985; SATO-OKOSHI & NOMURA, 1990). The present study summarizes the life history of *P. variegata* in Abashiri Bay where it causes considerable damage to the scallops.

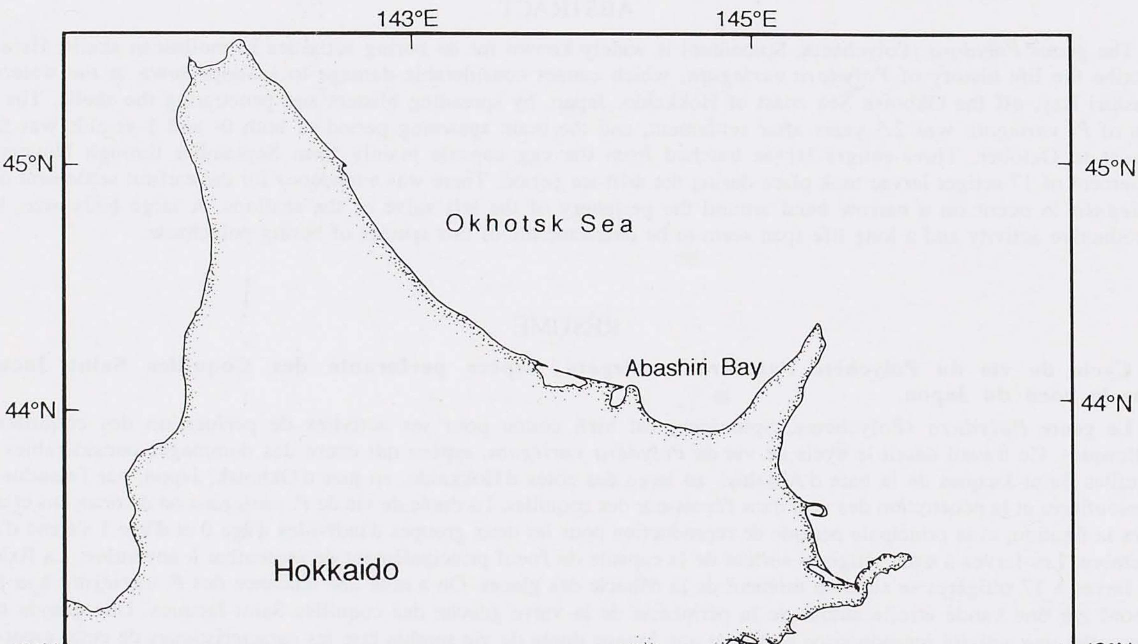

FIG. 1. — Location of sampling area.

MATERIALS AND METHODS

Three- to five-year-old scallops were collected monthly by dredging from April 1982 to December 1986 (excluding 1985) from a depth of 30 to 50 m in Abashiri Bay, on the Okhotsk Sea coast of Hokkaido, Japan (Fig. 1). The scallops collected in 1982-1984 were the same cohort and their juveniles were collected in 1979 and sown in 1980, and scallops collected in 1986 were sown in 1984 from their juveniles collected in 1983. Two to 11 scallops were examined each month.

The scallop flesh was removed, and the left valve was broken into small pieces with pliers, and *P. variegata* were removed with forceps under a stereomicroscope. The presence of gametocytes was checked by rupturing segments and transferring the coelomic contents onto a microscope slide. Body size was determined by measuring the width of the fifth setiger after fixation in a neutralized 10 % solution of formalin.

Egg capsules were collected from the burrows of adults. The egg capsules were carefully removed from the burrows with forceps and placed in culture dishes that contained filtered seawater. After hatching from the egg capsule, larvae were maintained in 200-300 ml of filtered seawater in glass beakers at 12 °C. Larval development was observed under a stereomicroscope until settling and metamorphosis. The seawater was changed every 3-5 days. Larvae were fed a mixture of *Skeletonema costatum* and *Chaetoceros* spp. taken from Onagawa Bay.

RESULTS

SETTLEMENT PATTERNS AND SIZE-FREQUENCY DISTRIBUTIONS. — Strong growth-inhibition rings were found on the shells of 4-year-old cultured scallops that had been sown in Abashiri Bay (Fig. 2). These rings corresponded to the times at which (1) scallops had been sown in June (R1); (2) the first winter season (R2); (3) the second winter season (R3); etc. (SATO-OKOSHI *et al.*,1990). In the winter season, the Okhotsk Sea coast of Hokkaido is generally covered with drift ice from January to March and referred to as the "drift-ice period".

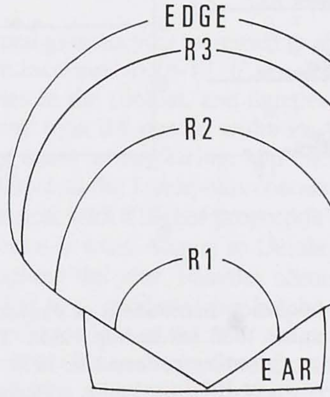

FIG. 2. — Growth-inhibition rings of scallops collected from Abashiri Bay. R1: Ring formed when scallops were sown in June; R2: ring formed during the first winter season; R3: ring formed during the second winter season (from SATO-OKOSHI *et al.*, 1990)

Size distributions of *P. variegata* in 1982, 1983, 1984 and 1986 are shown in Figure 3. A large number of *P. variegata* were observed to have bored around the inhibition rings, R2, R3 and R4, of the left valves. The size of the worms from each inhibition ring was investigated. The width of the fifth setiger was used as an index of the age of the worms (MORI *et al.*, 1985).

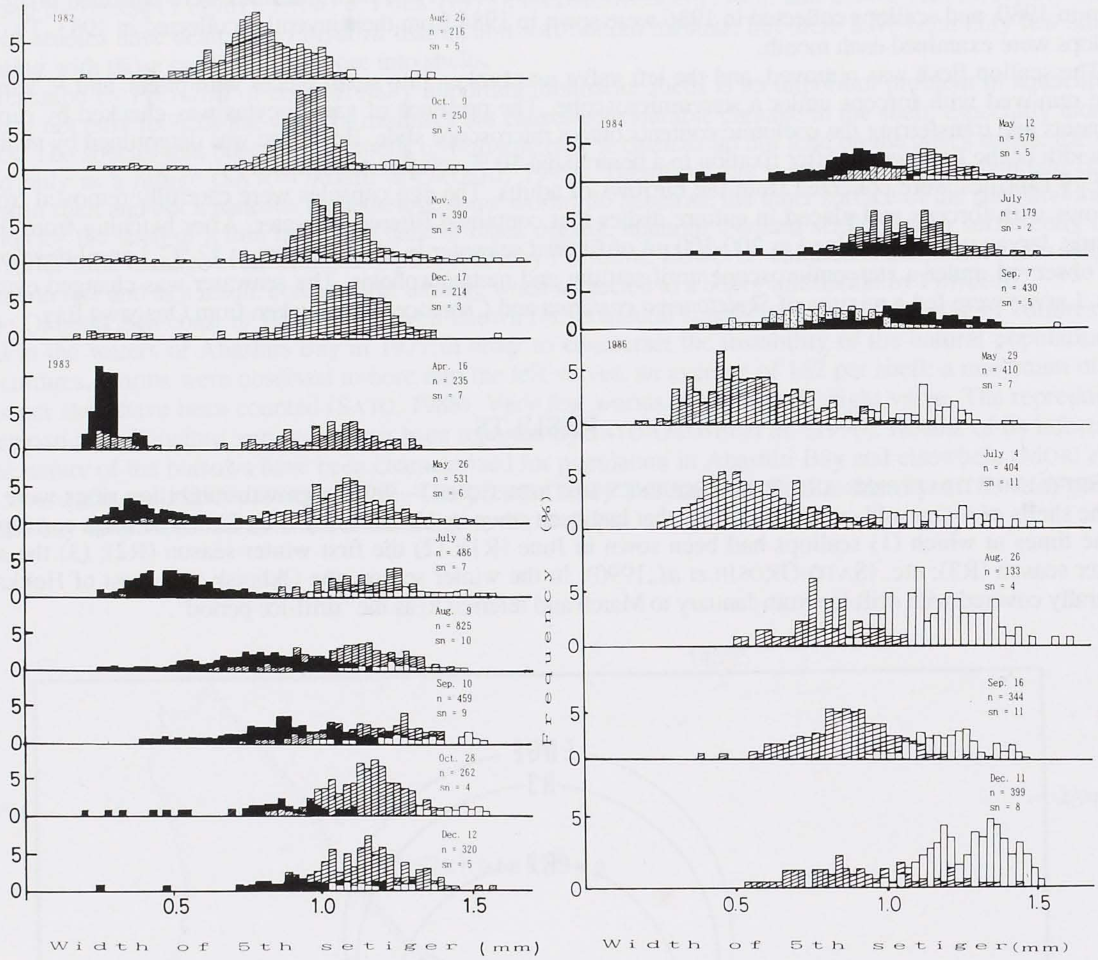

FIG. 3. — (1) on the left, (2) on the right. Size-frequency distributions of *Polydora variegata* that had bored into the left valves of scallops from April 1982 to December 1986 (excluding 1985). The worms in 1982-1984 were extracted from a population of scallops of the same age (juveniles collected in 1979 and sown in 1980). The worms in 1986 were extracted from scallops that had been sown in 1984 (juveniles collected in 1983). [open box], individuals that settled around R2; [hatched box], individuals that settled around R3; [black box], individuals that settled around R4; [dotted box], individuals that settled around R5. (adapted from MORI *et al.*, 1985 and from SATO-OKOSHI *et al.*, 1990). n, number of *P. variegata* examined; sn, number of scallop shells examined.

Young juveniles of about 20 segments appeared around the periphery of the left valve in April, after the drift-ice period. This observation suggests that the peripheral regions of the left valve during the drift-ice period subsequently become growth-inhibition rings, and that worms that settled on the peripheral regions grew around the inhibition rings. Thus, if both the age of the scallop and the boring region of the worms are known, it is possible to estimate the age of *P. variegata* individuals.

Worms around R3 appeared to have settled on the peripheral regions of the left valve during the period when the bay was frozen in 1982, while worms around R4 appeared to have settled on the peripheral regions during the same period in 1983.

The worms that settled on R3 in the drift-ice period of 1982 seemed to survive until the summer of 1984 but had disappeared by September. Thus, the life span of *P. variegata* seems to be approximately 2.5 years after settlement on a shell. The widths of the fifth setiger of newly settled worms varied from about 0.2 to 0.3 mm in April and grew to approximately 1.0 mm in December, about eight months after settlement. Once they had reached 1.0 mm in width, the worms grew slowly. The width of the fifth setiger did, however, varied from 0.8 mm to 1.5 mm in the second summer.

There was a small influx of newly settled worms around R3 throughout the period from August to December, 1982 (Fig. 3). Furthermore, some small worms found around R3 in April 1983 were obviously the newly settled young of 1983, demonstrating that, while almost all the juveniles settled around the peripheral region of the left valve, some settled around the other rings.

The same tendency was observed in 1986. Newly settled worms of 1986 during the drift ice period were observed to grow around R3 (0-year-olds) and larger worms which appeared to have settled in 1985 were observed to grow around R2 (1-year-olds).

From the data for 1982-1986, there seemed to be some years in which there was no settlement, for example, the winter of 1981. No worms were observed to settle around R2 in spite of the large number of worms around R3 and R4. These results suggest that the number of worms that settle on a shell fluctuates annually.

REPRODUCTION. — The reproductive patterns of 0- and 1-year-olds have been described previously (SATO-OKOSHI *et al.*, 1990). Table 1 shows the number and percentage of worms that contained gametocytes in the coelom and egg capsules in tubes in 1983 and 1986. Oocytes in the coelom of the female were shaped like an oval disc with the diameter of the long axis measuring 30 to 170 µm. Diameters of 130 to 140 µm were common in August in 0-year-olds and those of 130 to 140 µm were common in May to September in 1-year-olds in 1986 (SATO-OKOSHI *et al.*, 1990).

The proportion of worms that contained gametocytes increased to above 70 % among 0-year-olds in September and October, as the seawater temperature increased to 16-17 °C at a depth of 30 m. Some 0-year-olds measuring at least 0.6 mm wide contained gametocytes in the coelom, and females produced egg capsules. Brooding females appeared among the large worms of more than 0.8 mm in width in August and September, with an increase in October. Plural number of egg capsules made an egg string, and each egg string contained about 300 to 1,000 eggs. When the drift-ice period ended, almost all the 1-year-olds contained mature gametocytes. They were found in almost all the 1-year-olds throughout the year with a higher proportion of brooding females. Previous reports have indicated that the main reproductive season is from August to October (MORI *et al.*, 1985; SATO-OKOSHI *et al.*, 1990). Egg strings were observed throughout the year. Females seemed to have the potential for producing egg string repeatedly, with about 800 to 5,700 eggs produced per batch, during the period from August to October predominantly. The relationships between the width of the fifth setiger of the brooding female and the number of eggs per egg string for 0-year-olds and 1-year olds are, respectively, as follows:

$\ln Y = -1.10 \ln X + 7.80$ ($r^2 = 0.092$, $n = 7$) and $\ln Y = 1.05 \ln X + 6.19$ ($r^2 = 0.082$, $n = 25$) [X, width of 5th setiger (mm); Y, no. of eggs/string].

LARVAL DEVELOPMENT. — Larvae remained in the capsules until the three-setiger stage at which time they hatched. The time from the initial deposition of eggs to hatching was approximately 2 weeks at 15 °C. The long diameter of the oval fertilized egg was 150-160 µm with an average of 152.5 ± 11.0 µm. Asetigerous larvae measured 160 to 230 µm in length. Large macromeres filled the central portion of each larva. Two small circular eye spots were located dorsally. The larvae elongated and one or two distinct setigerous segments appeared. One- and two-setiger larvae measured 220-240 µm and 230-280 µm in length, respectively. Both early and late three-setiger larvae (Fig. 4A-B) were positively phototactic. Yolk was still present within the gut. Four eyes were located on the dorsal surface of the head. Black pigmentation was seen on the dorsal surface of the third setiger and at the posterior end. Both the number and the length of the setae increased as this larval stage grew.

TABLE 1. — Numbers and frequencies of sexually mature worms of *Polydora variegata* in Abashiri Bay in 1983 and 1986. Numbers in parentheses show the frequency (%).

Date	Total n°	Mature		Mature		Mature and mature		Brooding	Total
		males		females		males	females	females	females
(a) 0-yr-olds									
83 Apr. 16	108	0		0		0		0	
May 26	106	0		0		0		0	
July 8	173	26	(15.0)	13	(7.5)	39	(22.5)	0	
Aug. 9	280	110	(39.3)	63	(22.5)	173	(61.8)	4	(6.3)
Sep. 10	151	73	(48.3)	42	(27.8)	115	(76.2)	10	(23.8)
Oct. 28	46	18	(39.1)	19	(41.3)	37	(80.3)	7	(36.8)
Dec. 12	42	15	(35.7)	15	(35.7)	30	(71.4)	0	
86 May 29	314	16	(5.1)	8	(2.5)	24	(7.6)	0	
July 4	300	27	(9.0)	10	(3.3)	37	(12.3)	0	
Aug. 26	48	17	(35.4)	9	(18.8)	26	(54.2)	2	(22.2)
Sep. 16	232	111	(47.8)	62	(26.7)	173	(74.6)	8	(12.9)
Dec. 11	208	87	(41.8)	50	(24.0)	137	(65.9)	0	
(b) 1-yr-olds									
83 Apr. 16	93	35	(37.6)	30	(32.3)	65	(69.9)	1	(3.3)
May 26	370	153	(41.4)	151	(40.8)	304	(82.2)	18	(11.9)
July 8	219	106	(48.4)	100	(45.7)	206	(94.1)	13	(13.0)
Aug. 9	349	154	(44.1)	170	(48.7)	324	(92.8)	48	(28.2)
Sep. 10	215	102	(47.4)	102	(47.4)	204	(94.9)	44	(43.1)
Oct. 28	141	69	(48.9)	66	(46.8)	135	(95.7)	23	34.8)
Dec. 12	207	95	(45.9)	93	(44.9)	188	(90.8)	0	
86 May 29	100	50	(50.0)	42	(42.0)	92	(92.0)	1	(2.4)
July 4	104	52	(50.0)	52	(50.0)	104	(100)	0	
Aug. 26	87	39	(44.8)	48	(55.2)	87	(100)	19	(39.6)
Sep. 16	158	72	(45.6)	83	(52.5)	155	(98.1)	43	(51.8)
Dec. 11	209	109	(52.1)	90	(43.1)	199	(95.2)	4	(4.4)

Larvae were released from the egg capsules during the late three-setiger stage, and they were able swimmers. Larvae were planktotrophic until they reached the 17-setiger stage, a process that required more than two months at 15 °C. The length of planktonic three-setiger larvae was 250-320 µm. The embryonic yolk was no longer present by the six-setiger stage. The 13-setiger larvae were about 750 µm long, and palps were present. Gastrotrochs were located on setigers 3, 5, 7 and 10. The 14- (Fig. 4C) and 15-setiger larvae were about 800 and 950 µm long, respectively. A modified prostomium and yellow pigmentation were apparent. The 16- and 17-setiger larvae (Fig. 4D) were 1.0 and 1.25 mm long, respectively. Palps were elongated to the end of the fifth setiger and four eye spots were in trapezoidal arrangement. Distinct black pigmentation was present on the dorsal surface of the 15th, 16th and 17th setigers, and gastrotrochs were present on setigers 7, 10, 13 and 15. The modified spines and accompanying companion setae on setiger 5 developed and emerged at this stage; they were present on some worms at the 15-setiger stage. A caruncle gradually developed and appeared at the 14-setiger stage. The 17-setiger stage was reached in a minimum of 36 days and a maximum of 65 days.

The larvae of *P. variegata* were not easily induced to settle and metamorphose. Only five out of 200 larvae completed metamorphosis. These larvae took more than two months to settle and metamorphose after hatching. Almost all the 17-setiger larvae were alive for more than two months and up to as much as three months without settling and metamorphosing. There was no apparent change in morphology of these larvae apart from slight elongation.

DISCUSSION

A large number of worms of the genus *Polydora* were found to have bored into the shells of sown cultured scallops in Abashiri Bay. The boring species were *P. variegata, P. websteri, P. concharum, P. concharum* subspecies and *P. convexa.* The relative frequencies of these species were 55.5 %, 17.3 %, 0.4 %, 26.6 % and 0.2 %, respectively, throughout the year. We have studied the reproductive characteristics and settling periods of *P. websteri* and *P. concharum* subspecies.

FIG. 4. — Photographs of larvae of *Polydora variegata.* A, Early three-setiger larva; B, late three-setiger larvae; C, 14-setiger larva; D, 17-setiger larva.

There are two reproductive populations of *P. websteri* which are found in early summer and in autumn (SATO, 1988). Females apparently produce egg string only once with approximately 500 eggs per batch. Their juveniles tend to settle on the ventral edge of the left valve, in the same way as *P. variegata,* after approximately one month's planktonic life. Their life span seems to be one year.

No mature individuals were observed in the case of *P. concharum* ssp. The strong regenerative activity and the fact that more than two worms inhabit each burrow suggest that asexual reproduction might be occurring in this species. Five species of the genus *Polydora,* which coexist in the same scallop shell, seem to have different life-cycle patterns.

There are many reports with descriptions of the reproduction of the genus *Polydora* (WILSON,1928; HEMPEL, 1957; HATFIELD, 1965; MIZUMOTO, 1966; BLAKE, 1969; RASMUSSEN, 1973; DAY & BLAKE, 1979; ANGER, ANGER & HAGMEIER, 1986; RADASHEVSKII, 1986). For many species of *Polydora,* the life span has been reported to be about one year or less and they die after their first or several spawnings within a year (SÖDERSTROM, 1920; LAMBECK & VALENTIJN, 1987). Under natural conditions, only the example from northeast England offers the possibility of some worms surviving for more than a year and spawning again (GUDMUNDSSON, 1985). In the case of *P. variegata,* however, all the worms seem to survive for 2.5 years after having settled on the scallop shells. They spawn during the first year and also in the subsequent year, producing one to several batches of egg strings during the main spawning season. *P. variegata* produced 300 to 1,000 eggs per batch in the first year and 800 to 5,700 eggs in the second. Moreover, the 1-year-olds apparently produced egg strings year round. The maximum body size of 30 mm in length and 1.6 mm in width, the high reproductive activity and a long life span are characteristic of the boring polychaete *P. variegata*.

The life history of *P. variegata* is shown schematically in figure 5.

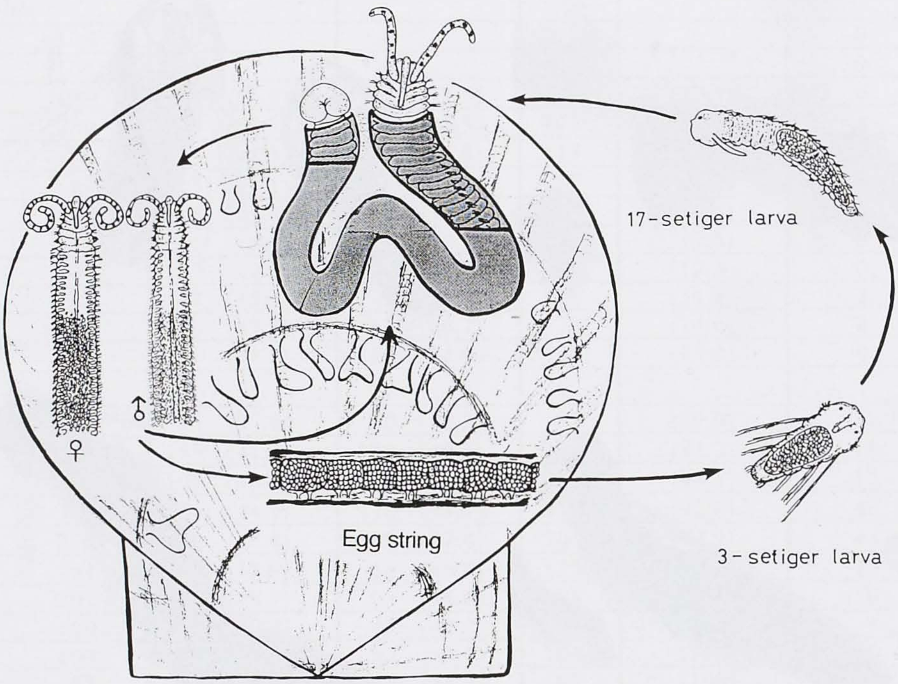

FIG. 5. — Schematic diagram showing life history of *Polydora variegata*.

Live *Polydora* worms were found only in the shells of live scallops or in shells just after the death of scallops. No worms were collected from the benthos. From a depth of 15 to 45 m in Abashiri Bay, *Tectonatica janthostomorides, Mercenaria stimpsoni, Fusitriton oregonensis, Glycymeris yessoensis, Chlamys swifti* and *Buccinum ochotence* live among high densities of natural and sown scallops. We have observed live *Polydora* species only in the shells of *T. janthostomoides* and *F. oregonensis.* Some worms of *P. websteri* were taken from the shells of *T. janthostomoides,* and many worms of *P. concharum* ssp. were extracted from those of *F. oregonensis. P. variegata* was never extracted from any of these species.

P. variegata and *P. websteri* settle on the ventral edge of the left valve. In contrast, *P. concharum* ssp. seems to have no tendency in settling region. However, its burrows are found in aggregates. In the case of *P. websteri* and *P. concharum,* each species was found in only a few shells into which no other species had bored. Very few worms of *P. variegata* were taken from these shells. The number of *Polydora* extracted from one shell fluctuated greatly which may be the result of patchy distribution of larvae.

The tendency of *P. variegata* to settle on the ventral edge of the left valve seems to suggest that (1) larvae are induced to settle by some chemical substance(s) contained in the newly formed periostracum, and (2) it is more advantageous to settle on this edge of the left valve for feeding. Indeed, *Polydora* worms are basically suspension feeders and the scallop always tends to face the oncoming water current.

Identification of the species in the genus *Polydora* has been somewhat confused in Japan. *P. variegata* was mistaken for *P. ciliata* until it was redescribed as a new species by IMAJIMA & SATO in 1984. The distribution of *P. variegata* has not yet been investigated. We have reported that *P. variegata* is distributed in the Okhotsk Sea, Mutsu Bay and along the Pacific coast of Tohoku district (MORI *et al.*, 1985; SATO-OKOSHI & NOMURA, 1990). Our present data indicate that *P. variegata* is distributed extensively in the northern part of Japan.

It would be advantageous to prevent the settlement of *P. variegata* on the shells of scallops during the first winter season after sowning, and it would seem better to harvest scallops after two years in Abashiri Bay. We mentioned previously that when numerous worms settle on the ventral edge of the left valve of 1-year-old sown scallops in the first winter season after sowing, the site of attachment of the adductor muscle to the left valve overlaps the region of the shell that is heavily infested with 1-year-old worms because the adductor muscle inceases in size and shifts its position toward the ventral side during growth in the following year (MORI *et al.*, 1985; SATO-OKOSHI *et al.*, 1990). Scallops that are heavily infested with *Polydora* at the site of attachment of the adductor muscle may be weakened and penetration at this site may be fatal (MORI *et al.*, 1985). Furthermore, worms become a year old before harvesting the scallops when they settle on scallop shells during the first winter season, and the 1-yr-old worms produce many offsprings.

It would be of importance to determine the length of the planktonic period and the mechanism of settling of the worm, as well as to determine why the larvae prefer to settle on the ventral edge of the left valve rather than the right valve of the scallop. Experimentation in the laboratory may help to clarify these issues.

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