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Studies on Life History and Systematics of the Japanese Commensal Hydroids Living in Bivalves, with Some Reference to Their Evolution

By

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(*With 28 Text-figures, 38 Tables, and 1 Plate*)

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Introduction

It is well known that most of the hydroid species pass through the sessile life during the polypoid generation. They grow on the surface of various kinds of living or nonliving organisms such as algae, aquatic plants, and many diverse animal groups from sponges to fishes, as well as on the surface of inorganic matters. Among the epizoic hydroids, only a few ones attach to the interior body surface of other living animals. They are divided into two groups: members of one group are dwellers in the mantle cavity of bivalves (e.g. *Eutima* and *Eugymnanthea*) and those of the other group are dwellers inside the pharyngeal chamber of tunicates (e.g. *Endocrypta*). In the present research the former group is treated with. The inside of the mantle cavity of bivalves is one of the most unique habitats where hydrozoans immigrated, and the modification of body structure in connection with such peculiar ecological niche is supposed to be biologically and phylogenetically noticeable.

As mentioned below, a relatively small number of investigations of the hydroids harbored within bivalves are available to us at present, though several decades have passed since the first record of such hydroids. In Japan, following the researches by Uchida (1925, '64), Yamada (1950, '59), and Kakinuma (1964), the author has been studying the biology of the Japanese hydroids harbored within bivalves, particularly on their life-history (Kubota 1978, '79a, b). This paper reveals not only the detailed observations on the metamorphosis from polyp to primary polyp through medusa and planula of the Japanese commensal hydroids associated with various bivalves from various localities but also biological aspects such as nematocyst equipment, host preference, commensal life of polyp within a host, distribution, local variation, etc. The taxonomy on the Japanese hydroids harbored in bivalves is reviewed, and moreover, phylogeny and evolution of the commensal hydroids hitherto recorded in the world are considered from their mode of life history.

The first record of the hydroid species harbored in a bivalve was made by Palombi in 1935, and he established a new genus *Eugymnanthea*, describing a new species *Eugy. inquilina*. The polyp of this species was living in the mantle cavity of the bivalve *Tapes decussatus* from Naples, Italy and it liberated peculiar medusa which was degenerated but sexually mature and short-lived. Since then similar or related hydroids have been sporadically found in the world. In 1941 Cerruti found *Eugy. inquilina* from *Mytilus galloprovincialis* at Taranto, Italy, though it was referred at first to a different species, *Mytilhydra polimantii*. In 1957 Crowell found the same species at Naples in not only the above-mentioned two hosts but also four other pelecypods such as *Tapes aureus*, *Cardium tuberculatum*, *C. edule*, and *Ostrea* sp., and some biological observations on this hydroid were made by him. On the other hand, Mattox and Crowell, in 1951, reported a new hydroid *Eugymnanthea ostrearum* from Boqueron, Puerto Rico, of which polyp was associated with *Crassostrea rhizophorae* and it liberated immature medusa which is clearly different from that of *Eugy. inquilina*. In 1950, Yamada who firstly reported a commensal polyp harbored in bivalves in Japan, proposed a new genus *Ostreohydra*, describing a new species, *O. japonica*, which was associated with *Crassostrea gigas* from Onomichi, southern Japan. This Japanese species was afterwards emended by Crowell (1957) and Yamada (1959) as *Eugymnanthea japonica* without clarifying its medusan generation. In 1964 Kakinuma described a new hydroid, *Eugy. cirrhifera* associated with *Mytilus edulis* from Hachinohe, northern Japan, and she reported immature medusa with cirri which was liberated from polyp. In the same year, in his review of the hydroids harbored in bivalves in the world, Uchida reported the same species from *Mytilus coruscus* at the same locality. However, the mature medusa of *Eugy. cirrhifera* has been unclarified despite of their efforts of rearing. In 1969 Santhakumari and Balakrishnan Nair described a peculiar commensal polyp associated with some wood-boring bivalves such as *Nausitora hedleyi*, *Teredo furcifera*, and *Martesia striata* from Cochin, India. The polyp liberated immature medusa with cirri, and it was assigned to the genus *Eugymnanthea*, though its specific name has remained unsettled because of lack of information of the mature medusa. Ramachandra Raju *et al.* (1974) and Kalyanasundaram (1975) reported that several specimens of *Mytilopsis sallei* from Visakhapatnam, India (an immigrant bivalve from American waters) were found to be infected with similar polyp to *Eugymnanthea* sp. from Cochin, India.

In all the above-mentioned species except for *Eugy. inquilina* their mature medusae have been unknown. Consequently the systematic position, particularly of the higher categories, of these hydroids has been unsettled and it was a matter of speculation mainly due to their unique morphology of polyp. As to *Eugy. inquilina* too it was the same case because of its peculiar polyp and mature medusa (see Picard 1958, Kramp 1961, Reisinger 1961, Uchida 1964, Rees 1967, etc.).

In 1970, among the plankton samples from Cochin where the above-mentioned peculiar polyp of *Eugy.* sp. was described, Santhakumari found various developmental stages of a certain type of medusa belonging to the genus *Eutima* (cf. Vannucci *et al.* 1970); and she concluded that the polyp and medusa are of different generations of the same species. From this time on clarification of the morphology of mature medusa and more reasonable assignment of the systematic position of these hydroids have been made. For the species from Cochin, India the assignment of a new specific name and an emendation of its generic status was made by Santhakumari in 1970, and it was designated as *Eutima commensalis.* In 1975, by Narchi and Hebling the polyp and medusa of a commensal hydroid from São Paulo, Brazil, of which polyp was associated with *Tivela mactroides,* were connected directley by laboratory rearing. This hydroid was named as *Eutima sapinhoa,* a new species in the genus *Eutima,* as was the same case in the Indian species. Recently the author studied a commensal hydroid from Oshoro, northern Japan, of which polyp is associated with *Mytilus edulis,* and the polyp and medusa were connected by laboratory rearing and also by field work. After identified this hydroid with *Eugymnanthea cirrhifera,* it was transferred to the genus *Eutima,* mainly based on the morphology of mature medusa (Kubota 1978a). This species was found also from Akkeshi, northern Japan, associated with *Clinocardium californiense,* an unrecorded bivalve as a host of the hydroid (Kubota 1979b), A very noticeable fact was the occurrence of *Eugymnanthea inquilina* at Shimoda, central Japan, associated with *Mytilus* (Kubota 1979 a). It was assigned to *Eugymnanthea inquilina japonica,* a new subspecies of *Eugy. inquilina,* based on some distinguishable characters of the medusa, particularly of male one.

Materials and Methods in General

In order to investigate the life-history and systematics as well as some other biological aspects of the hydroids harbored in Japanese bivalves, a large number of specimens of various kinds of bivalves were collected from various localities in Japan (Table 1; cf. Tables 32–34).

On most of the occasions, almost all of the bivalve specimens were examined promptly after the collection, but some were preserved in formalin solution *in situ* and were examined afterwards. As the fundamental biological investigations on the hydroids in Japanese bivalves have not yet been much made, the certain identification is difficult unless the life-history is clarified for each material. Therefore at first rearings were made for different materials as many as possible, that is for at least 50 bivalve specimens of nine species from various localities (Table 2).

The method of rearing of hydroid and that of observations are as follows. Many polypoid specimens were picked up from the host, and after rinsing them several times they were transferred into a covered small polystyrene vessel filled with clean sea water. The polyp or sometimes its youngest medusa liberated *in*

Table 1. Materials collected from various localities in Japan (cf. Tables 32, 33).

	Locality	Collecting date of bivalves	NBS[1)]	NBSP[2)]	NB[3)]	NBP[4)]
Hokkaido	Teuri Is.	3–VIII–'79	3	0	433	0
	Yagishiri Is.	3–VIII–'79	2	0	269	0
	off Ishikari	2–IV–'79	3**	0	54	0
	Tarukawa	20–VIII–'78, (20–24)–VII–'79, 22–VIII–'79	4	0	399	0
	Zenibako	23–VII–'78, 29–VII–'79, 20–VII–'80	4	1	195	1
	Oshoro	(21–VI–'77)–(11–XII–'80)	18	4	6129	765
	Utasutsu	2–VIII–'80	3	2	114	32
	Akkeshi	2–XI–'78, (6–13)–VII–'79	12	1	918	1
	Muroran	(21–22)–VI–'78, (28–29)–IV–'79	4	0	201	0
	Kuroiwa	1–VIII–'80	1	1	72	20
	Mori	1–VIII–'80	1	1	98	1
Honshû	Asamushi	(11–13)–VIII–'79	8	0	290	0
	Fukaura	(9–10)–VIII–'79	5	0	140	0
	Sasagawanagaru	31–V–'80	1*	0	117	0
	Ogi	(21–23)–VIII–'80	1*	0	79	0
	Oozakai	9–VIII–'80	1*	0	114	0
	Miyazu	19–IV–'80	1*	0	82	0
	Amanohashidate	19–IV–'80	1*	0	52	0
	Amino	19–IV–'80	1*	0	20	0
	Kumihama	8–I–'79	1*	0	65	0
	Yokosuka	25–III–'80	1	0	147	0
	Kannonzaki	27–III–'80	1	0	56	0
	Jôgashima Is.	25–III–'80	1	0	245	0
	Enoshima Is.	26–III–'80	1	1	153	27
	Shirahama	(18–23)–I–'81	5	0	277	0
	Ushimado	18–II–'80	1*	0	183	0
	Mukaishima Is.	9–V–'79, (30–III)–(1–IV)–'80	7	3	999	15
Shikoku	Usa	(12–16)–V–'79	6	4	991	6
	around Mitsuhama	27–XII–'78, 9–I–'79, 10–V–'79, (10–12)–IV–'80	3**	1	88	2
	Mitsuhama	11–I–'79, 18–V–'79, 10–IV–'80	6	2	589	29
	Nuwajima Is.	11–I–'79	1	1	166	2
	Total		36	12	13735	901

1) NBS: number of bivalve species examined (when NBS is 1, the bivalve is *Mytilus edulis* except Sasagawanagaru and Amino where the bivalve is *Septifer virgatus*).
2) NBSP: number of bivalve species associated with polyp. 3) NB: number of bivalves examined.
4) NBP: number of bivalves associated with polyp. *,**: All bivalves were collected by fishermen (**) or some members of our laboratory (*).

Table 2. Materials reared and their rearing conditions, and sex appeared.

Locality	Collecting date	Host bivalve	NH[1]	Host size (cm)[2]	PM[3]	WT (°C)[4]	RP[5]	Sex
Oshoro	21–VI–'77, 16–VII–'77	*Mytilus edulis*	16[6]	4.5-5.6(APA)	+	18-25	40	♂♀
	23–IV–'80, 21–V–'80	*Mytilus edulis*	14	4.4-6.0(APA)	−	20	90	♂♀
	24–VIII–'79	*Septifer virgatus*	1	3.7(APA)	+	20	30	♂?
	6–VII–'80	*Crenomytilus grayanus*	5	5.7-13.4(APA)	+	15-25	125	♂♀
	5–X–'80	*Chlamys swifti*	1	7.6(SH)	+	20	35	♂
Zenibako	29–VII–'79	*Peronidia venulosa*	1	7.6(SL)	+	20	60	♂
Utasutsu	2–VIII–'80	*Mytilus coruscus*	1	3.7(APA)	+	20	60	♂
Kuroiwa	1–VIII–'80	*Mytilus edulis*	5	2.9-5.7(APA)	+	20	30	♂♀
Mori	1–VIII–'80	*Mytilus edulis*	1	4.6(APA)	+	20	60	♀
Akkeshi	2–XI–'78	*Clinocardium californiense*	1[7]	5.8(SL)	−	20	30	♀
Usa	16–V–'79	*Mytilus edulis*	1	5.5(APA)	+	20	100	♀
Mitsuhama	27–XII–'78	*Paphia schnelliana*	1	7.2(SL)	+	12-20	15	?
Mukaishima Is.	9–V–'79	*Mytilus edulis*	1	4.2(APA)	+	20	90	♀
	31–III–'80	*Crassostrea gigas*	1	4.0(SH)	+	15-24	90	♂

1) NH: number of hosts from which polyps were picked up and reared.
2) APA: anterior-posterior axis, SH: shell height, SL: shell length.
3) PM: presence (+) or absence (−) of medusa-bud when the host was collected.
4) WT: water temperature of rearing.
5) RP: approximate rearing period of medusa, in days.
6) Kubota 1978a.
7) Kubota 1979b.

situ at the localities in southern Japan was carried back to the laboratory in Sapporo, keeping them cool in an icebox, as soon as possible after collection. And as a general rule, the specimens were reared in the filtered sea water supplied from Oshoro near Sapporo and kept at about 20°C in an incubator, fed with newly hatched *Artemia* nauplii. Under this rearing condition, the polyps began to liberate their medusae within a few weeks. The medusa was kept in the same manner as for polyp, while each medusa was kept separately in one rearing container. The food was given to each specimen sufficiently, nearly once a day. Even the newly

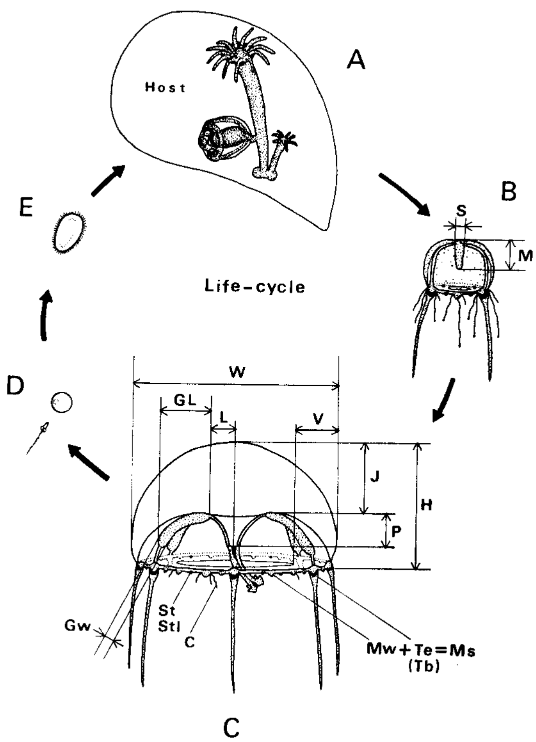

Fig. 1. A schematic illustration of the life-history of the present eutimid hydroid. A: a polyp with a daughter polyp and a medusa-bud within a host bivalve, B: a newly liberated medusa, C: a mature medusa, D: an egg and a spermatozoon, E: a planula larva. Abbreviations used for measurements of various body portions of medusa examined are as follows. C: total number of cirri, GL: length of gonad, GW: maximum width of gonad, H: umbrellar height, J: thickness of jelly at the umbrellar apex, L: length from center of stomach to proximal portion of gonad, M: length of manubrium, Ms: total number of marginal swellings (number of tentacular bulbs (Tb) plus that of marginal warts (Mw)), P: length of peduncle, S: breadth of stomach, St: number of statocysts, Stl: number of statoliths, Te: number of tentacles (=Tb), V: breadth of velum, W: umbrellar width (GL, GW, L, S, V, W: measured in aboral view; H, J, M, P: in side view).

liberated medusae could catch and swallow *Artemia* nauplii easily by themselves. The sea water and the rearing container were exchanged nearly every day after the specimen was satiated with the food.

Fig. 1 shows the schematic illustration of the life-history of a bivalve-inhabiting hydroid belonging to the genus *Eutima* and indicates various body portions examined and measured. The abbreviations in the figure are used in the following figures and tables of this paper. With the aid of an ocular micrometer set in binocular microscope, various body portions of the polyp and medusa were measured on the living specimens in starved and well-extended conditions, often dropping a small quantity of 8% $MgCl_2$ solution for narcotization. After the measurements, the medusa was transferred onto a deep-hole slide glass and further detailed examinations were made on the characters such as C, Mw, St, Stl, and Te (=Tb). And the drawings of the specimens such as Figs. 2–5, 19, 22–24 were made with the aid of a drawing apparatus. The photographs (Plate X) and the above drawings except Fig. 2, B-D, F-H; Figs. 3, 5; Fig. 4, A-G; Fig. 23, H were made from living specimens.

The detailed explanations for the methods for the study of the biological aspects on the hydroids in bivalves, i.e. the commensal life made within the mantle cavity of a bivalve, the morphological variation of medusa in different rearing conditions, host preference, gametes, larva, and primary polyp, and on the nematocyst equipment are given in each part of the following text.

I. Polypoid Generation

A. Morphology of Polyp

The morphology of polyp was examined in living specimens as a rule. Besides many living specimens picked up from various hosts collected from various localities, the examination was extended to a great many preserved specimens from various localities, for example ca. 80000 ones from Oshoro, in order to reveal the morphological variation as much as possible.

1. General external morphology

Among the specimens found within many bivalve species from northern to southern Japan no distinct morphological difference was found (Table 3).

The polyp (Fig. 2; Plate X, C) is solitary and no creeping stolon is present. Instead of the stolon the base of the polyp forms a flattened pedal disk, with which the polyp attaches to the soft body surface of the host. The pedal disk is usually oval in shape (Fig. 2, A, B, H, etc.), though a concave or protruded portion was present in some specimens (Fig. 2, F, G). The hydranth, which is indistinguishable from the hydrocaulus, is provided with a conical hypostome surrounded by a single verticil of filiform tentacles with a membraneous web at each base between neighboring tentacles (Fig. 2, A; Plate X, D). The hydranth and hydrocaulus are slender

Table 3. Morphology of polyp associated with various bivalves from northern and southern Japan.

Locality and Host bivalve	No. of hosts examined	No. of specimens examined	Body length (mm)	Body width (mm)	No. of tentacles	Presence of medusa-bud
Oshoro						
*Mytilus edulis*1)	4	16	0.96-2.7	0.14-0.20	18-30	+
Crenomytilus grayanus	5	many	up to 7.8	0.15-0.20	up to 31	+
Septifer virgatus	1	4	1.0-1.8	up to 0.15	14-16	±
Akkeshi						
*Clinocardium californiense*2)	1	many	up to 4.4	up to 0.19	17-28	+
Hachinohe						
*Mytilus edulis*3)	several	many	0.50-5.0	0.20-0.30	18-28	±
Usa						
Mytilus edulis	1	9	0.63-2.3	0.08-0.20	14-26	+
Septifer virgatus	1	5	0.60-1.2	—	—	—
Crassostrea gigas	1	many	up to 0.69	up to 0.09	up to 14	—
Coecella chinensis	1	8	0.25-0.69	0.04-0.06	8-15	—
Mitsuhama						
Paphia schnelliana	1	12	1.1-1.8	0.16-0.22	up to 30	±
Mukaishima Is.						
*Crassostrea gigas*4)	several	many	1.4-2.6	0.4	15-20	±
Crassostrea gigas	1	many	up to 5.0	0.2	22	+
Mytilus edulis	1	21	0.86-2.8	0.09-0.14	19-26	±
Total 7 species			up to 7.8	up to 0.4	up to 31	

1) Kubota 1978a. 2) Kubota 1979b. 3) Kakinuma 1964.
4) Yamada 1950, in preserved specimens.

and gradually taper toward the pedal disk, and the body is very contractile (Fig. 2, A-C). No secretion of periderm is found on the entire body surface. The polyp is usually 0.5–3.0 mm in length and 0.1–0.3 mm in greatest width when it is well-extended, and 15–30 tentacles are usually present. It was observed that the largest polyp attained 7.8 mm in length and a very tiny polyp (Fig. 2, D) was 70 μm in length, and that when the polyp attached to the host it was often much more extended than after the polyp was picked up from the host.

The color of polyp is variable, showing yellow, orange or red, pale green, etc. This variation may be due to the kinds of food ingested. It was observed that the polyp sometimes swallow such a relatively large food as copepods, ostracods, etc.

Although the fundamental structure of the polyp is stable, there is a conspicuous morphological variation of the polyp in connection with the age of polyp, the environmental condition, and some other factors. A polyp with a daughter polyp and/or a medusa-bud, a degenerating polyp, and an aberrant polyp were often found and they are treated below.

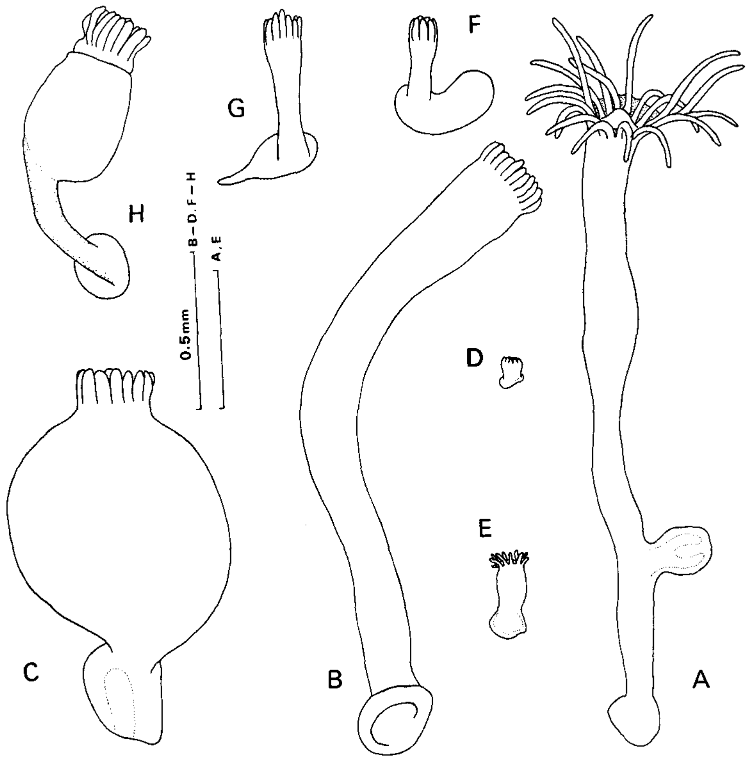

Fig. 2. Morphology of polyp from Oshoro, host: *Mytilus edulis* (A, E: in living state, from Kubota 1978a; B-D, F-H: in preserved state). A-C: an ordinary polyp (A,B: in well-extended state; C: in contracted state), D: a tiny polyp, E: a regenerated polyp after liberation of medusa, F, G: a polyp with an unusual pedal disk, H: a polyp in which the lower part of hydrocaulus is very lean and the hydranth is constricted.

2. Asexual reproduction of polyp

a. Formation of daughter polyp

It was often encountered among the specimens collected directly from bivalves that a larger and a smaller polyps are jointed with a common pedal disk (Fig. 3, E-I), and as a rare case three polyps are jointed (Fig. 3, O-Q). A series of this kind of form showing the asexual formation of a daughter polyp(s) were also found in the specimens reared in laboratory and this process was observed and ascertained each time. A daughter polyp is produced on the pedal disk of mother polyp in principle; and at one time one daughter polyp is usually formed, while several daughter polyps are sometimes produced. As a rare case five daughter polyps were budded one after another in one specimen from Akkeshi, and they attached to the mother polyp

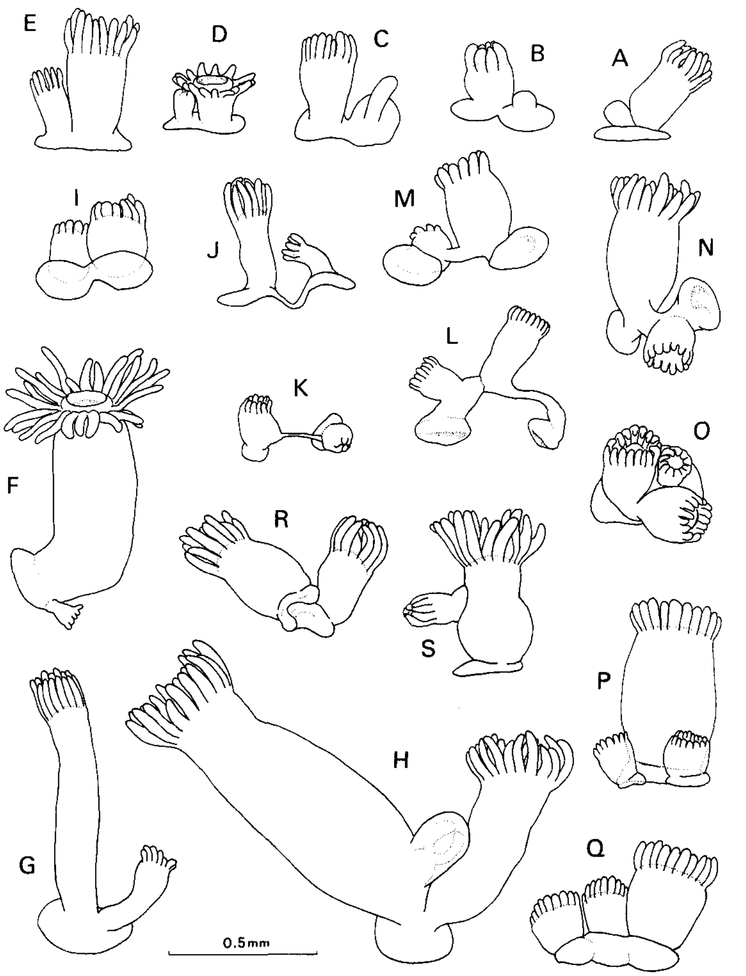

Fig. 3. Asexual formation of daughter polyp (preserved specimens from Oshoro, host: *Mytilus edulis*). A-D: a mother polyp with an undeveloped daughter polyp, E-I: a mother polyp with a daughter polyp, J: a mother polyp with a daughter polyp, both connected with a fine extension of pedal disk, K-N: a daughter polyp produced on lower part of hydrocaulus of mother polyp, O-Q: a mother polyp with two daughter polyps, R, S: a daughter polyp attaching to the body of mother polyp.

for a short time (see Kubota 1979b). Very rarely the formation of daughter polyp took place on the lower part of hydrocaulus (Fig. 3, K-N). It is noticeable that even if a polyp is very small (e.g. 140 μm in length in the preserved state) it had an ability to bud a daughter polyp (Fig. 3, A-D). It was observed that the daughter polyp was not produced for several months at about 6°C in laboratory even in a larger polyp. The daughter polyp produced in laboratory was usually 0.3–1.2 mm in length and had 10–18 tentacles.

In laboratory the polyp sometimes moved on the bottom of the polystyrene container, only a short distance (several mm) in one day. And the separation of a daughter polyp from the mother polyp depends on this locomotion of polyp and/or the division of the pedal disk (cf. Fig. 3, I, J). It was sometimes observed that a daughter polyp attached to the body of the mother polyp after the separation (cf. Fig. 3, R, S).

b. Formation of medusa-bud

Another often encountered form is a polyp with a medusa-bud. The medusa-bud is found usually on the lower part of hydrocaulus near the pedal disk (Fig. 4), but some larger polyps bore their medusa-buds nearly on the middle of hydrocaulus. A series of this kind of form showing the asexual formation of a medusa-bud were found (Fig. 4, A-E). It is noticeable that only larger polyp bore the medusa-bud, differing in the case of the budding of the daughter polyp. In laboratory the medusa-bud was always produced on the hydrocaulus not on the pedal disk when a specimen was reared at the water temperature of above 15°C, and usually one bud was produced in one polyp at one time. The bud develops from a small protrusion with a short stalk to a free-swimming medusa within one or two weeks at 15–25°C in laboratory. And the higher the temperature is, the shorter the time to liberation is. Although it was not so often encountered in laboratory, a polyp bearing two or three medusa-buds of different growths was found at the same time (Plate X, C). Such a polyp was often found when the specimens were kept in higher temperature (ca. 20–25°C) in laboratory. In not only laboratory but also in the sea this kind of formation of two or more medusa-buds by a polyp took place but the frequency was somewhat different according to the locality. Namely it was rarely found among the specimens from northern Japan (Fig. 4, F), while often found among those from central and southern Japan (Fgi. 4, G). It was noticed that a polyp from Mukaishima Island (host: *Mytilus edulis*) was reared for about a month, without any extreme change of its morphology. The polyp was 3.8 mm in length and had 27 tentacles, and the position of medusa-bud on the hydrocaulus (length from the medusa-bud to the lower end of hydrocaulus/length of polyp) is 0.15–0.28. In this specimen two medusa-buds were produced at one time (Plate X, C), and before degeneration of polyp five medusae were liberated. Among these four* medusae of same origin a wide morphological variation is found as follows: W=0.97–1.6 mm; H=0.75–1.0 mm; Te=0–4; Tb+Mw=7–8; St=6–8; Stl=7–24, the number of lateral cirri=11–31; the number of abaxial cirri=0–4; and the total number of cirri=11–35 (cf. II. A.).

A remarkable reduction of hydranth and most parts of the hydrocaulus often

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* Measurements were not taken in one specimen.

occurred as the medusa-bud developed, in both the specimens reared in laboratory and those collected from the sea. In a well-developed medusa-bud shortly before liberation, which is usually 0.6–1.0 mm in diameter, the tentacular bulbs with black

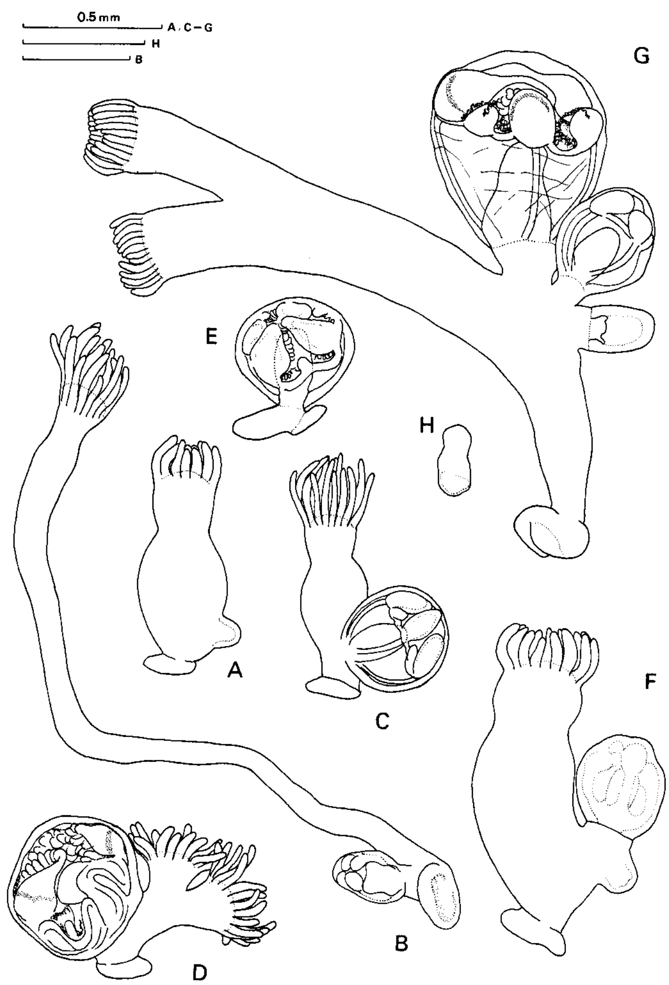

Fig. 4. Asexual formation of medusa-bud (A-F: preserved specimens from Oshoro, G: a preserved specimen from Mitsuhama, H: a living specimen from Oshoro; host: *Mytilus edulis*). A: a polyp with a tiny medusa-bud, B: a markedly long polyp with a medusa-bud developed on hydrocaulus just above pedal disk, C: a polyp with a well-developed medusa-bud, D: a double-headed polyp with a fully developed medusa-bud, E: a fully developed medusa-bud with a remnant of polyp, F: a polyp with two medusa-buds of different growths, G: a double-headed polyp with three medusa-buds of different growths, H: a remnant of polyp remained after the liberation of medusa.

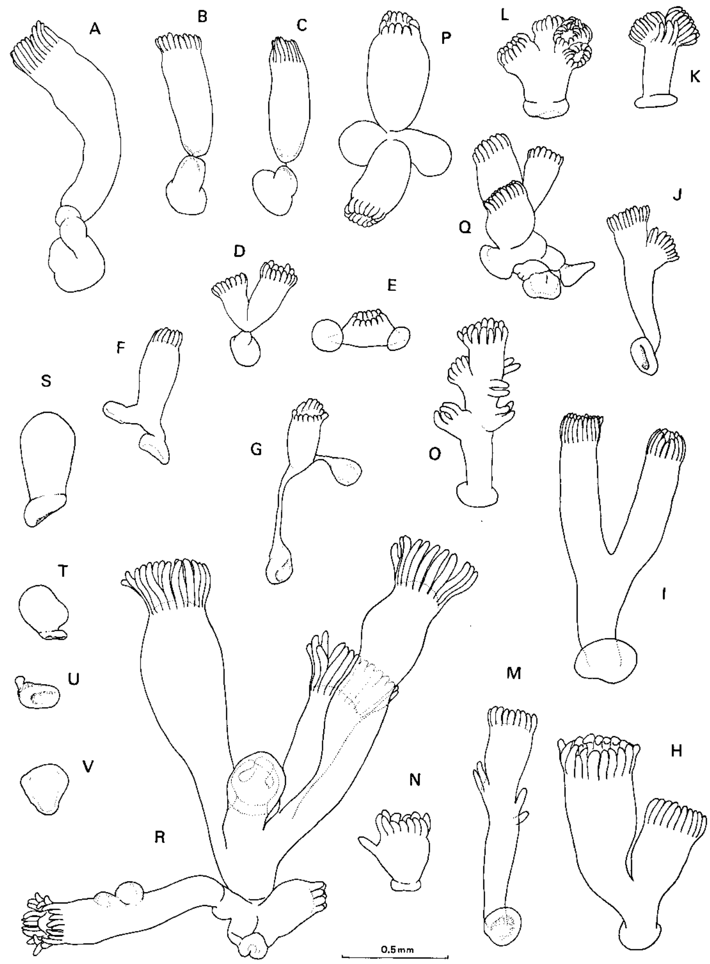

Fig. 5. Morphology of aberrant polyps, host: *Mytilus edulis* (A-Q: preserved specimens from Oshoro, R: a preserved specimen from Kuroiwa). A-D: a ployp of which lower part of hydrocaulus is constricted (C: upper and lower parts are connected with a filament-like extension), E-G: a polyp with two pedal disks (G: with a fine thread-like extension between the body and a pedal disk), H-J: a double-headed polyp, K-O: a branched polyp with several hydranths and/or some tentacle-like protuberances (K: a double-headed polyp with three protuberances, L: a branched polyp with five hydranths, M: a polyp with four protuberances, N: a polyp with one protuberance, O: a branched polyp with four hydranths and five protuberances), P-R: a branched polyp consisting of several hydranths and several pedal disks (P: two polyps with two pedal disks, Q: three hydranths with three pedal disks, R: a markedly branched polyp with five hydranths, some pedal disks, and one medusa-bud, moreover a bump attached to one zooid, S-V: a degenerating or regeneraing ployp (S, T: hydranth absent, U: only a very small body present, V: no hydrocaulus). A-U: side view, V: top view.

band, statocysts, and exumbrellar nematocysts are found. The medusa-bud is covered with a thin and membraneous envelope throughout its development. And it becomes free after tearing of the envelope and the contraction toward the apex of the umbrella. A reduced body of polyp (Fig. 4, H; cf. Fig. 5, S-V) often remains on the apex of the newly liberated medusa or on the bottom of the rearing container. It is very small and usually 0.2–0.5 mm in length. Some of these polyp remnants were transformed into tiny polyps within several days after the liberation of their medusae either directly on the apex of the umbrella of the youngest medusa or on the bottom of the rearing container. And the regenerated polyp (Fig. 2, E) was usually 0.3–0.6 mm in length and 0.1–0.2 mm in greatest width, and had 8–12 tentacles.

On the other hand, the polyp sometimes produced both a daughter polyp and a medusa-bud at the same time, and the polyp of this type was also found among the specimens collected in bivalves from the sea (Fig. 3, H).

3. Morphology of aberrant polyp

The following aberrant polyps showing a greater to lesser degree of 'abnormality' were found: (1) a polyp of which lower part of hydrocaulus is constricted (Fig. 5, A-D); (2) a polyp with two pedal disks (Fig. 5, E-G); (3) a branched polyp with two to several hydranths and/or many tentacular protuberances on hydrocaulus (Fig. 5, H-O); (4) a remarkably irregular form with some hydranths and some pedal disks (Fig. 5, P-R).

The reason why these polyps appear is uncertain. It was observed, for example, that in one polyp reared in laboratory a hydranth divided into two ones and the polyp became a double-headed one (cf. Fig. 4, D, G). In this specimen further division of the body did not proceed, never assuming the polyp shown in Fig. 5, I. No longitudinal fission was observed even if several double-headed polyps including the above one were reared in laboratory. Although the number of the double-headed polyp was very small in one host, it was most frequently found among the above-described aberrant polyps; it was found at Oshoro all the year round (in every month), in nearly half the specimens of *Mytilus edulis* examined (73 hosts out of 135 ones). And it was frequently found also in other localities than Oshoro.

B. Commensal Life of Polyp in the Mantle Cavity of *Mytilus edulis* at Oshoro, Northern Japan

1. Materials and Method

In the intertidal region of Oshoro Bay and its neighboring coasts a wave cut bench is developed well, and in this habitat two bivalves, *Mytilus edulis* and *Septifer* (*Mytilisepta*) *virgatus*, are found as dominant species.

In order to reveal the commensal life of the polyp as a sessile generation in the life-history of the present hydroid harbored in bivalves, the following investigation

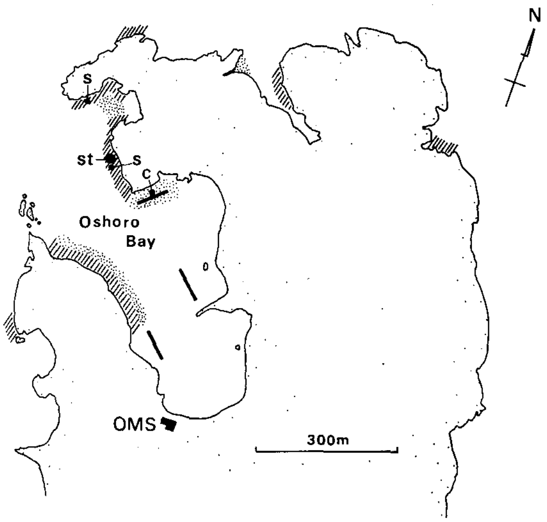

Fig. 6. A map of Oshoro Bay and its neighboring coasts, showing the sampling station (St) of commensal polyp within *Mytilus edulis* and the distribution of four bivalve species associated with polyp. Obliquely lined: *Mytilus edulis* on wave cut bench, Thick line: *Mytilus edulis* on buoy or rope, Dotted: *Crenomytilus grayanus* on subtidal rock wall, S: *Septifer virgatus* on wave cut bench, C: *Chlamys swifti* on subtidal rock. OMS: Oshoro Marine Biological Station.

was carried out at Oshoro, Hokkaido, northern Japan. A large mussel bed on the intertidal wave cut bench in the bay was selected for a station of sampling of material (Fig. 6, St). From a quadrat, 15×15 cm, set in the station all the mussels of different growths were collected once in a month during a year from August, 1977 to July, 1978. All the materials collected were immediately preserved by formalin solution then and there. Each bivalve was examined afterwards under a binocular microscope in laboratory.

It should be mentioned here that selection and collection of *Mytilus edulis* as a host bivalve of the commensal polyp were made in the present investigation for the following reasons: (1) the polyp was frequently associated with *M. edulis* in this locality as well as other localities in Japan (see Table 1, cf. VI); (2) collection of the host is possible even in the severe winter season; (3) size of the host is appropriate for the detailed examination, etc.

In order to supplement the above-mentioned quantitative sampling, a large number of specimens of *Mytilus edulis* were arbitrarily collected from various stations on the wave cut bench of Oshoro inside the bay as well as outside the bay from June, 1977 to December, 1980 (Fig. 6). Besides the above-mentioned specimens collected from the intertidal region, the following other specimens of

M. edulis were collected and examined: (1) specimens attached to the fishermens' buoys and ropes which were just below the sea surface and constantly submerged in the sea water; (2) specimens attached to the wave cut bench constantly submerged in the sea water; (3) specimens found in the subtidal region attaching to the rock wall at the depth of several meters.

In this connection it may be added that range of tides in this locality is only several tens centimeters, and the intertidal wave cut bench has been often dried up for a relatively long time in winter, which is a well-known phenomenon especially on the coasts facing Sea of Japan in our country. Accordingly the organisms living on the wave cut bench are exposed to danger of their life in severe winter.

2. Observations and discussion

a. Association rate of polyp with the host and the number of polyp per host

In all 2363 specimens of *Mytilus edulis* were collected from the intertidal wave cut bench, and they were within 6.9 cm in size* and most of them (82%) were 2.5–4.9 cm in size. At every station surveyed both outside and inside Oshoro Bay the polyp was always found (see Fig. 6), and no distinct difference of the association rate was found among the hosts from various stations despite of the difference of the microhabitat; and the association rate was 27.6% in these 2363 mussels (see Table 4, left half). Of these many hosts examined the commensal polyp was found in the specimens of the size above 1.5 cm, and the association rate was very high in the specimens of the size above 4.5 cm among them. And the larger the host was, the higher the association rate was (Table 4, left half).

On the other hand, in 135 polyp-associated mussels out of 825 ones collected quantitatively for a year at the sampling station (Fig. 6, St) the number of polyp per host varied considerably from 11 to 2043 (mean 587, SD 497) (Table 5, left half; Fig. 7), while in more than half the number of these hosts 201 to 1000 polyps were found in one host (Table 5, right half). By the way, in a square of 225 cm^2 (15×15 cm^2) 29–89 mussels (mean 69, SD 16.4) were present and 9.6–41.4% of them (mean 17.5%, SD 8.7) harbored the commensal polyp. And the total number of polyps in the square (see Fig. 8) varied 1425–16866 (mean 6598, SD 4267).

A certain tendency was found between the host size and the number of polyp per host (Table 5; Fig. 7). The commensal polyps were very few in number in every smaller host of the size below 3.0 cm, and the number of polyp per host was less than 180. To larger hosts of the size 3.0–4.7 cm numerous polyps often attached, namely in most of them (80%) the number of polyp was over 200. And in these hosts more than 1000 polyps were found in 22% of them. However, in the largest hosts of the size above 4.8 cm the number of polyp suddenly decreased

* Host size is always indicated by the maximum anterior-posterior axis of the shell in this paper.

Table 4. Relationship between the association rate of polyp and the host size in both the hosts collected in the intertidal zone and those in the habitat constantly submerged in the sea water.
Host: *Mytilus edulis.*

Host size (cm)	No. of mussels examined (no. with polyps) found on the intertidal wave cut bench			Association rate (%)	Ditto found in submerged place, collected arbitrarily during Nov. '78 – Oct. '80	Association rate (%)
	collected quantitatively during Aug. '77 – July '78	collected arbitrarily during June '77 – Dec. '80	Total			
0.1-0.4	8 (0)		8 (0)	0		
0.5-0.9	14 (0)	5 (0)	19 (0)	0	1 (0)	0
1.0-1.4	18 (0)	12 (0)	30 (0)	0	6 (0)	0
1.5-1.9	30 (1)	32 (1)	62 (2)	3.2	49 (0)	0
2.0-2.4	37 (2)	82 (12)	119 (14)	11.8	93 (1)	1.1
2.5-2.9	53 (2)	206 (38)	259 (40)	15.4	121 (0)	0
3.0-3.4	137 (17)	302 (79)	439 (96)	21.9	29 (0)	0
3.5-3.9	259 (44)	277 (77)	536 (121)	22.6	7 (0)	0
4.0-4.4	197 (46)	262 (109)	459 (155)	33.8	18 (0)	0
4.5-4.9	59 (16)	185 (98)	244 (114)	46.7	16 (2)	12.5
5.0-5.4	12 (6)	105 (62)	117 (68)	58.1	26 (10)	38.5
5.5-5.9	1 (1)	52 (32)	53 (33)	62.3	14 (6)	42.9
6.0-6.4		15 (7)	15 (7)	46.7	14 (9)	64.3
6.5-6.9		3 (2)	3 (2)	66.7	9 (3)	33.3
7.0-7.4					3 (3)	100
7.5-7.9					3 (1)	33.3
8.0-8.4					1 (1)	100
Total	825 (135)	1538 (517)	2363 (652)	27.6	410 (36)	8.8

Table 5. Relationship between the host size and the number of polyp per host (*Mytilus edulis*). Host size is classified into three groups according to Fig. 7.

Host size (cm)	No. of hosts examined	No. of polyp per host: range (mean), SD	No. (percentage) of hosts associating polyps of which number are:			
			<200	201–1000	1001–2000	2000<
1.6-2.9	5	18- 173(106), 58	5(100)			
3.0-4.7	115	11-2043(643), 507	23(20.0)	67(58.3)	23(20.0)	2(1.7)
4.8-5.6	15	54-1052(315), 293	8(53.3)	6(40.0)	1(6.7)	
1.6-5.6	135	11-2043(587), 497	36(26.7)	73(54.1)	24(17.8)	2(1.5)

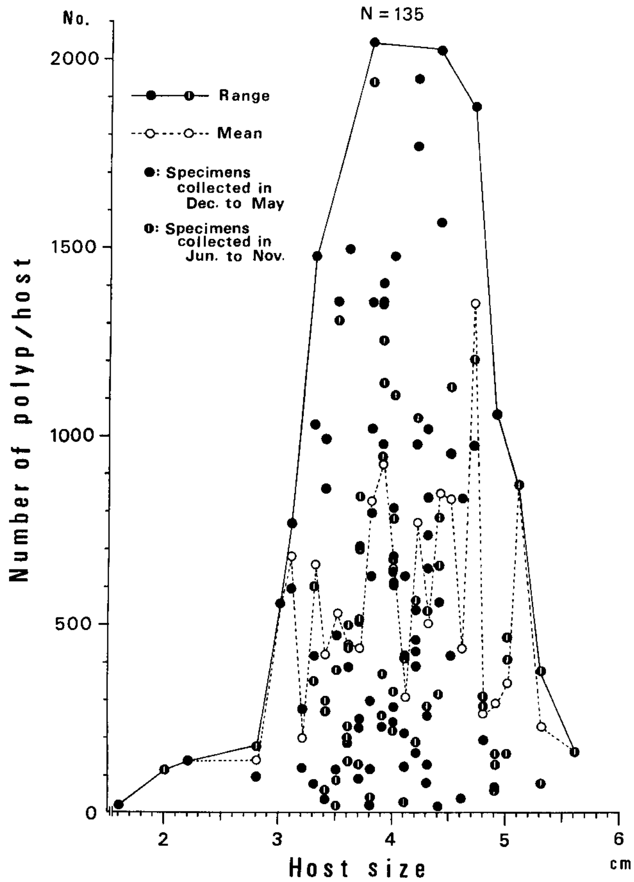

Fig. 7. Relationship between the host size and the number of polyp per host (*Mytilus edulis*). Host specimens are divided into two groups according to the season or activity of budding of polyp (see I. B. 2. b). Note the same relationship between these host groups.

and less than 500 polyps were present in most of them (87%). It is noteworthy that against the very frequent association of polyp with these very large hosts the number of polyp in each host was rather few.

The number of polyp per host varied according to the season, and the number tended to be small in all the hosts in June and July (Fig. 8). The reason why this phenomenon appeared is inferred later.

On the other side, the polyp was also associated with the hosts collected from the constantly submerged habitat in the sea water (410 in number), which grew larger than the above-mentioned ones collected in the intertidal region. Although, the association rate of polyp with these hosts was not high (only 8.8%), the same manner of association of polyp was found (see Table 4, right half): (1) the larger the host was, the higher the association rate of polyp was and no polyps were found in the hosts of the smaller size below 4.5 cm except one specimen; (2) the number of polyp tended to be fewer in larger and aged hosts. The difference of size in the non-polyp-associated hosts between the intertidally inhabited ones mentioned above and the ones in the subtidal habitat probably due to the difference of their growth in the different environment*. It was observed that the shell of the hosts attached to the ropes or buoys was thin and weak.

From the facts described above it can be concluded that the association of polyp is closely connected with the life-history of host: no settlement of the commensal polyp to the young host, a frequent and prosperous association with the host which is in the prime of life, and with senility of the host the colonization of polyp becomes declining.

b. Life-cycle of polyp

The life-cycle of the commensal polyp within the mantle cavity of the host, particularly the period of the asexual reproduction of a daughter polyp and/or medusa-bud, was analyzed mainly using the materials collected quantitatively during a year. The commensal polyp was always associated with the host all the year round (Fig. 8), showing nearly the same association rate in most of the months except for August when the rate was high.

In the hosts associated with polyp asexual budding of a daughter polyp took place all the year round (Fig. 9, Rp). Activity of the budding (percentage of hosts with the daughter polyp-bearing polyp) decreased gradually from December to April in connection with the coming of winter and with the increase of its severity such as a great deal of snowfall, very low temperature, rough weather by a seasonal wind, and frequent and long-term exposure of a wave cut bench in the air, etc. But when the climate was improved in May, the polyp began to show more frequent budding again. And in the next month, in June, the budding occurred in every

*As described in VI. B., the specimens inhabiting the subtidal region grew up to giant ones, with which very frequent association of polyp was found despite of the very rare occurrence.

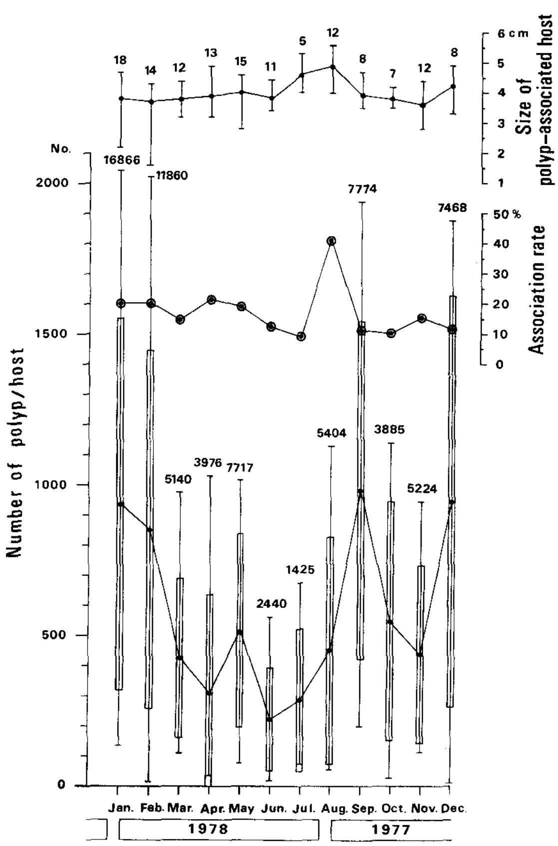

Fig. 8. Successive change of the number of polyp per host in a year (bottom), association rate (middle), and the host size associated with the polyp (top). The vertical line is the range, the circle is the mean, and the vertical bar represents SD. The number above the range of host size is the number of host specimens examined, and that above the range of number of polyp per host is the total number of polyp in a quadrat of $15 \times 15\ cm^2$.

host associated with polyp. Then the budding was performed very actively until December, though in July it decreased a little.

The formation of a medusa-bud began in June and it occurred in every host associated with polyp in July and August; and then it continued until November, while the rate decreased month after month. In all the hosts associated with polyp no medusa-bud formation, however, took place during the period from December to May (Fig. 9, Rm). Therefore it is apparent that the medusa-bud was formed in the warm or hot season. The above-mentioned period of the medusa-bud formation (June to November), on the other hand, was precisely in accord with the seasonal appearance of the planktonic medusae in Oshoro Bay (see II. C), and especially the peak of medusa-bud formation in July and August precisely coincided with that of the appearance of the youngest medusae in the sea.

It is noticeable that even when the medusa-bud formation actively took place the daughter polyp formation occurred actively at the same time; namely during the period from June to November, particularly in July and August, both buddings were performed simultaneously (cf. Fig. 10). Moreover in this period both buds were sometimes (the rate was below 40%) produced in one polyp at the same time (Fig. 9, Rpm).

On the other hand, among the polyps found in one host the polyps bearing a daughter polyp and/or a medusa-bud were very few in number in almost all of the hosts all the year round; and the active time of asexual budding was not clearly appreciated from the viewpoint of the rate of polyp with the bud to the total number of polyp in one host (Fig. 10) in contrast with that of host shown in Fig. 9. During the period from January to May only a very few polyps bore daughter

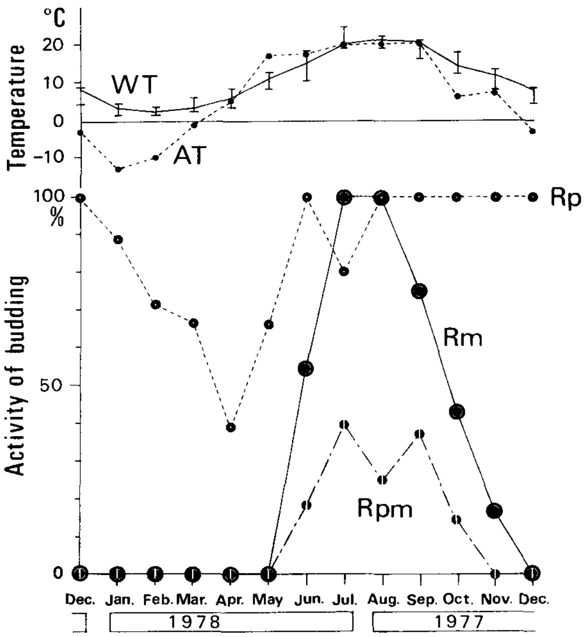

Fig. 9. The time and activity of asexual reproduction of a daughter polyp (Rp) and/or a medusa-bud (Rm) viewed from the monthly change of the rate of host specimens with the bud-formation polyp to the total bivalve specimens associated with polyp, showing together with the monthly change of the water temperature (WT, the vertical line shows the range of temperature in a month) and the air temperature (AT) of the collected day.

polyps and the rate was below 5% (below 1% on the average) and no medusa-bud formation took place, therefore the polyp is very inactive in this cold and severe season. But in the period from June to December the asexual budding of a daughter polyp and/or a medusa-bud frequently occurred, accordingly the polyp is active in the warm, mild, and even in cool seasons. The rate of daughter polyp formation was high in August and October, but was below 20% in almost all of the hosts. However, in one host collected in October in which the number of polyp per host was very small (27), the rate of budding of a daughter polyp was very high and it was more than 50%. Such kind of phenomenon is analyzed later. On the other side, the rate of budding of the medusa-bud was also not high and usually below 10%. And even in July and August when the production of a medusa-bud occurred most actively as described above, it was not high and below 12% from the present viewpoint (Fig. 10), but in some hosts collected in June and October when the budding was not so active the rate was higher (above 15%). It was observed that the rate of simultaneous formation of both medusa-bud and daughter polyp in one polyp was very low and usually below 1%.

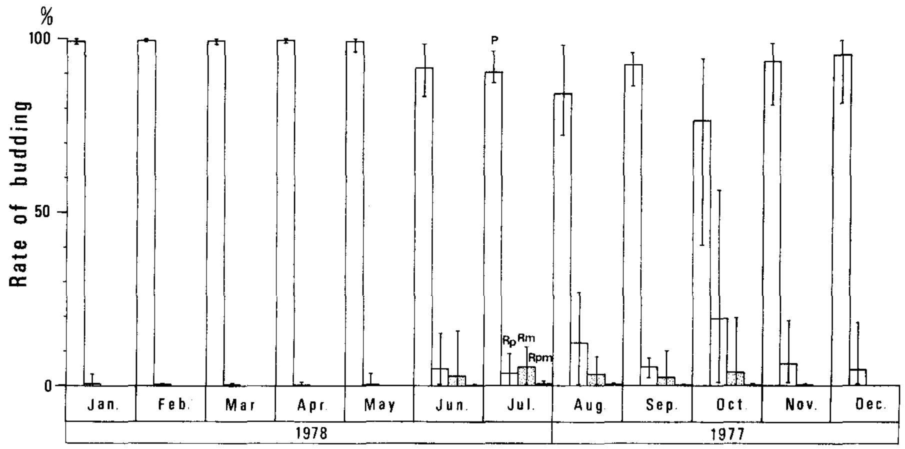

Fig. 10. The time and activity of asexual reproduction of daughter polyp and/or a medusa-bud viewed from the monthly change of the rate of polyp specimens with the bud to the total number of polyp specimens per host. In each month the rates are shown in the following order: the rate of polyp without buds (P), that with a daughter polyp (Rp), that with a medusa-bud (Rm), that with a daughter polyp and a medusa-bud (Rpm). The vertical bars represent mean values and the vertical lines the ranges.

From the two viewpoints of the time of asexual reproduction mentioned above it can be concluded that at Oshoro the life-cycle of polyp within the mantle cavity of the host (*Mytilus edulis*) in a year is grossly divided into the following four stages: (1) the inactive stage in winter from January to April; (2) the activity-beginning stage in spring from May to June; (3) the active medusa-liberation stage in summer from July to August; and (4) the daughter polyp production stage in summer and autumn from July to December. It may be worth mentioning here that the present hydroid seems to hold the elements of the groups living in the temperate regions judging from the above-summarized life-cycle. This is supported from the fact that all the hydroids harbored in bivalves are reported from the tropical or temperate regions (cf. Introduction). The present species is, therefore, the northernmost inhabitant and has an ability to tolerate against the very low temperature in winter.

The reason why the rate of asexual formation of a daughter polyp and/or medusa-bud is very low from the viewpoint of the number of polyp may be due to: (1) separation of the daughter polyp from the mother polyp as well as the liberation of a medusa takes place for a short time; (2) the budding ability is different in proportion to the age of polyp, etc. In order to ascertain the second reason for the low rate of budding, the following analysis was made. Selecting 43 specimens of *Mytilus edulis* which were collected quantitatively during the period from June to October, the relationship between the number of polyp per host and the rate of formation of daughter polyp or that of medusa-bud was analyzed. The result is shown in Table 6 in which the degree of the number of polyp per host is classified into four ranks with reference to the Fig. 7. As a result, the less the number of polyp per host was, the more frequently the formation of daughter polyp took place while the less frequently the formation of medusa-bud occurred. If the production of a daughter polyp took place similarly in every mother polyp the above-mentioned result would never happened and rather a reversal result must have taken place. It could be generally conceivable that the more the number of polyp in one host is, the older the age of polyp is. It is very likely that among 29 hosts with which a small number of polyps associated (below 500 in number) some hosts give harbor to the colonies of the newly settled generation (cf. next section) and some others do the regenerating colonies after liberation of medusae or the degenerating colonies nearly accomplishing their life-span. The small number of polyp in the latter two hosts is thus superficial and their colonies are older than the aged colony consisting of a large number of polyp. And the presence of such colonies must have lowered the rate of daughter polyp formation and raised that of medusa-bud formation, that is they broaden the range of both rates. Despite of the probable mixture of these colonies the above-shown result is clear, therefore the age of polyp may be one of the intrinsic factors for the medusa-bud formation.

To supplement the above analysis Fig. 11 was prepared in which the number of polyp bearing daughter polyp and that bearing medusa-bud was counted and their percentage ratio was calculated in every rank of the number of polyp/host used in Table 6. As a result, the same tendency mentioned above can be recognized as shown in the left column of the figure. Furthermore even when the host size is arbitrarily divided into four ranks the above-mentioned tendency is nearly the same in each rank (Fig. 11, right columns), though the number of host specimens

Table 6. Relationship between the number of polyp per host and the rate of daughter polyp formation or that of medusa-bud formation. Values are shown in the order: range, (mean), SD. Host: *Mytilus edulis.*

No. of polyp per host	No. of host examined	Rate of daughter polyp formation (%)	Rate of medusa-bud formation (%)
1- 200	13	2.2-55.6(14.4), 14.7	0- 8.5(1.7), 2.7
201- 500	16	0-28.1(9.6), 9.0	0-16.0(3.4), 4.7
501-1000	6	2.3- 8.0(4.5), 2.6	0.2-11.1(5.1), 4.5
1001-2000	8	1.2- 8.1(5.2), 2.1	0-19.8(4.1), 6.5

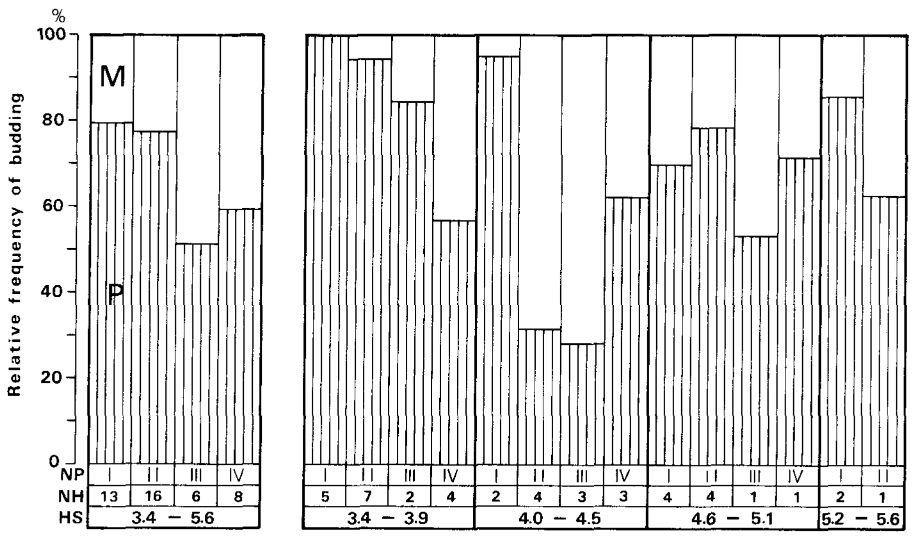

Fig. 11. Change of the relative frequency (%) of the budding of daughter polyp (P) and that of medusa-bud (M) according to the number of polyp/host (NP, I: below 200; II: 201–500; III: 501–1000; IV: 1001–2000). The left column is divided into four ranks in terms of the host size (HS, in cm) as shown in the right columns. And the number of host examined (NH) is also shown.

examined is few. Hence the above deduction is ascertained. It is noteworthy that in the larger host within which even if only a small number of polyp are associated (NP: I, II) the rate of budding of medusa-bud is relatively high.

By the way, Fig. 11 could be interpreted from another viewpoint: the relative frequency of the budding of medusa-bud and daughter polyp is different according to the density of polyp. In each rank it has a trend that the higher the density is, the more frequently the budding of medusa-bud takes place while the budding of daughter polyp occurs less frequently.

In conclusion, in a younger colony the formation of a daughter polyp is very active but that of a medusa-bud is markedly inactive, to the contrary in an older colony the formation of a daughter polyp is inactive but that of a medusa-bud is active. It is reasonable for the commensal life of the polyp that the polyp would not actively liberate its medusa as a sexual generation until the dwelling space of the host is occupied by its numerous daughter polyps and that not all the sessile polyps metamorphose into the planktonic medusae at the same time even in the breeding season and many daughter polyps are left within the host for the subsequent commensal life.

Although the exact life-span of one zooid or one colony has been unknown, judging from the supposition on the settlement and spread of the polyp within the host (cf. next section) the newly settled polyp might spend its life at least for one year at Oshoro, asexually reproducing a number of polyps in the warm and mild season (August to October), and after resting in the cold and severe winter it may become to produce and liberate its medusa in the favorable season in the next year. In this time an extrinsic factor for the medusa-bud formation, the rising of the water temperature above 15°C, must play an important role (cf. Fig. 9, WT). By the way, if the regeneration of polyp always occurs after liberation of medusa and production of daughter polyp also takes place without cease, the life of polyp or colony would continue perpetually until the host dies if once the polyp settles on the host.

c. Settlement of the new generation

As the outline of the life-cycle of the commensal polyp within the host has been clarified, the time and the place of settlement of the new generation are analyzed in this section. Firstly the time of settlement is surmised from the following five facts: (1) a large number of the youngest medusae appeared in July and then they matured at least within a month (cf. II); (2) the association rate of polyp with the host was lowest in July and highest in August (Fig. 8), which was ascertained by other several samplings in the Bay; (3) the number of polyp per host and also the total number of polyp in a quadrat were small in June and July (Fig. 8); (4) considerable reduction of polyp was often found with the development of a medusa-bud, and some of them completely degenerated and some others regenerated as tiny polyps (cf. I. A. 2); (5) most of the polyps found during the period from July to December were small. These facts are combined each other and result in the following inference: the lowest association rate of polyp and the small number of polyp per host in July are due to the degeneration of polyp accompaning with the liberation of medusa, and the tiny polyps in August are partly the regenerated ones and partly the newly settled generation; accordingly the invasion of the new generation occurred at least in August in this locality.

Next it was analyzed what body portions of the mantle cavity of the host the polyp settles on. In the above-mentioned 135 mussels associated with polyp the frequency of attachment of polyp to the various body portions was examined (Table 7, left half). As a result, the polyp could attach to all the body portions of the

Table 7. Frequency of attachment of polyp

Collec. month	No. of hosts examined	Freq. of attachment (%) on:				
		mantle	gill	labial palp	visc. mass	foot
I	18	89	78	17	94	11
II	14	93	93	29	79	0
III	12	83	83	42	92	8
IV	13	77	46	15	62	0
V	15	93	53	20	87	0
VI	11	100	18	18	55	0
VII	5	100	20	20	40	0
VIII	12	100	67	50	92	17
IX	8	100	88	25	75	25
X	7	100	100	14	43	14
XI	12	75	83	17	75	0
XII	8	100	88	13	88	0
I–XII	135 (11)[2)]	91	69	24	77	6

1) This is made for examination in both

host, among which the polyp most frequently attached to the mantle and frequently to the visceral mass or the gill, but rarely to the foot. The frequency of attachment to the various body portions of the host was analyzed further in each side of the mantle cavity of these 135 hosts (Table 7, right half). The polyp attached to the mantle very frequently and to the visceral mass or gill frequently as was nearly the same frequency mentioned above, accordingly the polyp was usually found on the mantle, the visceral mass, and the gill in both sides of the mantle cavity. It should be mentioned here that when the polyp attached to the gill, most polyps were usually found on its base, where these polyps seem to move from the mantle or the visceral mass. In 17 mussels out of these 135 ones the polyp was found only one side of the mantle cavity, and the similar analysis was especially made (Table 8). The polyp was most frequently found on the mantle and in six hosts the polyp was exclusively found on it. However, differing from the above-mentioned order, the polyp was frequently found on the gill in the next place and in one host the polyp was exclusively attached to it. The polyp was sometimes found on the visceral mass and in one host it probably exclusively on it. But no polyps were found on the labial palp and the foot. Both the foot and the labial palp are the small body portions and they have the ability to swing, accordingly the polyp might not be easy to settle on them as is also indicated in Table 7.

Consequently it would be inferable that the polyp at first settles on the mantle and then it spreads to the other body portions. If this inference were right the medusa-bud formation should firstly take place on the polyps attached to the mantle. In order to ascertain this, among many polyp-associated specimens of *Mytilus edulis* quantitatively collected during the period from June to November on various body portions of *Mytilus edulis.*

(No. of hosts) X2[1)]	Freq. of attachment (%) on:				
	mantle	gill	labial palp	visc. mass	foot
36	83	72	17	89	6
28	86	82	25	79	0
24	79	63	38	83	4
26	73	31	8	58	0
30	90	43	13	83	0
22	73	14	9	45	0
10	80	20	20	40	0
24	83	50	33	79	8
16	100	75	19	75	19
14	93	71	7	43	7
24	63	63	8	67	0
16	94	75	6	75	0
270 (23)[2)]	82	56	17	71	3

sides of mantle cavity. 2) Total (mean).

Table 8. Frequency of attachment of polyp to the body portions of *Mytilus edulis* on which the polyp is found in one side of the mantle cavity.

Collect. month	Host size (cm)	No. of polyp per host	No. of polyp detached*	Freq. of attachment (%) on:		
				mantle	gill	visc. mass
I	4.3	253	many			100?
II	3.8	18	0		100	
	4.1	210	52	96	4	
IV	4.3	125	0	100		
VI	3.5	15	0	100		
	3.8	39	some	100		
	3.4	56	0	89		11
	3.5	82	16	100		
	4.1	414	171	97	3	
VII	4.0	217	0	100		
VIII	4.9	126	3	83	5	12
	5.0	153	19	82	18	
X	4.1	27	0	93	7	
XI	3.6	135	0	100		
	3.4	267	0	99	1	
	3.3	348	0	66	32	2
XII	4.4	11	8	33	33	33

* Probably most of these specimens originally attached to any soft part of the host.

Table 9. Medusa-bud formation of polyp on various body portions in both sides of mantle cavity of *Mytilus edulis* collected from June to November. Arrangement is in the order from the host with a small number of polyps.

Collect. month	Host size (cm)	No. of polyp per host	One side of mantle cavity with more polyps			Opposite side of mantle cavity with less polyps		
			Mantle and labial palp	Gill	Visc. mass and labial palp	Mantle and labial palp	Gill	Visc. mass and labial palp
X	4.1	27	+	−				
VIII	4.9	126	+	−	−			
VIII	5.0	153	+	−				
VII	4.0	217	+					
VI	4.1	414	+	−				
VII	4.9	152	+			+		
VIII	5.6	161*	+		−	−		+
VI	3.6	227	+			−		−
VI	3.9	255	+			+		
VIII	4.8	281	+		+	+		+
VI	3.4	294	+		−	−		−
VII	4.8	307*	+		−	−		+
VIII	5.3	374*	+		−			+
VIII	5.0	404	+	+	−	+	−	−
VIII	5.0	466	+		+	+		−
IX	3.7	512	+	+	−	+	−	+
IX	4.3	531	+	+		+		
VI	4.2	560	+	+	+	+		−
XI	4.0	674**	−	+	−	−		−
XI	4.4	781	+	−		−		
IX	3.7	838	+	+		−		
VIII	5.1	870	+	+	+	+	−	−
X	4.2	1047	+	−	+	+	−	+
VIII	4.0	1108	+	+	+	+	+	+
VIII	4.5	1129*	+	+	+	−	+	+
X	3.9	1139	+	+	+	+	+	+
IX	4.7	1201	+	−	+	+	−	+
IX	3.5	1303**	−	+	−	−		+
IX	3.8	1938	+	−	−	+	−	−

+: Presence of medusa-bud formation. −: Absence of medusa-bud formation.
*,**: See text.

(excluding some specimens in which attachment of polyp to each body portion of the host is not completely grasped due to detachment of many polyps and some other specimens without budding of the medusa-bud) the following analysis was made: what body portions in both sides of the mantle cavity the polyp attached to and produced the medusa-bud. As a result, in five hosts within which polyps were found in only one side of the mantle cavity, the medusa-bud formation was exclusively took place on the mantle even if the polyp attached to other body portions (Table 9, upper columns). In many other hosts within which polyps were found in both sides of the mantle cavity (22 specimens out of 24 ones except two ones asterisked twice in Table 9, lower columns), the polyp attached to the mantle always produced the medusa-bud in one or both sides of the mantle cavity. Among these 22 hosts, in four ones asterisked the medusa-bud formation took place on other body portions than the mantle in one side of the mantle cavity (the polyp attached to the mantle in this side), but in all of them more number of polyps were present in the other side of the mantle cavity and the polyp on the mantle in this side always produced the medusa-bud.

These facts verify the above-mentioned inference that the polyp at first settles on the mantle, and the polyp on the mantle is oldest and comes first of the age to produce the medusa-bud. It is noticeable that the polyps which attached to the gill of the two exceptional hosts asterisked twice were markedly larger than the other polyps. They probably also come of the age to produce the medusa-bud (cf. I. A. 2. b).

On the other hand, in the hosts with which numerous polyps were associated (above ca. 500 in number) and in which the polyps passed certain long period after their settlement, the polyp often spread nearly to all over the host body portions in both sides of the mantle cavity and on every body portion the medusa-bud formation sometimes took place (Table 9, lower columns), though the rates on each portion are different.

By the way, among the polyp-associated *Mytilus edulis* which were collected quantitatively throughout the year, the specimens with which less number of polyp associated (below 200; cf. Fig. 7) were chosen and the following analysis was made: what body portions of the host polyps were attached to. In 24 host specimens (except nine ones asterisked) more than half the number of polyps in one host were found on the mantle in one side of the mantle cavity (Table 10). Above all in every host collected in June to October, when the planktonic medusae appeared in the sea, this tendency is clearly appreciable. It was often observed that on the anterior portion of the mantle just beneath the labial palp where the narrow opening space is formed many polyps were densely aggregated. As was assumed above, these polyps collected in this period may be mostly newly settled ones and were actively colonizing by the asexual reproduction. However, the reason for the appearance of hosts associated with a small number of polyps during the period from November to May is uncertain. Moreover, the reason why the polyp did not attach to the mantle in the nine hosts asterisked is also uncertain. It is likely that these unusual hosts appear as a result of (1) the degeneration and disappearance of many polyps after accomplishing their life-span or (2) the accidental or voluntary removal of polyp from one host to another. As already described, in laboratory the polyp could live well for a relatively long time even if it was picked up from the host and the re-attachment to the rearing container often took place. Furthermore, from the mussels reared in laboratory polyps were put out many times, sometimes mingled with the pseudofaeces of the host, and some of them re-attached to the

Table 10. Percentage ratio of attachment of polyp on various body portions of *Mytilus edulis* associated with a small number of polyp below 200.

Collect. month	Host size (cm)	No. of polyp per host	One side of mantle cavity with more polyps				Opposite side of mantle cavity with less polyps			
			Mantle	Gill	Labial palp	Visc. mass	Mantle	Gill	Labial palp	Visc. mass
I	2.2	137	55			12	26			7
II	3.8	18*		100						
	1.6	18	67				33			
III	3.5	110*		14		37				49
	3.2	115*				50				50
	3.6	182	60	1		10	29			
IV	3.8	111*				68				32
	3.4	36	92				8			
	4.3	125	100							
	4.9	64	86	5	2		8			
	4.8	190*			5	60				35
	3.7	89	75				25			
	4.6	37*				86				14
	4.1	120	68				33			
V	2.8	92	51				49			
	4.3	78*				63				37
VI	3.5	15	100							
	3.5	82	100							
	3.8	39	100							
	3.4	56	89			11				
	4.2	186	80			9				12
VII	4.9	152	73				27			
VIII	5.0	153	84	16						
	4.9	126	83	5		13				
	4.9	54	44	2		22	24			7
	5.6	161	42			12	35			12
IX	3.6	199	50			3	36			11
X	4.1	27	93	7						
XI	2.8	173*		1		62		5		32
	2.0	111*		2		51		1	1	45
	3.6	135	100							
	3.7	126	93	3		2	2			
XII	3.3	71	72				28			

* See text.

rearing container. On the other hand, the host *Mytilus edulis* was densely aggregated, forming a mussel bed on the wave cut bench at Oshoro. Considering these facts, it might not be impossible for the polyp to migrate from the host on which it originally settled to the next-door or near-by host.

By the way, in the whole life-history of the present hydroid, the larval stage plays a role of an invader to the host (see III). How many planulae invade a host at one time (see III) or whether a further invasion into the host associated with polyp occurs have been unknown. In every rearing case of the materials from various localities, both sexes were not appeared at the same time in one host (cf. Table 2). If the sex is determined at fertilization and unchangable through the life of the present hydroid, it may be safe to say at present that only very small number of planulae invade the unexploited host (probably usually smaller hosts, cf. Table 4) and they firstly settle on the mantle of the host just beneath the labial palp, and from that place the polyp spreads gradually to all over the body portions by the asexual budding as shown in Fig. 12 (though within a host detachment of polyp from one site and re-attachment to another site might occur). The aged polyps which had been lived for probably several or more years would usually associate with the senile host, and they would not produce their daughter polyps and rather leave from the host as medusae (cf. Table 6), as a result, the number of polyp in such host would markedly decrease (see Fig. 7).

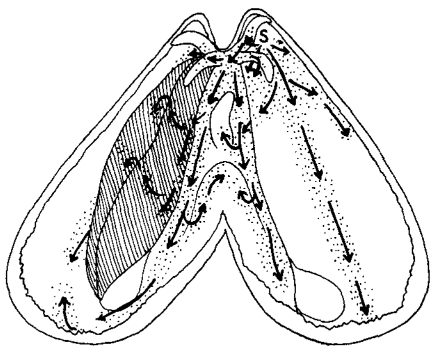

Fig. 12. A hypothetical process of settlement (S) and dispersal of polyp (arrows indicate the direction and dots represent the zooids) within the mantle cavity of host (*Mytilus edulis*). The gill of one side is omitted.

3. Supplementary note of the commensal life of polyp within a mantle cavity of bivalves from various localities

At Oshoro the commensal polyp was frequently associated with *Crenomytilus grayanus* and rarely with *Septifer virgatus* or *Chlamys swifti* (see VI). Within the mantle cavity of *Crenomytilus* the polyp seemed to spend the similar commensal life to that within *Mytilus edulis* described above. As is the same case in the polyp associated with *M. edulis* (cf. Table 4), the polyp was very frequently commensal with larger specimens of *Crenomytilus* (of the size above 5 cm) but it was rarely associated in small immature ones (Table 11). In almost all the *Crenomytilus* a great number of the polyps (probably tens of thousands ones) attached to the various body portions in proportion to the size of host which grows much larger than *Mytilus edulis* (cf. Table 36).

In not only these four bivalve species from Oshoro but also in other three bivalve species in Hokkaido, northern Japan the formation of medusa-bud in the

Table 11. Relationship between the host size of *Crenomytilus grayanus* and the association rate of polyp at Oshoro (cf. Table 32).

Host size (cm)	Total no. of hosts examined	No. of hosts with polyps	Association rate (%)
0.1- 2.9	22	2	9.1
3.0- 5.9	7	3	42.9
6.0- 8.9	11	10	90.9
9.0-11.9	36	34	94.4
12.0-14.9	25	24	96.0
Total	101	73	72.3

polyp usually occurred in July and August (Table 12, upper columns). In contrast with these northern bivalve species, in various bivalve species including *Mytilus edulis* from central and southern Japan the formation of medusa-bud occurred in December and January, when the bud developed well and liberation of medusa often took place soon after the collection. And the period of medusan formation seems to continue until May in southern Japan (Table 12, lower columns). This difference in the time of medusa-bud formation between the northern population and the central or southern one is due to the clear difference of the climate or environment; and each population spends its commensal life in proportion to the circulation of the season in the given locality. It will be interesting to know how the polyp lives within the mantle cavity of a bivalve for a year in various localities.

On the other hand, in every bivalve including *Mytilus edulis* from various localities frequent attachment of polyp to the mantle was found, and in many cases the polyp was on the mantle exclusively. Consequently the above-mentioned conclusion that the polyp at first settles on the mantle of the host and from there it spreads to the other body portions is supported. However, it is possible that in some other bivalves than *Mytilus edulis* (e.g. *Paphia* and *Peronidia*) the settlement was firstly made on other body portions than the mantle (see Table 12).

The pinnotherid crabs (*Pinnotheres* spp.) were sometimes found in the bivalves associated with polyp as shown in Table 12. This simultaneous commensalism was rare in northern Japan, for example at Oshoro it was found only in three specimens of *Mytilus edulis* and no crabs were found in *Crenomytilus*, *Septifer*, and *Chlamys*. And in this region only one commensal crab was found together with a number of commensal polyps in one host. Compared with this, in central and southern Japan simultaneous commensalism between the polyp and the crab was frequently found, moreover two or three crabs were sometimes associated in one host. The crab seems to invade the host earlier than the polyp, because of its high association rate with the host and even in the small host in which no polyps were usually found the crab often inhabited there. It was not observed that polyp was attached to the carapace of the crab.

Table 12. Time of medusa-bud formation and body portions on which polyps are found in various bivalves from northern and southern Japan.

Locality and Host bivalve[1)]	Collect. time[2)]	No. of hosts with polyps	No. of hosts with medusa-buds	Rate of medusan formation (%)	Attachment of polyp to:				
					mantle	gill	labial palp	visc. mass	foot
Oshoro									
Septifer virgatus	VIII-l	1	1	100		+			
	IX-l	1	0	0	+			+	
	XI-l	1	0	0	+	+	+	+	+
Chlamys swifti	X-f	1	1	100	+			+	
Zenibako									
Peronidia venulosa	VII-l	1	1	100		+	+	+	+
Utasutsu									
Mytilus coruscus	VIII-f	1	1	100	+				
*Mytilus edulis**	VIII-f	31	26	84	+	+	+	+	+
Kuroiwa									
Mytilus edulis	VIII-f	20	12	60	+	+	+	+	
Mori									
*Mytilus edulis**	VIII-f	1	1	100	+				
Akkeshi									
Clinocardium californiense	XI-f	1	0	0	+	+			
Enoshima Is.									
*Mytilus edulis**	III-l	27	12	44	+	+	+	+	
Usa									
Mytilus edulis	V-m	1	1	100			+	+	+
Septifer virgatus	V-m	1	0	0		+			
Crassostrea gigas	V-m	1	0	0	+				
Coecella chinensis	V-m	3	0	0	+			+	+
Mitsuhama									
Mytilus edulis	I-m	3	2	67	+			+	
*M. edulis**	IV-m	20	19	95	+	+	+	+	+
*Modiolus auriculatus**	IV-f	2	2	100	+	+	+		
Paphia schnelliana†	XII-l	1	1	100	+	+	+		
P. schnelliana†	I-f	1	0	0			+		
Nuwajima Is.									
Mytilus edulis	I-m	2	1	50	+	+	+	+	
Mukaishima Is.									
*Mytilus edulis**	III-f	10	6	60	+	+	+	+	
*M. edulis**	V-f	2	1	50	+	+	+	+	
Crassostrea gigas	III-l	1	1	100	+		+		
*Barbatia virescens**	V-f	2	2	100	+	+	+	+	

1) †: Not collected directly in that locality, but bought at the sea food market at Mitsuhama; *: Pinnotherid crab present.

2) f: The first decade of a month; m: the middle ten days of a month; l: the last ten days of a month.

Besides the pinnotherid crabs, parasitic copepods or turbellarians and probably symbiotic gammarids were found in the bivalves associated with polyp. Of these animals harboring in bivalves the commensal polyp seems to be the most prosperous animal because of its wide distribution in Japanese waters and the great number of zooids occupying nearly all the space of the mantle cavity of the host.

C. Some General Remarks on the Commensal Life of Polyp within a Bivalve

The exact nature of the commensal relationship between the hydroid and the host bivalve remains unknown, namely the advantage and the disadvantage of the commensal life for both organisms has been unclarified; and only the following some reports are available. By the attachment of the polyp of *Eugymnanthea inquilina* from Italy Cerruti (1941) reported loss of cilia and the presence of granules in the epithelial cells of the host mussel *Mytilus galloprovincialis*. On the contrary, Mattox and Crowell (1951) reported that the cilia of the host *Crassostrea rhizophorae* did not appear being damaged by the attachment of polyp of *Eugymnanthea ostrearum* from Puerto Rico. Santhakumari and Nair (1969) reported that in *Eutima commensalis* from India no evidence of damage to the host tissue was observed in any host specimen and hosts were healthy and normal despite of the heavy infestation of the polyp, though picking up the polyp from the host invariably leads to the damage of the host tissue because of its particular way of attachment. It was also observed in the present investigation that in any bivalve species from any locality all the hosts except the senile ones were healthy despite of the very heavy infection of the polyps. It was noticeable that probably by the pinnotherid crabs a portion of gills was sometimes damaged. In conclusion a host bivalve does not receive any harmful effects by the settlement of the commensal polyp.

As was originally stated by Mattox and Crowell (1951) and similarly thought by some other workers (Rees 1967, Santhakumari and Nair 1969, etc.) the mantle cavity of a bivalve is an excellent dwelling place for an unprotected and naked polyp. An abundant and nearly steady flow of the sea water took in by the host supplies a polyp for a variety of food and indispensable oxygen for respiration. And it is suitable for a polyp that the space of dwelling place of mantle cavity becomes enlarged by the growth of the host bivalve, especially in a large *Crenomytilus* which could live more than ten years. And furthermore even in the intertidal region the polyp can live and is saved from the dessication by harboring within the bivalve. It is noteworthy that on the outer shell surface of nearly all the specimens of *Mytilus edulis* in the intertidal region at Oshoro no hydroid species were found. On the other side, the disadvantage for the polyp would be the difficulty in settlement and holding on the soft body portions of the host on which mucus is often secreted and cilia were sometimes present and furthermore a water current occurs around these body portions. In correlation with these characteristics of the habitat the polyp evolved to spend a reasonable commensal life by modifing the body, particularly the elaboration of the pedal disk as discussed later (see VII).

In other commensal hydroids than the present hydroid the body portions to which polyps are attached, the seasonal occurrence of polyp, and the time of medusa-bud formation, etc. were known, and they are summarized in Table 37. Of all these commensal hydroids except one, *Eutima commensalis*, their polyps could attach to nearly all the body portions of the host and probably live within the mantle cavity throughout the year, liberating their medusae at a certain time. In *E. commensalis* of which host is unusual in both its morphology and mode of life among the hydroids harboring in bivalves, the dwelling place is restricted (exclusively to the ctenidia) and the seasonal occurrence in both the polypoid and the medusan generations is quite limited mainly due to the conspicuous change of the environment by the south-west moonsoon (see Santhakumari and Nair 1969; Vannucci *et al.* 1970).

II. Medusan Generation

A. Morphology of Newly Liberated Medusa

Many youngest medusae liberated from the polyps associated with various bivalves from various localities were examined. As a result, no morphological difference in connection with the host difference was found and the general morphology is as follows (Table 13).

The umbrella is nearly hemispherical and is 0.6–2.0 mm in height and 0.8–3.0 mm in width. It is usually wider than high, though sometimes it is reversed. At the apex of the umbrella either a small concavity or a remnant of polyp and/or umbilical canal are often present. The mesogloea is transparent and very thin, with about 1/6 the length of the umbrellar height. Nematocysts of one kind are found all over the exumbrellar surface except the umbrellar margin just above the ring canal and the marginal swellings. The manubrium is not long and occupies nearly 1/2 of the umbrellar height. The small stomach, occupying about 1/7 of the umbrellar diameter, is quadrate in shape and no peduncle is present on it. There are four (very rarely three) small and simple oral lips. No trace of gonad is found on manubrium and four radial canals. The velum is relatively wide and the umbrellar aperture is small.

At perradii there are four large conical bulbs, on each of which 2–9 lateral cirri and a abaxial U-shaped black band are present. And from all these four bulbs or from the opposite two ones marginal tentacles are extended. At interradii there are four small marginal warts (of the first set) without tentacles, and on each of which 0–6 lateral cirri and one abaxial cirrus are present. The abaxial cirrus is very contractile and about as long as the umbrellar width when it is well-extended. It tapers distally and at the distal end one nematocyst knob with cilia is present. It was observed that in some specimens the abaxial cirrus was not present in every interradial bulb.

The lateral cirri are usually present on both sides of the perradial and interradial marginal swellings, though they were sometimes found on the free

Table 13. Morphology of the newly liberated medusa within Japan, associating with various bivalves.

Locality	Host	No. of hosts and medusae examined	W (mm)	H (mm)
Oshoro	*Mytilus edulis*[1)]	4, 47	0.88-1.8 (1.3)	0.56-1.1 (0.83)
	Crenomytilus grayanus	5, 30	1.6 -2.8 (2.1)	0.88-1.6 (1.2)
	Septifer virgatus	1, 2	0.94-1.4 (1.2)	—
	Chlamys swifti	1, 6	1.1 -1.4 (1.3)	0.69-0.81 (0.74)
Zenibako	*Peronidia venulosa*	1, 5	0.95-1.4 (1.2)	0.81-0.94 (0.88)
Utasutsu	*Mytilus coruscus*	1, 5	1.4 -1.9 (1.6)	1.0 -1.2 (1.1)
Mori and Kuroiwa	*Mytilus edulis*	4, 5	1.6 -2.3 (2.0)	1.2 -1.7 (1.4)
Akkeshi	*Clinocardium californniense*[2)]	1, 15	1.3 -2.1 (1.7)	0.81-1.4 (1.2)
Hachinohe	*Mytilus edulis*[3)]	-, -	1.5-2.0	1.5-2.0
	M. coruscus[4)]	-, -	3.0	1.5
Usa	*Mytilus edulis*	1, 10	0.94-1.4 (1.2)	0.63-1.0 (0.86)
Mitsuhama	*Paphia vernicosa*	1, 8	0.94-1.4 (1.1)	0.88-1.3 (1.1)
Mukaishima Is.	*Mytilus edulis*	1, 31	0.84-1.4 (1.1)	0.63-1.1 (0.81)
	Crassostrea gigas	1, 18	0.88-1.2 (1.0)	0.75-1.1 (0.96)
Total	9 species		0.84-3.0	0.56-2.0

1) Kubota 1978a. 2) Kubota 1979b.

marginal portion of the umbrella, mostly near the perradial bulb, rarely near the statocyst. As an unusual case, it was observed that in many medusae originated from the polyp in *Crenomytilus grayanus* (20 specimens out of 30 ones examined) several or many marginal cirri (up to 10 in one specimen) were found. Some lateral cirri are well-developed ones similar to the abaxial cirrus and some are short ones like finger-like processes without a distinct nematocyst knob. The lateral cirri on the perradial bulbs are always more in number and they are usually well-developed ones, while those on the interradial warts are less in number and the cirri are sometimes absent on one side of the base and the finger-like ones are often present. The total number of cirri in a medusa is highly variable, namely 12–52 in number.

There are eight (very rarely six or seven) statocysts as closed marginal vesicles in adradii, each containing usually one to three statoliths while rarely up to seven ones. The statoliths are usually composed of one large statolith and one or two small ones which are possibly undeveloped ones, while in some statocysts all the statoliths are large ones. The number of statoliths in a medusa is variable and 6–35 ones are counted.

The medusa is mostly transparent, while the stomach and eight marginal swellings are orange and the ring canal is green in color. As a rare case the subumbrellar surface is green in color. On the perradial bulb a black U-shaped band is usually present markedly, but it is sometimes indistinct or absent.

one-day-old from polyp found in both northern and southern
Measurements: range (mean).

Te	Ms	St	Stl	Stl/St	C	No. of cirri/marginal swelling at perradii and interradii
4 rarely 2	8	8 rarely 7	6-22 (10)	0-3	20-38 (30)	2-5, 2-4
4	8	8	8-27 (20)	0-5	33-52 (40)	3-9, 2-6
4	8	8	8-16 (12)	1-3	28-29 (29)	4, 2-3
4	8	8	8	1	28-31 (29)	4-5, 2
4	8	8	8-24 (14)	1-3	28-44 (35)	4-7, 2-5
4	8	8	8-10 (8)	1-2	41-46 (43)	4-7, 3-5
4	8	8	12-29 (22)	1-4	28-39 (34)	3-6, 2-3
4	8	8	16-35 (24)	1-7	31-45 (40)	3-7, 2-6
4	8	8	—	1-4	up to 12	3-4, —
4	8	8	—	—	—	2-3
2 rarely 3	8	8	8-16 (9)	1-3	16-27 (22)	2-4, 1-2
1-4	8	8	8-22 (17)	1-3	29-40 (35)	4-6, 2-4
2 rarely 0, 1, 4	8	8 rarely 6	7-20 (12)	0-4	15-31 (26)	2-5, 0-3
2-4	8	8	9-18 (13)	1-3	31-41 (37)	4-6, 2-4
2 or 4 rarely 0, 1, 3	8	8 rarely 6, 7	6-35	0-7	12-52	2-9, 0-6

3) Kakinuma 1964. 4) Uchida 1964.

Although almost all of the characteristics of the specimens from every locality surveyed coincide with each other, a morphological variation, which could be conceivable as a local variation, is found in the number of tentacles (Table 13). Namely the specimens from southern Japan tend to have two tentacles (Plate X, E, F), while those from northern Japan four tentacles (cf. Fig. 17, A).

In addition to the above-described normal specimens three abnormal specimens were found, and their morphology was as follows. One specimen from Mukaishima Island of which host was an oyster had three radial canals, and there were three large bulbs with marginal tentacles, two marginal warts, and five statocysts (W= 0.88 mm). In this specimen no abaxial cirri were found, while 22 lateral cirri (4–5 cirri on both sides of one marginal swelling) were present. Each statocyst had 1–3 statoliths and in all 10 statoliths were found. Furthermore on the apex of the umbrella a finger-like process lied, containing the nematocyst which was the same kind as the exumbrellar nematocyst. Another specimen from the same locality and the same host (W=H=0.75 mm) had also three radial canals, and one of which bifurcated. In this specimen there were four large bulbs, and two of which protruded tentacles. And four marginal warts, eight statocysts, nine statoliths, and 20 cirri were present. In one quadrant of this specimen two statocysts were found on the abnormal position, namely just beside one marginal wart. The other specimen from Oshoro of which host was *Mytilus edulis* had five radial canals due to the bifurcation of one radial canal. The arrangement of marginal equipment is, however, regular and five marginal tentacles, five marginal warts, and 10 statocysts were present. The metamorphosis of this specimen could be observed for about three months and was summarized in Table 20.

B. Metamorphosis of Medusa

The rearing of medusa in laboratory could be easily carried out and the metamorphosis proceeds rapidly for about a month in every material. Using the specimens from both Oshoro and Akkeshi, Hokkaido, northern Japan, the development of medusa from the newly liberated medusa to the mature one was observed in the previous studies (Kubota 1978a, '79b). On the present occasion the metamorphosis of medusa was fully investigated, namely it was observed covering all the life-span of medusa in not only many specimens from Usa and Mukaishima Island, southern Japan but also those from Oshoro, northern Japan again. Furthermore observations were made on the metamorphosis of medusae from several localities in Hokkaido and on the morphological variation of medusa appeared in different rearing conditions.

1. Metamorphosis in the material from Usa, Kôchi Prefecture, southern Japan

Nine newly liberated medusae originated from the polyp in *Mytilus edulis* were reared and the metamorphosis was observed in detail (Tables 14, 15), especially analyzing the subsequent appearance of marginal warts and cirri (Fig. 13). As to the morphology of the present youngest medusa (cf. Fig. 13, A), it should be better to make a note of the following: (1) the abaxial cirri were not present in some interradial marginal warts, (2) the black U-shaped band was usually absent. Within a few days after liberation all the abaxial cirri completely disappeared. Three to five days after liberation when the umbrellar diameter was 1.5–2.1 mm, from the other opposite two perradial bulbs marginal tentacles were extended, though they were still as half as long the former tentacles already produced at the youngest stage. Three to eight days after liberation when the umbrella was 1.9–2.9 mm in diameter, the rudiment of gonad appeared on the radial canal just beside the stomach, and at this time the formation of marginal warts of the second set began. Seven to eleven days after liberation when the umbrellar diameter was 3.5–4.3 mm the marginal warts of the second set were completely produced on both sides of eight statocysts, so they were in all 16 in number (Fig. 13, B). Nine to twelve days after liberation when the umbrella was 3.8–4.4 mm in diameter the peduncle and the marginal warts of the third set began to appear. During these 12 days after liberation disappearance of the lateral cirri on the perradial and interradial marginal swellings did not take place, the exumbrellar nematocysts were still present, and the formation of lateral cirri on the marginal warts of the second or the third set was not found except one specimen in which one lateral cirrus was produced on one marginal wart of the second set (see Fig. 13, B).

Thirteen to sixteen days after liberation when the umbrella was 5.4–6.4 mm in

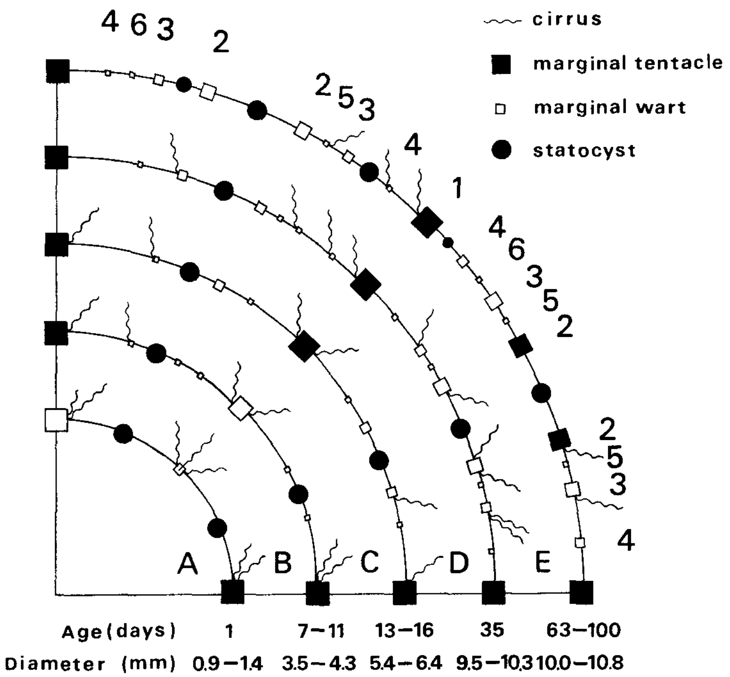

Fig. 13. Diagram showing the subsequent appearances of marginal warts, lateral cirri, marginal tentacles, and statocysts in a quadrant of the material from Usa (host: *Mytilus edulis*), from oral side.

diameter four interradial bulbs began to put forth marginal tentacles, accordingly eight tentacles of different lengths were present in every specimen. And in this stage, a number of the marginal warts of the third set were produced. The lateral cirri remained on the perradial and interradial bulbs, and the formation of lateral cirri on the marginal warts of the second set was sometimes found (only one cirrus was present on each of one or two warts of some specimens). The peduncle was still short and a black band appeared on the interradial upper region of the manubrium (Fig. 13, C). Nineteen to twenty-three days after liberation when the diameter was 7.6–8.4 mm the marginal warts of the third set were completely produced, 16 in number, on the umbrellar margin between the marginal warts of the second set and the perradial or interradial tentacular bulbs; moreover the marginal warts of the fourth set began to appear the outer side of the marginal warts of the third set near the perradial or interradial bulbs. In this stage lateral cirri on eight tentacular bulbs still remained, and the manubrium protruded from the umbrellar aperture due to the elongation of the peduncle. The morphology of the well-grown medusa 25 days old is shown in Table 15.

The maturation of gonad began on and after about a month after liberation and

Table 14. Morphology of mature medusa from Usa, host:

Specimen no.	W	H	J	P	M	S	V	L	GL	GW	Te	Mw	St
1	9.8	6.4	3.2	3.2	2.4	0.40	0.79	0.95	3.7	0.19	8	54	8
2	9.5	-	-	-	-	-	-	-	-	-	8	47	8
3	9.5	6.4	3.2	3.2	2.2	0.32	0.79	0.63	3.5	0.19	9	49	8
4	10.2	7.1	4.0	2.4	2.4	0.35	0.95	0.79	3.8	0.19	8	50	8
5	10.0	7.6	4.0	2.7	2.4	0.35	0.95	0.79	3.8	0.24	8	47	8
6	9.8	7.5	3.7	2.9	2.4	0.35	0.79	0.87	3.7	0.24	8	45	8
7	9.8	7.0	3.8	3.2	2.4	0.32	0.87	0.63	3.8	0.19	8	51	8
8	9.8	7.1	3.8	2.9	2.4	0.35	0.95	0.79	3.8	0.19	8	45	8
9	10.3	7.9	4.0	3.2	2.5	0.32	0.79	0.63	4.0	0.29	8	49	8
Mean	9.9	7.1	3.7	3.0	2.4	0.35	0.86	0.76	3.8	0.22	8	49	8

Table 15. Subsequent morphological changes in some important characters in the

Age (days)	Sex	No. of specimens examined	W (mm)	Te	Mw	C	No. of cirri/1Tb or 1Mw	St	Stl
1	?	10	0.94-1.4 (1.2)	2 rarely 3	6 rarely 5	16-27 (21.9)	1-4	8	8-16 (9.3)
25	?	9	8.3-9.7 (9.2)	8	33-44 (38.1)	3-27 (17.7)	0-2	8	60-79 (67.2)
35	♀	9	9.5-10.3 (9.9)	8 rarely 9	45-54 (48.6)	14-34 (22.9)	0-2	8	71-88 (76.9)
40	♀	8	9.7-11.0 (10.3)	8 rarely 9	47-56 (52.1)	11-28 (21.9)	0-2	8	78-93 (86.3)
63	♀	4	10.0-10.6 (10.5)	8 rarely 9	55-60 (57.8)	0-33 (9.8)	0-2	8	79-106 (91.8)
70	♀	2	10.3-10.8 (10.6)	9	57-60 (58.5)	1-4 (2.5)	0-2	8-20	103-108 (105.5)[1]
100	?	1[2]	-	14	67	0	0	21	ca. 300

1) In the newly produced statocysts Stl: 0–40, Stl/St: 1–5 (3.3).

on the 35th day all the specimens turned out female medusae with eight tentacles, eight statocysts, many cirri, well-developed peduncle, etc. The morphology of mature medusa 35 days old is as follows (Tables 14, 15; Fig. 13, D; Fig. 14). The jelly was very thick, with about 1/2 the length of the umbrellar height; and the

Mytilus edulis, (35 days old, ♀). Size: in mm.

Stl	Stl/St	C	Ms with cirri (total no. of cirri)/total Tb or Mw in each set: 0	1st	2nd	3rd	4th	5th
73	7-11	19	0 (0) /4	1 (2) /4	9 (9) /16	7 (7) /16	1 (1) /14	0 (0) /8
79	7-11	14	0 (0) /4	2 (2) /4	5 (6) /16	5 (6) /16	0 (0) /12	0 (0) /3
71	7-12	30	0 (0) /4	2 (2) /4	12 (16) /16	9 (9) /16	3 (3) /14	0 (0) /4
74	7-12	34	0 (0) /4	1 (1) /4	14 (17) /16	13 (15) /16	1 (1) /15	0 (0) /3
73	7-11	17	0 (0) /4	0 (0) /4	11 (13) /16	4 (4) /16	0 (0) /14	0 (0) /1
88	8-13	27	0 (0) /4	0 (0) /4	14 (16) /16	9 (11) /16	0 (0) /13	0 (0) /0
80	8-12	19	0 (0) /4	0 (0) /4	11 (14) /16	5 (5) /16	0 (0) /14	0 (0) /5
68	7-11	24	0 (0) /4	0 (0) /4	12 (17) /16	6 (7) /16	0 (0) /13	0 (0) /0
86	9-12	22	0 (0) /4	0 (0) /4	11 (12) /16	10 (10) /16	0 (0) /15	0 (0) /2
77	10	23	0 (0) /4	1 (1) /4	11 (13) /16	8 (8) /16	1 (1) /14	0 (0) /3

medusa from Usa, host: *Mytilus edulis*. Measurements: range (mean). —: absent.

Stl/St	Mean value of Ms with cirri (mean value of cirri)/total Tb or Mw in each set: 0	1st	2nd	3rd	4th	5th	6th
1-3 (1.2)	4 (12.4) /4	4 (9.4) /4	—	—	—	—	—
6-12 (8.4)	0.2 (0.2) /4	1.4 (1.8) /4	8.8 (10.2) /16	5.0 (5.4) /16	0 (0) /6.1	—	—
7-13 (9.6)	0 (0) /4	0.7 (0.8) /4	11.0 (13.3) /16	7.6 (8.2) /16	0.6 (0.6) /13.8	0 (0) /2.9	—
7-14 (10.8)	0 (0) /4	0.5 (0.5) /4	10.0 (12.1) /16	7.8 (8.5) /16	0.6 (0.6) /15.0	0.1 (0.1) /5.1	—
6-16 (11.5)	0 (0) /4	0.3 (0.3) /4	2.8 (3.3) /16	2.8 (2.8) /16	2.5 (3.0) /16	0.3 (0.5) /9.5	0 (0) /0.5
8-16 (13.2)[1)]	0 (0) /4	0.5 (0.5) /4	1.0 (1.5) /16	0.5 (0.5) /16	0 (0) /16	0 (0) /11.0	0 (0) /0.5
5-ca. 20	0 (0) /4	0 (0) /4	0 (0) /16	0 (0) /16	0 (0) /16	0 (0) /10	0 (0) /5

2) With hat-shaped umbrella due to degeneration.

peduncle reached near the umbrellar aperture. The linear gonad extended on the most parts of the radial canal from the middle of peduncle to near the ring canal. The marginal warts of the fourth set were almost completely produced beside the perradial and interradial bulbs (12–15 warts in a medusa); and furthermore the marginal warts of the fifth set were produced between the marginal warts of the second and the third sets, though their number was very small (0–8 warts in a medusa). As a rare case, two marginal warts of the fourth set* (or those of the five set ?), only one wart in each of two specimens (Nos. 1, 2 in Table 14), were produced between the marginal warts of the second and the third sets. As to the lateral cirri, they completely disappeared on the perradial bulbs and no cirri were yet produced on the marginal warts of the fifth set, and they nearly disappeared on the interradial bulbs and barely produced on the marginal warts of the fourth set, while most of the marginal warts of the second and the third sets had cirri. Most of the marginal swellings bore one lateral cirrus, while only 1–6 marginal swellings per medusa had two cirri on one or both sides of them. The oral lips became folded and frilled. A black band was still present on the interradial upper region of the manubrium, while the tentacular band disappeared. It was observed that as an unusual case one specimen bore the 9th tentacle on one marginal wart of the second set on the 30th day when the umbrellar diameter was 8.7 mm.

On the 40th day the marginal warts of the fourth set increased in number and 13–16 warts were found in a medusa, while the marginal warts of the fifth set were still few in number (1–9) and no cirri were found on them except one wart (Table

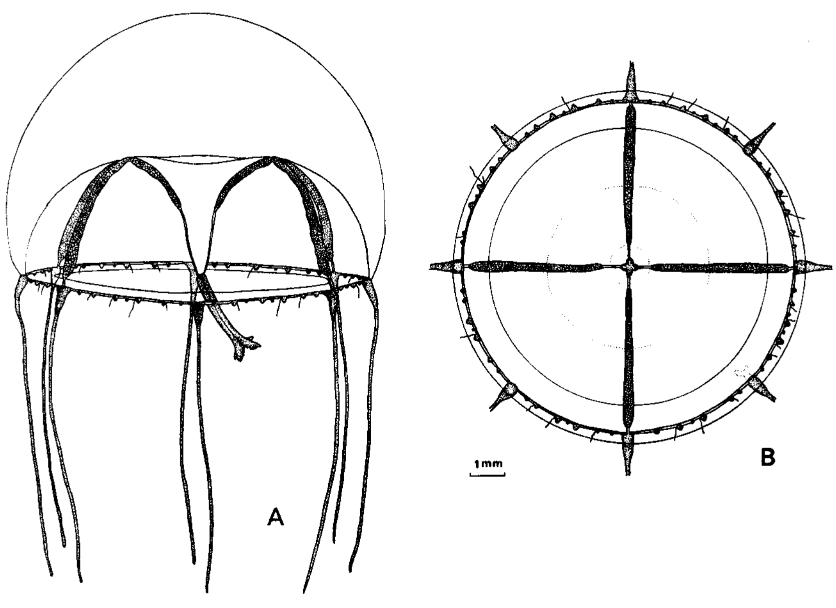

Fig. 14. A female mature medusa from Usa (host: *Mytilus edulis*), 35 days old. A: side view, B: aboral view (marginal tentacles are omitted).

* Set number of these warts was tentatively determined to the fourth by the order of appearance (not by the position produced).

15). On and after the 45th day the discharge of eggs was observed, and it had been continued for about a month. The gonad was long and lean and the greatest width was 0.32 mm. On the 63th day, the marginal warts of the fourth set completely produced (16 in number). The lateral cirri were produced on some of the marginal warts of the fifth set and the marginal warts of the sixth set appeared between the marginal warts of the third and the fourth sets (only two in number) (Table 15; Fig. 13, E; Plate X, I, J). It was noticed that in a quadrant the marginal wart of the sixth set appeared in one side of an octant while in the other side of an octant the marginal warts of the fifth set has not yet produced.

In the spent specimens about 70 days old irregular morphological changes were observed. The radial canal was somewhat branched, and 1–3 short branches were found in one radial canal, and furthermore a short canal extended from the interradial tentacular bulb. Moreover statocysts were increased in number and in a quadrant 2–5 statocysts were newly produced, so up to seven statocysts were found in a quadrant (cf. Fig. 13, E). And disappearance of the lateral cirri was observed in almost all the margianl swellings.

The life-span was within 100 days, during which the peduncle did not protrude from the umbrellar aperture and the gonad did not appear on the manubrium and the lower part of the peduncle. The black band on manubrium was consecutively present, but was restricted on its interradial upper region, while the tentacular band had been disappeared. In the specimen near degeneration, subsequent marginal tentacles were put forth from one or two of the marginal warts of the second sets, and up to four tentacles were found in a quadrant (cf. Fig. 13, E). As was the same case in the formation of tentacles on the interradial bulb, these marginal warts became larger before putting forth the tentacles.

Summarizing the above-described metamorphosis of medusa from Usa, most of the metamorphic characters appeared and their development was mostly completed concurrently with the maturation of gonad for about a month after liberation. However, marginal warts and statoliths still continuously increased in number until degeneration. The lateral cirri, a most variable character, was produced or disappeared on marginal swllings of different growths with the development of medusa, though they still remained in the spent medusa over two months old. The metamorphosis proceeded regularly, but in the specimens near degeneration irregular and conspicuous morphological changes took place in the characters such as the radial canals, statocysts, and the tentacles.

2. Metamorphosis in the materials from Mukaishima Island, Hiroshima Prefecture, southern Japan

Metamorphosis of medusa was examined in detail in the specimens of which polyps were associated with both *Mytilus edulis* and *Crassostrea gigas*, particularly in order to clear the systematic status of *Ostreohydra japonica* Yamada (see V).

a. In the case that the host is *Mytilus edulis*

Three young medusae survived (abbr. a-c) after the transference from southern Japan and three youngest medusae (abbr. 1–3) liberated from one polyp in laboratory at Sapporo (see I. A. 2. b) were reared until degeneration and the metamorphosis was observed (Tables 16–18; Fig. 15; Plate X, G, H). And in the two latter specimens (Nos. 2, 3) the subsequent morphological changes as to the number of lateral cirri, marginal tentacles, marginal warts, and of statoliths were examined every day till the stage in which they had eight tentacles.

It was noticed in the present youngest medusa that as was the same case in the medusa from Usa the abaxial cirri were sometimes absent in some interradial bulbs and the U-shaped black band was often absent, moreover the oral lip was very indistinct and the manubrium and the marginal swellings were cream-colored. The early metamorphosis during 10 days was as follows (Table 16; cf. Fig. 13, A, B). Within a few days the abaxial cirri entirely disappeared, and four tentacles were found in all due to the formation of tentacles on every perradial bulb. The marginal warts of the second set began to appear on the third day. When most of them were produced on about a week after liberation the marginal warts of the third set began to appear. The lateral cirri on both the perradial and the inter-

Table 16. Early metamorphosis of two specimens (Nos. 2

Age (days)	W (mm)	Stl (St=8)	Stl/St	Te+Mw	No. of cirri (lateral+abaxial)	Max. no. of cirri/ 1Tb, 1Mw
1	0.97, 1.1	24, 7	3, 0-1	0+ 7, 4+ 4	11+0, 31+4	4, 6
2	1.4, 1.7	24, 14	3, 1-3	4+ 3, 4+ 4	13+0, 33+2	3, 6
3	2.1, 2.8	24, 22	3, 2-3	4+ 8, 4+12	15+0, 42+2	5, 8
4	2.8, 3.7	24, 25	3, 3-4	4+ 8, 4+16	26+0, 54+0	6, 9
5	4.1, 4.1	29, 25	3-5, 3-4	4+13, 4+17	44+0, 49+0	8, 6
6	4.8, 5.1	36, 29	3-6, 3-5	4+17, 4+19	47+0, 40+0	8, 6
7	5.4, 5.9	43, 39	5-7, 4-6	4+20, 4+21	45+0, 42+0	7, 6
8	6.4, 6.2	44, 43	4-8, 5-7	5+22, 4+23	42+0, 42+0	5, 5
9	7.1, 6.7	54, 50	6-9, 5-8	7+23, 7+24	53+0, 32+0	6, 3
10	7.9, 7.3	59, 54	5-9, 5-9	8+23, 8+27	45+0, 40+0	6, 4

–: Absent.

Table 17. Morphology of three mature medusae from Mukaishima

Specimen no.	W	H	J	P	M	S	V	L	GL	GW	Te	Mw
a	10.3	6.2	3.0	1.6	1.6	0.3	0.8	1.6	2.9	0.1	8	40
b	9.8	6.3	2.9	1.7	1.6	0.3	1.0	1.4	2.7	0.1	8	35
c	11.3	6.3	3.2	2.1	1.7	0.3	0.8	1.3	2.9	0.1	8	36

radial bulb increased in number soon after the liberation and up to nine cirri were found on one bulb. However, their number became decreased on and after about one week after liberation in contrast to the formation of many lateral cirri on the marginal warts of the second set. In this early metamorphic stage so many marginal warts of the third set were not yet produced (up to nine in number), and the marginal warts of the fourth set were rarely found (up to four in number); and on both of them no cirri were yet present. The number of statoliths increased rapidly and up to nine statoliths were counted in one statocyst. When the umbrella with about 7–8 mm in diameter they had eight tentacles, while the peduncle was short then. It was observed that in the other specimens reared, eight tentacles were found when they were 6.3–8.1 mm in diameter.

Compared these early morphological changes with those in the specimens from Usa described above, the formation of the lateral cirri on the marginal warts of the second set and the appearance of the marginal warts of the fourth set were earlier in the present specimens.

Within three weeks after liberation the metamorphosis proceeded rapidly, attaining about 10 mm in diameter, and the specimens began to assume the adult form. The gonad did not mature well in every specimen except for two specimens

and 3) from Mukaishima Island (host: *Mytilus edulis*).

Ms with cirri (total no. of cirri)/ total Tb or Mw in each set:				
0	1st	2nd	3rd	4th
4(10)/4, 4(24)/4	1(1)/3, 4(7)/4	– , –	– , –	– , –
2(10)/4, 4(24)/4	2(3)/3, 4(9)/4	– , –	– , –	– , –
4(14)/4, 4(26)/4	1(1)/4, 4(16)/4	0(0)/ 4, 0(0)/ 8	– , –	– , –
4(18)/4, 4(30)/4	4(8)/4, 4(24)/4	0(0)/ 4, 0(0)/12	– , –	– , –
4(25)/4, 4(22)/4	4(14)/4, 4(22)/4	5(5)/ 9, 5(5)/13	– , –	– , –
4(27)/4, 4(16)/4	3(12)/4, 4(19)/4	6(8)/12, 5(5)/15	0(0)/1, –	– , –
4(22)/4, 4(13)/4	3(12)/4, 4(17)/4	7(11)/13, 9(12)/15	0(0)/2, 0(0)/2	0(0)/1, –
4(12)/4, 4(13)/4	3(14)/4, 4(13)/4	8(16)/13, 10(16)/15	0(0)/5, 0(0)/4	0(0)/1, –
4(15)/4, 4(9)/4	3(16)/4, 4(8)/4	9(22)/13, 11(15)/15	0(0)/6, 0(0)/8	0(0)/3, –
4(17)/4, 4(11)/4	3(13)/4, 4(8)/4	7(15)/13, 12(21)/16	0(0)/6, 0(0)/9	0(0)/4, 0(0)/2

Island (30 days old). Size: in mm. Host: *Mytilus edulis*.

St	Stl	Stl/St	C	Ms with cirri (total no. of cirri)/total Tb or Mw in each set:				
				0	1st	2nd	3rd	4th
8	56	6- 9	35	3(4)/4	4(5)/ 4	13(13)/16	13(13)/16	0(0)/8
8	64	6-10	74	4(10)/4	4(11)/4	16(33)/16	14(20)/16	0(0)/3
8	62	6-10	63	4(13)/4	4(10)/4	16(23)/16	14(16)/16	1(1)/4

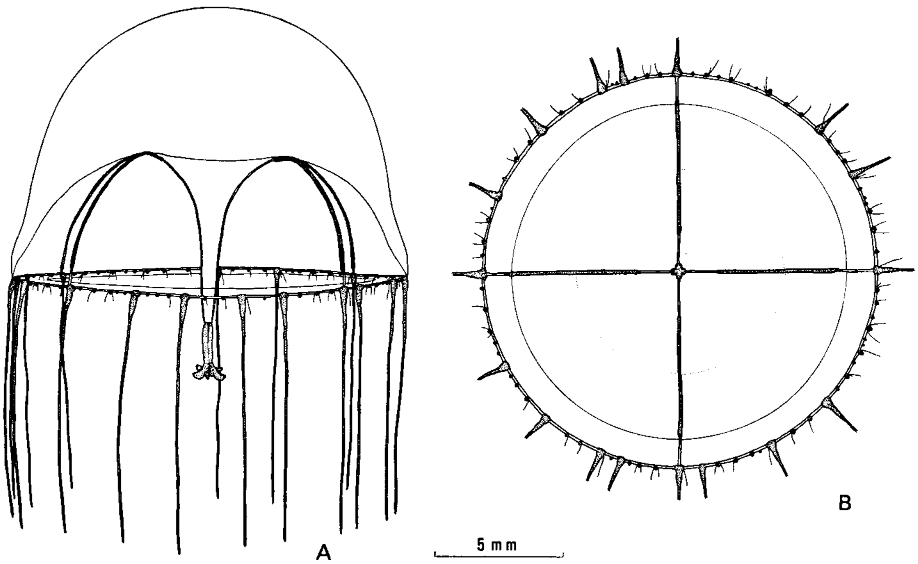

Fig. 15. A well-grown medusa from Mukaishima Island (host: *Mytilus edulis*) 60 days old. A: side view, B: aboral view (marginal tentacles are omitted).

in which full maturation was observed after 5–6 weeks and they turned out female (Table 18, Nos. 1, 2).

Some marginal warts of the second set began to put forth tentacles about on and after six weeks after liberation, and the number of tentacles attained up to 20. In some specimens the number of statocysts also increased and up to 19 ones were present. The marginal warts and statoliths increased further in number; up to 73 marginal swellings per specimen and 20 statoliths per statocyst were counted. The number of lateral cirri was highly variable and usually many cirri were present in the well-grown medusa. It is noteworthy that in two specimens (Table 18, Nos. 1, 2) all or almost all the cirri disappeared only when the gonad matured, but the cirri reappeared afterwards with the age (Table 18; Fig. 20). In addition to the lateral cirri, adaxial cirri were sometimes found (see Fig. 19, E), and the total number of cirri in a medusa attained 98 and in one marginal swelling up to five cirri were present. A black band was always present on the upper interradial region of manubrium, while a U-shaped black band was often indistinct or absent on tentacular bulbs. The life-span was about two to three months and during which the umbrella attained 13 mm in diameter. In the old-aged specimens the size slightly decreased and branching of the radial canal occurred. As a rare case, in one specimen (Table 18, No. 3) the radial canal became considerably reticulated on the peduncle on the 35th day.

It is noticeable that in the present well-grown specimens the marginal warts

Table 18. Subsequent morphological changes of six medusan specimens from Mukaishima Island (host: *Mytilus edulis*).

Specimen no.	Age (days)	W (mm)	Te	Mw	Ms	Ms with cirri	C	Max. no. of cirri on 1Tb or 1Mw	St	Stl	Stl/St
1	21	11.9	8	53	61	33	89	5	7	66	8-13
	42	11.4	8	58	66	0	0	0	7	75	9-13
	50	12.7	9	58	67	21	38	4	17	140	1-15
	66	11.1	12<	-	-	-	-	-	-	-	-
2	18	11.1	8	38	46	18	48	4	8	68	7-10
	35	11.1	8	53	61	1	1	1	8	90	10-13
	43	11.4	13	48	61	16	30	3	14	126	3-15
	78	11.9	16	45	61	19	26	2	19	195	2-20
3	18	10.3	8	33	41	20	41	3	11	86	4-10
	35	9.5	8	42	50	19	39	4	11	105	7-11
	43	10.8	8	47	55	25	62	4	11	107	8-11
	73	8.7	11	50	61	25	45	3	11	92<	7-11
a	30	10.3	8	40	48	33	35	2	8	56	6- 9
	60	13.0	17	55	72	42	60	2	8	99	11-14
b	30	9.8	8	35	43	38	74	4	8	64	6-10
	60	13.0	14	50	64	55	94	4	9	100	0-13
	84	12.7	20	48	68	52	87	3	8	123	11-18
c	30	11.3	8	36	44	39	63	4	8	62	6-10
	60	12.7	15	58	73	53	98	3	8	100	11-14

of the last two sets (the fifth and sixth sets) were produced on both sides of the marginal warts of the second set. This position was different from that of the specimens from Usa in which they were produced on both sides of the marginal warts of the third set (see Fig. 13). Moreover in the specimens from Usa no adaxial cirri were produced.

It was observed that in one present specimen after degeneration of umbrella only a manubrium remained, and it could survive at least for three months by rearing. But neither regeneration of medusan body nor further differentiation took place.

b. In the case that the host is *Crassostrea gigas*

A number of the youngest medusae liberated in the laboratory at Sapporo were reared at such various water temperatures as 15–20°C (room temperature), ca. 20°C (in an incubator), and ca. 24°C (ditto) until they became degenerated, and the metamorphosis was observed. This observation was carried out with the following three purposes: (1) comparison of the metamorphosis of the present material with that of the above-described material of which host is *Mytilus edulis*, (2) grasp of the morphological variation caused by the different water temperatures,

Table 19. Measurements of various body portions of male medusa from
gigas). Measurements:

Age (days) No. of medusae examined Water temperature	30 7 15-20°C	30 22 20°C	30 9 24°C
W	9.5-11.9 (11.0)	10.0-12.2 (11.1)	10.8-11.9 (11.6)
H	5.2-7.1 (6.4)	6.3-7.5 (6.8)	6.3-7.0 (6.6)
J	3.2-4.0 (3.3)	2.9-3.7 (3.2)	3.2-3.5 (3.4)
P	3.2-4.8 (3.8)	2.9-4-8 (3.9)	3.5-5.7 (4.9)
M	1.7-1.9 (1.8)	1.6-2.2 (2.0)	1.7-1.9 (1.9)
S	0.40-0.48 (0.44)	0.40-0.48 (0.43)	0.32-0.48 (0.39)
V	0.63-0.79 (0.70)	0.63-0.79 (0.75)	0.63-0.79 (0.71)
L	1.6-1.9	1.4-1.9	1.3-1.9
GL	2.4-3.5	3.0-3.8	3.2-4.0
GW	ca. 0.16	ca. 0.16	ca. 0.16
Te	8	8 rarely 11	8
Mw	53-77 (66.6)	61-77 (69.9)	56-75 (68.9)
Ms	61-85 (74.6)	69-85 (78.0)	64-83 (76.9)
St	8	8 rarely 7, 9	8
Stl	50-60 (54.9)	45-65 (56.5)	53-63 (57.3)
Stl/St	5-9	4-12	5-9
Tb with cirri	7-8 (7.7)	0-8 (4.9)	5-8 (6.9)
Mw with cirri	7-14 (9.0)	0-8 (3.2)	0-12 (3.7)
Ms with cirri	12-22 (18.1)	1-15 (8.0)	6-20 (10.6)
No. of cirri on Tb	9-21 (16.3)	0-19 (7.6)	9-26 (14.7)
No. of cirri on Mw	6-20 (11.7)	0-9 (3.7)	0-16 (4.3)
C	17-39 (28.0)	1-28 (11.3)	9-42 (19.0)
Max no. of cirri on 1Tb, 1Mw	4, 2	4, 2	4, 2

and (3) settlement of the systematic status of *Ostreohydra japonica* Yamada.

It was noticed as to the morphology of the present youngest medusa that a very few abaxial cirri had many large nematocysts, probably the same kind as the exumbrellar nematocysts, on their proximal portions. All the specimens reared at any water temperature became to have eight tentacles when the umbrella was ca. 5–8 cm (mean 7 cm) in diameter on the 8–12th day after liberation (observed in 40 specimens). In this stage immature gonad, short peduncle, and a black band on the manubrium had appeared; and the cirri on the tentacular bulb had not disappeared and on some marginal warts the lateral cirri were newly produced.

About a month after liberation all the specimens began to mature and assumed the adult form (Table 19, left column). No distinct morphological difference was found among the specimens reared at various water temperatures, while in many specimens reared at ca. 24°C the peduncle was more elongated and protruded from the umbrellar aperture. The lateral cirri still remained in every specimen, and most of them were found on the tentacular bulbs and the marginal warts of the second set

Mukaishima Island at various developmental stages (host: *Crassostrea*
range (mean), in mm.

60	60	91	67
8	3	5	1
20°C	24°C	20°C	24°C
11.6-14.6 (12.8)	13.0-14.3 (13.8)	11.6-14.3 (12.7)	10.3
6.3-7.9 (7.2)	6.3-7.9 (7.1)	6.3-8.7 (7.8)	7.1
3.2-4.0 (3.5)	3.8-4.0 (3.9)	3.7-4.0 (3.9)	4.0
5.7-7.1 (6.6)	5.6-6.3 (6.1)	3.5-6.3 (5.1)	2.7
1.9-2.2 (2.0)	1.7-1.9 (1.9)	1.6-1.8 (1.7)	1.1
0.48	0.40-0.48 (0.43)	0.40-0.48 (0.44)	0.32
0.79-0.95 (0.94)	0.63-0.79 (0.68)	0.48-0.79 (0.65)	0.32
1.6	-	-	-
3.7-4.9	-	-	-
up. to 0.24	-	-	-
8-12 (9.5)	10-18 (14.0)	9-17 (12.8)	16
80-94 (89.0)	79-88 (83.0)	78-94 (86.2)	63
92-102 (98.5)	96-98 (97.0)	93-103 (99.0)	79
8 rarely 9	8	8	8
67-101 (82.8)	58-82 (69.0)	56-96 (73.6)	50
6-14	5-12	2-17	4-8
1-9 (4.4)	9-11 (10.3)	9-12 (10.4)	8
11-41 (16.9)	0-27 (11.7)	4-34 (12.8)	0
13-45 (23.3)	11-29 (19.7)	14-44 (23.2)	8
1-15 (6.3)	16-20 (18.0)	14-23 (18.2)	9
11-50 (21.8)	0-37 (15.3)	4-37 (13.8)	0
13-57 (28.0)	20-55 (33.3)	18-53 (34.2)	9
2, 2	4, 2	4, 2	2, 0

which were produced on both sides of a statocyst and became larger than the other warts. The number of lateral cirri showed a wide individual variation, hence no apparent distinction was found among these specimens reared at different water temperatures; while it had a tendency that the specimens reared at a lower temperature (15–20°C) had more lateral cirri than those reared at a higher temperature (20–24°C).

The male gonad was white in color, the ring canal still green, and the distal and proximal part of the manubrium and the tentacular bulbs were red in color. As an unusual case one specimen had 10 tentacles on the 22nd day and it had 11 tentacles on the 30th day, and two radial canals were slightly branched and the arrangement of marginal warts was somewhat irregular. It was observed that several specimens reared together in one container were smaller and they were different in their size with each other, though no cannibalism was found. The measurements of these specimens were not included in Table 19.

After one month the room temperature rose to 20–25°C and all the specimens reared in that temperature were degenerated. But the specimens reared in an incubator at 20° or 24°C were still healthy; and on and after about the 40th day the umbrellar diameter began to increase markedly. The diameter attained ca. 14 mm and with the further elongation of peduncle the manubrium completely protruded from the umbrellar aperture. The gonad fully matured and extension to the upper part of the peduncle was found. And then all the specimens turned out male. The lateral cirri still remained, and marginal warts and statoliths increased in number, and furthermore complication of oral lips was found (Fig. 16).

On the 60th day many specimens reared at 20°C and all the specimens reared at 24°C became spent. No further elongation of manubrium and complication of oral lips were observed, though all other characters developed further, particularly further elongation of the peduncle from the umbrellar aperture and further increase in the number of marginal warts, of statoliths, and of lateral cirri were observed. And most of the speicmens had more than eight tentacles (Table 19, middle column). In some specimens little branches of radial canal on peduncle and both the adaxial and the marginal cirri were found.

One specimen continuously reared at 24°C began to degenerate on the 67th day, and its umbrellar diameter and all the body portions such as peduncle, manubrium, velum, tentacular bulbs, and marginal warts became smaller, and furthermore the shape of oral lips became simpler and most of the lateral cirri became finger-like processes. Moreover, some of marginal warts, statoliths, and

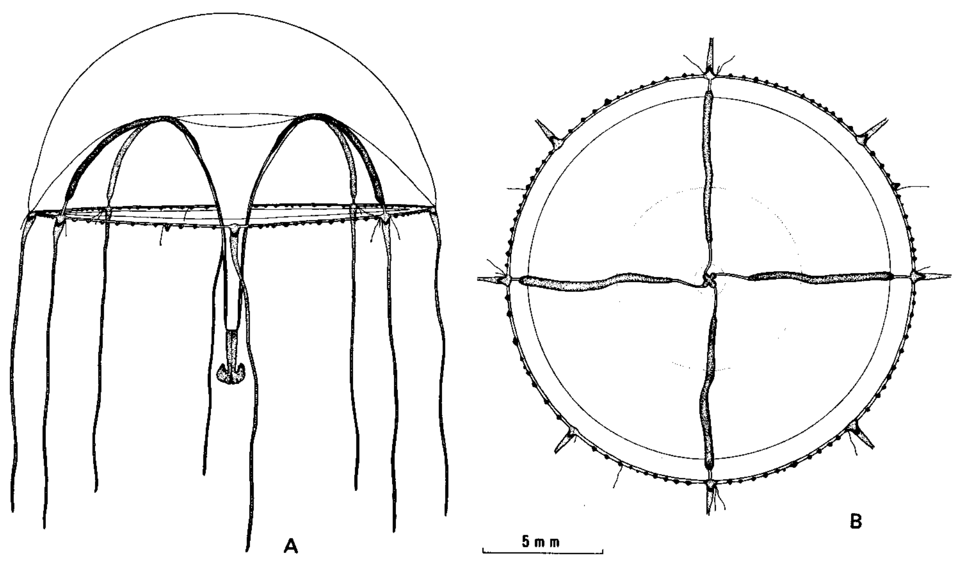

Fig. 16. A male mature medusa from Mukaishima Island (host: *Crassostrea gigas*), 45 days old. A: side view, B: aboral view (marginal tentacles are omitted).

of lateral cirri disappeared (Table 19, right column). This specimen seemed to be completely atrophied within a week afterwards.

On the other hand, five specimens continuously reared at 20°C survived for 90 days, though all of them became spent and two of which were somewhat degenerating. In this stage, the umbrellar diameter did not increase further and not exceeded 14.5 mm. The length of peduncle and manubrium and the width of velum became rather smaller (Table 19, right column), while the number of tentacles increased (up to 17). But the total number of marginal swellings was unchanged (about 100) on and after two months after liberation (cf. Fig. 20). The statocyst was still eight in number, while the number of statoliths increased still more in some statocysts and up to 17 ones were counted in one statocyst, but in some others the number decreased due to the degeneration. The lateral cirri did not disappear and the number in a medusa was unchanged, still showing a wide variation range; though it was noticed that the cirri on tentacular bulbs increased in number while those on marginal warts decreased. And as a rare case one marginal cirrus was present in one specimen. No further branching of radial canal and extension of the branches which appeared on the 30th day were found. There were black bands on tentacular bulbs and manubrium, and the band on the upper and lower regions of manubrium was darker. The oral lips were somewhat crenulated and the tip was slightly recurved.

One specimen reared at 20°C had been survived for just four months, but it began to degenerate thereafter. The umbrella became opaque, and the umbrellar margin of one quadrant was atrophied. The tentacle was lean and there were at least 15 ones, and the peduncle and the manubrium became smaller. It could not capture *Artemia* nauplii well and the swimming became weak. It seemed that this specimen completely degenerated within a week afterwards.

Summing up the above-described process of metamorphosis in the present material, the following is presented. The medusa began to assume a mature form on and after about a month, and within two months all the metamorphic characters nearly completely developed. Above all the elongation of the peduncle and increase of the number of marginal warts and statoliths were conspicuous. The lateral cirri were found in every developmental stage, though their number and position were highly variable. The life-span was about two to three months in most of the specimens, though it was different according to the rearing conditions. No distinct morphological difference was found among the specimens reared at various water temperatures, while the specimens reared at a higher temperature grew more rapidly and degenerated earlier. And the specimens reared at a constant water temperature survived well than those at a fluctuating water temperature.

Compared the metamorphosis in the present specimens of which host was *Crassostrea gigas* with that of the above-described specimens from the same locality of which host was *Mytilus edulis*, both materials developed nearly in the same way and assumed a similar morphology, while the following differences were found (cf. Tables 23, 24). In the present specimens, (1) the total number of marginal

Table 20. Measurements of various body portions of medusa
Measurements: range

Age (days)	14	23-35
No. of specimens examined	6	20[1]
(Sex)	(3♂+2♀+1?)	(17♂+3♀)
Water temperature	20-24°C	18-24°C
W	7.5-8.7 (7.9)	7.5-10.3 (9.1)
H	4.8-5.6 (5.0)	4.8- 7.1 (6.1)
J	2.1-2.7 (2.5)	2.4- 3.8 (3.0)
P	0.79-2.1 (1.5)	0.95- 2.9 (2.0)
Te	8	8 rarely 9, 10
Mw	30-41 (36.0)	28-59 (37.8)
Ms	38-49 (44.0)	36-69 (45.9)
St	8	8
Stl	52-67 (55.7)	46-86 (61.0)
Stl/St	6-9	5-13
Tb with cirri	0-8 (2.5)	0-5 (0.5)
Mw with cirri	0	0-16 (2.3)
Ms with cirri	0-8 (2.5)	0-16 (2.7)
No. of cirri on Tb	0-17 (4.3)	0-8 (0.7)
No. of cirri on Mw	0	0-18 (2.6)
C	0-17 (4.3)	0-18 (3.2)
Max. no. of cirri on 1Tb, 1Mw	3, 0	2, 2

1) Combined with the already

swellings is much more, (2) the peduncle is more elongated and far away protruded from the umbrellar aperture, (3) the black band is clearly present on the tentacular bulb in every specimen, (4) a marginal cirrus is rarely found.

3. Metamorphosis in the materials from Hokkaido, northern Japan

As described above, in the materials from southern Japan the medusa was reared until degeneration for several months. As a result, conspicuous morphological changes in some important taxonomic characters appeared and the medusa often grew into a giant one. In the material from northern Japan, however, the morphological change of medusa after maturation and the life-span have been unknown, therefore the following observations were made. A number of the newly liberated medusae of which polyps were associated with seven bivalve species from several localities in Hokkaido were reared (cf. Table 2). Among these, in the materials from Oshoro of which hosts were *Mytilus edulis* and *Crenomytilus grayanus* the metamorphosis for about three months was observed in detail, moreover to know the morphological variation the latter specimens were reared at various water temperatures and salinities.

from Oshoro at various developmental stages (host: *Mytilus edulis*).
(mean), in mm.

60-63	90-93	30	60	91
11	7	1	1	1
(9♂+2♀)	(4♂+1♀+2?)	(♀)	(♀)	(♀)
20°C	20°C	20°C	20°C	20°C
8.6-11.1 (10.1)	8.7-11.4 (10.3)	10.0	10.5	11.7
6.8- 8.4 (7.6)	7.1- 8.4 (7.8)	7.9	7.6	8.7
3.3- 4.1 (3.8)	3.5- 4.6 (4.1)	3.8	3.8	4.4
1.9- 4.3 (2.9)	1.3- 4.3 (2.7)	2.5	2.4	4.3
8-12 (8.8)	8-17 (13.0)	10	10	11
29-59 (42.6)	38-56 (43.6)	44	44	47
41-69 (51.5)	46-73 (56.6)	54	54	58
8	8 rarely 7	10	10	10
82-111 (91.5)	74-98 (85.0)	83	106	154
7-16	3-18	6-12	9-12	13-20
0-11 (1.8)	0-15 (3.9)	1	8	10
0-54 (8.7)	0-30 (8.9)	0	8	21
0-55 (10.5)	0-37 (12.7)	1	16	31
0-28 (4.9)	0-44 (9.0)	1	11	36
0-69 (14.1)	0-40 (13.9)	0	9	47
0-78 (19.0)	0-82 (22.9)	1	20	83
6, 3	6, 5	1, 0	3, 2	6, 3

reported description (Kubota 1978a).

a. Metamorphosis in the material from Oshoro of which host is *Mytilus edulis*

The present hydroid had a precocious medusa and many specimens were matured so soon on the 14th day after liberation, when eight tentacles were present and the black band was found on both the tentacular bulbs and the upper part of manubrium, while most of the cirri disappeared, the peduncle was still short, and a number of exumbrellar nematocysts remained (see Table 20).

On about a month after liberation, when every specimen became matured, the peduncle elongated and reached near the umbrellar aperture, the number of statoliths increased, and the jelly at the apex of umbrella became thick due to the further growth of the medusa (Fig. 17). In some specimens the ninth or the tenth tentacle was produced, though no other distinct morphological changes appeared (see Table 20).

On about two months after liberation many medusae were still matured, while some ones became spent. With the further increase of size the jelly became thicker and the peduncle elongated further (but not protruded from the umbrellar aperture), some marginal warts put forth tentacles, and the number of statoliths increased; though the number of marginal swellings did not so much increase. The most noticeable change was recognized in the character of lateral cirri; in nearly half

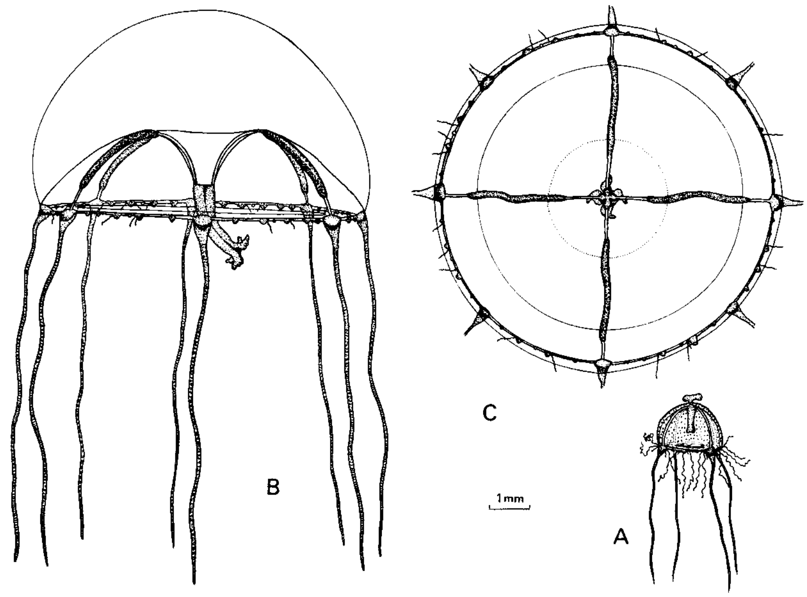

Fig. 17. A male medusa from Oshoro at the youngest (A) and the mature stage 28 days old (B, C) (host: *Mytilus edulis*). A, B: side view (from Kubota 1978a), C: aboral view (marginal tentacles are omitted).

the number of specimens examined (all the female ones and some male ones) the cirri reappeared (see Table 20), and up to 78 cirri were found in one specimen (cf. Fig. 20). It was observed that a well-developed cirrus attained 1.9 mm in length and that the end of two marginal tentacles was swollen in one specimen as a rare case.

On about three months after liberation the specimens became spent and some of the statocysts and statoliths degenerated. In this stage no subsequent morphological changes appeared except for tentacles of which number increased further (up to 17) due to the formation of tentacles on some of the marginal warts of the second set. As was the same case in the two-month-old specimen, two types were discriminated concerning the character of the lateral cirri; one was without cirri and the other was with numerous cirri (up to 82 in number) (cf. Fig. 20; Table 20). The black bands were still found on the tentacular bulbs and on the upper part of manubrium, while in some specimens the band on manubrium reached its lower part.

In addition to these normal specimens in morphology, in one abnormal specimen with five radial canals superficially due to the bifurcation of one radial canal, the metamorphosis was observed for about three months. The tentacles, marginal warts, and statocysts were produced subsequently and they arranged regularly in each of the five parts of the umbrellar margin; and the major morphological changes proceeded similarly to the above-described normal specimens. This specimen turned out female on the 30th day, when the cirri disappeared with maturation; but many cirri reappeared as the medusa became spent (Table 20, right column).

b. Metamorphosis in the material from Oshoro of which host is *Crenomytilus grayanus*, with reference to the morphological variation in connection with the difference of water temperature and salinity

The present specimen grew into a well-developed medusa of morphology similar to the above-described medusa when they were reared under the same conditions (in the filtered sea water from Oshoro and at ca. 20°C). In regard to the most variable character of the lateral cirri, almost all of them disappeared as the gonad matured, but in one male specimen many cirri reappeared afterwards (Table 21).

In addition to this observation, some specimens were reared for two months in the filtered sea water from Oshoro at 15°C and 25°C in an incubator; and after acclimation for a week, some specimens were reared in the instant sea water of different salinities such as 20‰, 30‰, and 40‰ at 20°C.

The medusa reared at any water temperature grew well and assumed a similar morphology with each other, while the following difference was found (Table 21). The specimen reared at the highest temperature (25°C) tended to be smaller and the gonad did not develop well, and the lateral cirri did not disappear and many cirri were found, mostly on tentacular bulbs and the marginal warts of the second set. Furthermore a black band on tentacular bulbs was indistinct or absent, while a black band was apparent on the manubrium. In contrast with this, in the specimen reared at the lowest temperature (15°C) lateral cirri entirely disappeared when matured, and marginal swellings were fewer in number. Furthermore black bands were apparent on tentacular bulbs, but those on manubrium tended to be indistinct. The fact that the black band on the tentacular bulbs was indistinct at higher temperature was already noticed in the material of which polyp was associated with *Mytilus edulis* from Oshoro by the author (see Kubota 1978a, p. 134).

On the other hand, the medusa reared in the instant sea water of any salinities also grew well and turned out female with normal eggs and spawning of eggs was observed. They assumed a similar morphology with each other, though the following difference was found (Table 22). All the specimens reared in the sea water of the highest salinity (40‰) had more lateral cirri. But all the other specimens reared in the sea water of lower salinities (20‰, 30‰) had no cirri except only one specimen which had two cirri. It is noticeable that almost all of these lateral cirri were found on the tentacular bulbs. In the specimens reared in the sea water of the lowest salinity (20‰) the statoliths were fewer in number on the 28th day, the peduncle did not elongate and remained short even on the 60th day, while the oral lip was more crenulated than the others; moreover black bands were

Table 21. Measurements of various body portions of medusa from
Measurements:

Age (days)	28	28	28
No. of specimens examined (Sex)	4	8	6
Water temperature	15°C	20°C	25°C
W	9.5-9.8 (9.6)	9.5-11.1 (10.1)	7.5-9.8 (8.7)
H	6.5-7.1 (6.9)	6.0-7.8 (6.8)	5.6-6.7 (6.1)
J	2.9-3.2 (3.1)	3.0-3.5 (3.2)	2.7-3.3 (3.0)
P	1.3-1.6 (1.5)	0.95-1.9 (1.6)	0.63-1.6 (1.1)
M	1.6-2.4 (2.1)	1.3-2.2 (1.8)	1.3-2.2 (1.7)
S	0.40-0.48 (0.41)	0.32-0.56 (0.46)	0.32-0.48 (0.40)
V	0.95-1.1 (1.0)	0.79-0.95 (0.87)	0.48-0.79 (0.71)
Te	8	8	8 or 9
Mw	31-34 (32.2)	32-50 (38.1)	34-48 (42.5)
Ms	39-42 (40.3)	40-58 (46.1)	42-56 (50.8)
St	8	8	8
Stl	56-76 (63.5)	58-81 (72.4)	65-85 (76.0)
Stl/St	5-12	6-11	7-12
Tb with cirri	0	0-3 (1.1)	6-9 (7.5)
Mw with cirri	0	0	8-25 (16.8)
Ms with cirri	0	0-3 (1.1)	16-33 (24.3)
No. of cirri on Tb	0	0-4 (1.4)	6-33 (16.3)
No. of cirri on Mw	0	0	9-36 (20.3)
C	0	0-4 (1.4)	22-69 (36.7)
Max. no. of cirri on 1Tb, 1Mw	0, 0	2, 0	5, 3

indistinct on all of the tentacular bulbs and sometimes on manubrium.

Compared these specimens reared in the instant sea water of various salinities at 20°C with those reared in the sea water from Oshoro at ca. 20°C, both were nearly of similar morphology, though the former was somewhat smaller in size, the manubrium was longer on the 30th day but shorter on the 60th day, and statoliths were fewer in number.

Judging from the facts described above, the present medusa survived well and developed normally under a wide range of environmental condition. And no distinct morphological difference appeared in spite of the considerable difference of the environment. However, as to the two characters, lateral cirri and black band, which are variable in the ordinary condition, a distinct difference was found. Namely many lateral cirri were present at the rearing condition of high water temperature or high salinity. The black band on tentacular bulbs was usually indistinct or absent at the rearing condition of high water temperature or low salinity, while that on manubrium was usually indistinct or absent at low temperature or low salinity.

Compared the present material from northern Japan with that from southern Japan (Mukaishima Island) of which polyp was associated with an oyster and reared

Oshoro reared at various water temperartures (host: *Crenomytilus grayanus*).
range (mean), in mm.

60	60	61	89	126
2	4	1	3	2
(2♀)	(3♀+1♂)	(1♀)	(2♀+1♂)	(1♀+1♂)
15°C	20°C	25°C	20°C	20°C
10.3, 9.5	10.3-12.2(11.3)	9.5	9.5-11.9(10.5)	8.9, 10.0
8.1, 8.6	7.1-9.5(7.9)	6.7	7.1-9.2(8.0)	6.3, 8.3
3.5, 3.8	3.3-4.4(3.9)	3.5	3.8-4.6(4.1)	3.7, 4.6
1.9, 1.7	3.2-4.4(3.6)	2.1	1.7-3.3(2.5)	1.6, 1.6
2.9, 2.4	2.5-2.9(2.7)	2.4	2.1-2.4(2.2)	2.4, 1.7
0.48, 0.40	0.48	0.48	0.48	0.48, 0.32
0.95, 0.95	0.79-0.95(0.86)	0.79	0.63-0.79(0.75)	—
8, 8	8-10(8.8)	10	9-10(9.7)	10, 9
35, 36	48-57(52.3)	46	49-56(53.0)	50, 55
43, 44	58-65(61.0)	56	59-65(62.7)	60, 64
8, 8	8	5	8 rarely 6	7, 5
99, 92	88-102(92.5)	52	68-112(93.0)	—
10-15, 9-13	0-16	5-15	0-17	—
0, 0	0-1(0.25)	7	0	0, 0
0, 0	0-30(7.5)	34	0-15(5.0)	0, 13
0, 0	0-30(7.8)	41	0-15(5.0)	0, 13
0, 0	0-2(0.5)	15	0	0, 0
0, 0	0-41(10.3)	49	0-15(5.0)	0, 18
0, 0	0-41(10.8)	64	0-15(5.0)	0, 18
0, 0	2, 2	3, 3	0, 1	0, 2

at various water temperatures (15–24°C), the degree of disappearance of the lateral cirri in connection with the difference of water temperature was different: the latter specimens reared at lower temperature had fewer lateral cirri (see Table 19), which was rather a reversed case to the former specimens described above (see Table 21).

c. Metamorphosis in the materials from Oshoro and its vicinity of which hosts are rarely commensal with polyps.

As rare cases, the commensal polyps were associated with the following four bivalve species, *Septifer virgatus* and *Chlamys swifti* from Oshoro, *Peronidia venulosa* from Zenibako, and *Mytilus coruscus* from Utasutsu, Hokkaido (see Table 2; cf. VI). Their newly liberated medusae were reared for about one to two months in order to examine their mature medusae and compare them with the materials of which polyps were associated with *Mytilus edulis* and *Crenomytilus grayanus* from Oshoro described above.

As a result, all these materials grew well and they were of similar morphology in spite of the difference of their hosts (see Table 23). They were also precocious medusae and on the 14th day maturation was observed in many specimens. And with the maturation the cirri entirely or mostly disappeared. The peduncle did

Table 22. Measurements of various body portions of medusa from *Crenomytilus grayanus*). Measure-

Age (days)	28	28
No. of specimens examined	4	4
Salinity (‰)	20	30
W	8.7-9.0 (8.8)	8.7-9.4 (9.0)
H	6.0-6.3 (6.2)	5.6-6.3 (6.1)
J	3.2	2.7-3.2 (3.0)
P	1.6	1.7-2.1 (1.9)
M	2.2-2.4 (2.3)	2.4-2.7 (2.5)
S	0.48-0.63 (0.52)	0.48-0.56 (0.49)
V	0.95	0.95
Te	8	8
Mw	33-34 (33.3)	32-36 (33.3)
Ms	41-42 (41.3)	40-44 (41.3)
St	8	8
Stl	57-62 (59.5)	71-82 (76.8)
Stl/St	4-10	7-13
Tb with cirri	0-2 (0.5)	0
Mw with cirri	0	0
Ms with cirri	0-2 (0.5)	0
No. of cirri on Tb	0-2 (0.5)	0
No. of cirri on Mw	0	0
C	0-2 (0.5)	0
Max. no. of cirri on 1Tb, 1Mw	1, 0	0, 0

not protrude from the umbrellar aperture. And the black band was always found on manubrium, while on tentacular bulbs it was indistinct or absent in some specimens. It is noticeable that in the materials from Utasutsu the lateral cirri were still present on the 30th (rather many in number) and the 59th days (in a small number), and a cirri attained 2.7 mm in length.

d. Metamorphosis in the materials from other localities in Hokkaido, northern Japan

From other three localities faced on the Pacific coast of Hokkaido, in addition to the above-mentioned three localities faced on the Japan Sea coast of Hokkaido, similar polyps were found and their metamorphosis was examimed (see Table 23). The materials from Akkeshi Bay of which host was *Clinocardium californiense* was reared for about a month until maturation and the metamorphosis was already reported by the author (Kubota 1979b). And the subsequent formation of marginal tentacles, marginal warts, and lateral cirri was analized in detail (Fgi. 18). From this locality despite of the examinations of a large number of various bivalves no commensal polyps have been re-discovered (cf. Tables 32, 34). Fortunately at the two localities in Uchiura Bay, Kuroiwa and Mori, similar polyps associated

Oshoro reared in the instant sea water of various salinities (host:
ments: range (mean), in mm.

28	58	58	58
4	2	2	2
40	20	30	40
9.2-9.5 (9.4)	8.7, 9.5	8.7, 11.1	10.6, 10.3
5.1-6.2 (5.8)	7.1, 7.8	6.3	7.0, 6.3
2.7-3.0 (2.9)	3.7	3.2	3.7, 3.2
1.3-1.7 (1.6)	1.7	2.4, 2.5	2.7, 3.2
2.2-2.4 (2.3)	2.2	2.2, 1.9	2.5
0.32-0.48 (0.41)	0.48	0.48	0.48
0.95	0.79	0.79, 0.63	0.79
8	8	8, 16	10, 12
35-36 (35.3)	40, 43	36, 43	37, 42
43-44 (43.3)	48, 51	44, 59	47, 54
8	8	8, 4	8
76-84 (80.3)	84, 90	109, 28	88, 112
8-13	8-15	9-16	10-18
7-8 (7.5)	0	0	0, 2
0-1 (0.25)	0	0	1, 0
7-9 (7.8)	0	0	1, 2
8-14 (11.3)	0	0	0, 3
0-1 (0.25)	0	0	2, 0
9-14 (11.5)	0	0	2, 3
3, 1	0, 0	0, 0	0, 2; 2, 0

with *Mytilus edulis* and their newly liberated medusae were reared for about one to two months.

As a result, both the specimens from Akkeshi Bay and Uchiura Bay were precocious medusae and on the 14th to 20th day maturation began to occur. Their mature medusae were of similar morphology and all the cirri disappeared (Fig. 18; Table 23), while the specimens from Uchiura Bay were more premature and had fewer tentacles and statoliths.

C. Seasonal Occurrence of Medusa at Oshoro, Northern Japan, with Some Planktonic Medusan Records in Japan

The seasonal occurrence of medusa was surveyed by the surface and vertical hauls at Oshoro during the five years from 1977 to 1981. The newly liberated medusa appeared at first in late June or early July every year, and it was usually captured for about two months (July and August) continuously as is shown below. In this period the asexual reproduction of medusa-bud actively takes place (see I. B. 2. b), therefore at Oshoro the liberation of medusa regularly occurs in early summer every year.

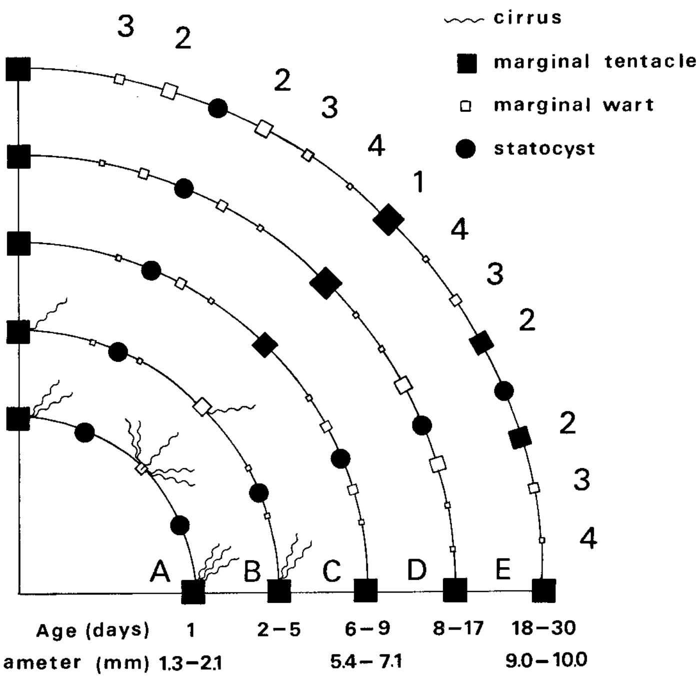

Fig. 18. Diagram showing the subsequent formation of marginal tentacles, marginal warts, and lateral cirri in a quadrant of medusa from Akkeshi (host: *Clinocardium californiense*), from oral side (from Kubota 1979b).

Year	Appearance of medusa
1977	July 5 – August 11
1978	June 30 – July 14
1979	June 30 – September 29
1980	July 5 – August 27
1981	July 2 – July 24

Almost all of the planktonic specimens were captured in July, and they were the youngest or immature medusae slightly developed with four tentacles and many cirri. The well-grown or the mature medusae with eight tentacles were, however, scarcely collected in spite of the abundant occurrence of the newly liberated medusa as well as the polyp in this locality.

Although the seasonal occurrence of medusa in southern Japan has not been studied, it is possibly different from that in northern Japan judging from the period of medusa-bud formation in that area (cf. I. B. 3). Up to the present, besides the above record in northern Japan, the following records on the occurrence of the planktonic medusa in central and southern Japan have been known. Two mature medusae with eight tentacles, eight statocysts, and many cirri were collected by Uchida (1925); one at Misaki in August, 1922 and the other at Yunohama in July, 1922, which was the first record of the present medusa in Japanese waters (see V and VI). And Yamazi (1958) listed the present species among the plankton organisms in Tanabe Bay and its environs. According to the list the medusa was captured in the bay in summer. At Mukaishima Island only one recently-liberated medusa was collected by the author on May 9th, 1979. It was 1.8 mm in umbrellar diameter and had three marginal tentacles, five marginal warts, eight statocysts, 22 statoliths, and 17 lateral cirri. This specimen had no trace of gonad and on each of eight marginal swellings a black band was present.

From the above-mentioned records it can be said that in Japanese waters the present planktonic young medusa appears at least in spring to summer in the year and it matures in summer, though the seasonal occurrence of medusa in northern Japan is somewhat different from that in southern Japan.

On the other hand, the morphology of the above-mentioned young or mature specimens collected in the sea well accords with that of the laboratory-reared ones. Furthermore as a result of rearing of some young specimens captured in the sea at Oshoro for one or two months, they grew up to the mature medusae with the similar morphology to the above-described laboratory-reared mature medusae.

D. Comparison of Metamorphosis between the Materials from Southern Japan and Those from Northern Japan, and Summary of Metamorphosis of Medusa

The above-described metamorphoses of medusae in Japanese commensal hydroids are summarized as follows (see Tables 23, 24). The small and immature newly liberated medusae grow rapidly and regularly into large and complicated mature medusa for about two to six weeks after metamorphosing. And after discharging of gametes for about a month the medusa finally becomes spent on about the 60th day. The life-span is usually two to three months, rarely four months, and in the senile medusa near degeneration irregular morphological changes such as branching of the radial canal and formation of many marginal tentacles occur.

The major features of the metamorphosis could be enumerated in the following. (1) The abaxial cirrus (cf. Fig. 17, A; Plate X, E), which is present on the interradial marginal wart of the youngest medusa, entirely disappears within several days after liberation. (2) The marginal tentacles, which are moniliform in shape (Fig. 19, A, B; Plate X, O), are always produced on the perradial and interradial bulbs and the number is usually eight. This number often exceeds eight due to the formation of some other tentacles mainly on the marginal warts of the second set (Fig. 19, C). (3) The marginal warts of several sets (at least three) are produced regularly and as a result many marginal swellings (at least about 40 in number) are found on the umbrellar margin. Further formation of marginal warts (more than the fourth

Table 23. Morphology of mature medusae one-month old from northern and southern

Locality	Host	No. of hosts and medusae examined	Sex	Age (days)	W (mm)	H (mm)
Oshoro	*Mytilus edulis*[1]	18, 20	♂, ♀	23-35	7.5-10.3 (9.1)	4.8-7.1 (6.1)
	Crenomytilus grayanus[2]	5, 20	♂, ♀	28	8.7-11.1 (9.4)	5.6-7.8 (6.5)
	Crenomytilus grayanus[3]	5, 10	♂, ♀	28	7.5-9.8 (9.1)	5.1-6.7 (6.0)
	Septifer virgatus	1, 1	♂?	30	8.9	—
	Chlamys swifti	1, 1	♂	35	8.4	5.7
Zenibako	*Peronidia venulosa*	1, 5	♂	29-31	8.7-10.0 (9.3)	—
Utasutsu	*Mytilus coruscus*	1, 4	♂	30	9.2-9.8 (9.5)	6.3-6.7 (6.5)
Mori and Kuroiwa	*Mytilus edulis*	7, 9	♂, ♀	30-31	8.7-9.7 (9.0)	6.3-7.1 (6.9)
Akkeshi	*Clinocardium californiensae*[4]	1, 15	♀	20-30	9.1-10.0 (9.5)	5.6-6.5 (6.1)
Usa	*Mytilus edulis*	1, 9	♀	35	9.5-10.3 (9.9)	6.4-7.9 (7.1)
Mukaishima Is.	*Myilus edulis*	1, 6	♀	30-42	9.5-11.4 (10.6)	6.2-8.3 (6.9)
	Crassostrea gigas	1, 38	♂	30-31	9.5-12.2 (11.2)	5.2-7.5 (6.6)
	8 speices	43, 138	♂, ♀	20-42	7.5-12.2	4.8-8.3

1) Together with the description already reported (Kubota 1978a). 2) Together with
3) Together with the measurements of specimens reared at 25°C and 40‰ (cf. Tables 21,

Table 24. Morphological range of medusa from mature

Locality	Host	Age (days)	W (mm)	H (mm)	P (mm)
Oshoro	*Mytilus edulis*[1]	14-93	7.5-11.4	4.8-8.4	0.79-4.3
	Crenomytilus grayanus[2]	28-126	7.5-12.2	5.1-9.5	0.63-4.4
Utasutsu	*Mytilus coruscus*	30-59	9.2-10.3	6.3-7.1	1.1-1.4
Mori and Kuroiwa	*Mytilus edulis*	30-59	8.7-9.7	6.3-7.1	1.3-2.4
Usa	*Mytilus edulis*[3]	25-100	8.3-11.0	5.2-7.9	1.4-3.2
Mukaishima Is.	*Mytilus edulis*[4]	30-90	8.7-13.0	6.2-8.7	1.6-4.8
	Crassostrea gigas[5]	30-91	9.5-14.6	5.2-8.7	2.7-7.1
	4 species	14-126	7.5-14.6	4.8-9.5	0.63-7.1

1) See Table 20. 2) See Tables 21, 22. 3) See Table 15. 4) See Table 18. 5) See
in every specimen).

set) often occurs regularly, while the position and order of the marginal warts produced lastly sometimes irregular (cf. Fig. 13). (4) Eight statocysts are usually present and the number does not increase during the life-span as a general rule, Japan, of which polyps are associated with various bivalves. Measurements: range (mean).

J (mm)	Te	Ms	Tb or Mw with cirri	C	Max. no. of cirri on 1Tb, 1Mw	St	Stl	Stl/St
2.4-3.8 (3.0)	8-10	38-69 (46)	0-5, 0-16	0-18 (3)	2, 2	8	46-86 (61)	5-13
2.7-3.5 (3.1)	8	39-58 (42)	0-3, 0	0-4 (0.5)	2, 0	8	56-82 (68)	4-13
2.7-3.3 (3.0)	8-9	42-56 (47)	6-9, 0-25	9-69 (24)	5, 3	8	65-85 (78)	7-13
—	8	46	0, 1	1	0, 1	8	67	5-11
2.5	8	39	0, 1	1	0, 1	8	61	6-9
—	8-9	43-62 (56)	0, 0	0	0, 0	8	65-72 (69)	6-12
3.0-3.3 (3.2)	8	52-55 (54)	4-7, 0	11-16 (14)	4, 0	8	65-80 (71)	7-12
3.2-3.7 (3.5)	8	32-53 (42)	0, 0	0	0, 0	8	66-91 (77)	6-14
2.4-3.0 (2.8)	8-14	39-48 (43)	0, 0	0	0, 0	8	80-102 (91)	8-15
3.2-4.0 (3.7)	8-9	53-62 (57)	0-2, 10-28	14-34 (23)	2, 2	8	68-88 (77)	7-13
2.9-3.7 (3.3)	8	43-66 (53)	0-8, 0-31	0-74 (35)	4, 3	7-8	56-105 (75)	6-13
2.9-4.0 (3.3)	8-11	61-85 (77)	0-8, 0-14	1-42 (19)	4, 2	7-9	45-65 (56)	4-12
2.4-4.0	8-14	32-85	0-9, 0-31	0-74	5, 3	8	45-105	4-15

the measurements of specimes reared at 15°C, 20°C, 20‰, and 30‰ (cf. Tables 21, 22). 22). 4) Kubota 1979b.

to spent stage in northern and southern Japan.

Te	Mw	Ms	Tb with cirri	Mw with cirri	C	St	Stl	Stl/St	Black band[6]
8-17	28-59	36-73	0-15	0-54	0-82	7-8	46-111	18	M, Tb
8-16	31-57	39-65	0-9	0-34	0-69	4-8	28-112	18	M, Tb
8	44-59	52-67	3-7	0	3-16	8	65-91	13	M
8	24-45	32-53	0	0	0	8	66-97	14	M, Tb
8-14	33-67	41-81	0-5	0-29	0-34	8-21	60-300	20	M
8-20	35-65	43-73	0-15	0-41	0-98	7-19	56-195	20	M, Tb
8-18	53-94	61-103	0-12	0-41	1-57	7-9	45-101	17	M, Tb
8-20	24-94	32-103	0-15	0-54	0-98	4-21	28-300	20	M, Tb

Table 19. 6) Black band present on manubrium (M) or on tentacular bulbs (Tb) (not present

while the number of statoliths rapidly increases after liberation and it usually more than seven in one statocyst (Fig. 19, C, D; Plate X, N). (5) The apex of jelly becomes remarkably thick and occupies about 1/2 of the umbrellar height.

(6) The peduncle is produced on the manubrium and usually hang down within the subumbrellar cavity, while sometimes protrudes from the umbrellar aperture far away. (7) The manubrium is quadrate in cross section and the length is usually about as long as the peduncle (Fig. 19, F), while it sometimes considerably shorter than the peduncle when the latter is greatly elongated. The oral lips are four in number and they are folded and frilled (Fig. 19, F, G; Plate X, K). (8) The gonad is linear in shape (Fig. 19, D, H; Plate X, L) and extends along the radial canal from its distal part near the ring canal to the proximal part on the upper part of the peduncle. (9) The exumbrellar nematocysts disappear

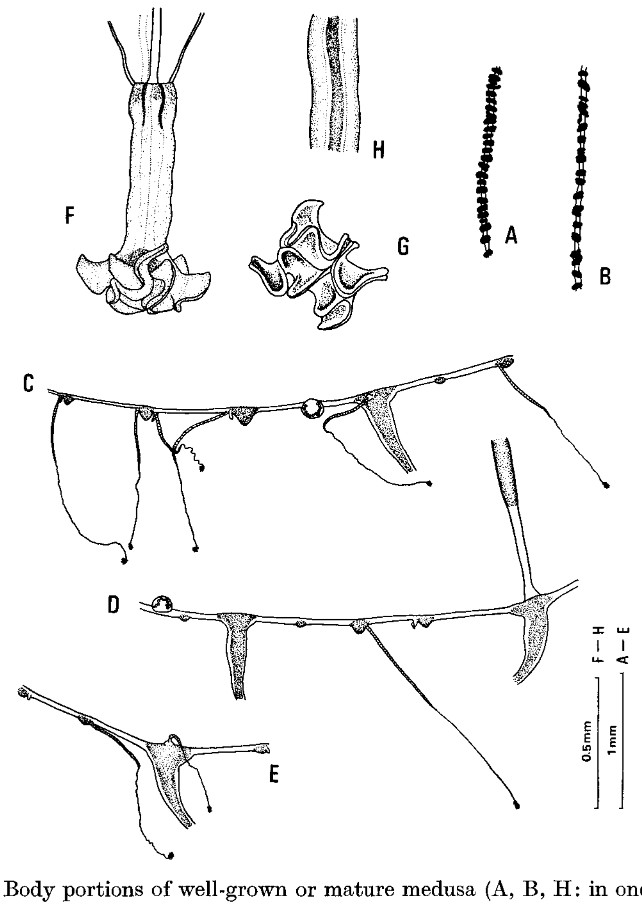

Fig. 19. Body portions of well-grown or mature medusa (A, B, H: in one male mature medusa 60 days old from Oshoro, C-G: in one well-grown medusa 60 days old from Mukaishima Island). A, B: a portion of marginal tentacle, C-E: several portions of umbrellar margin (oral view), F: a manubrium (side view), G: oral lips (oral view), H: a portion of male gonad. Hosts: *Mytilus edulis.*

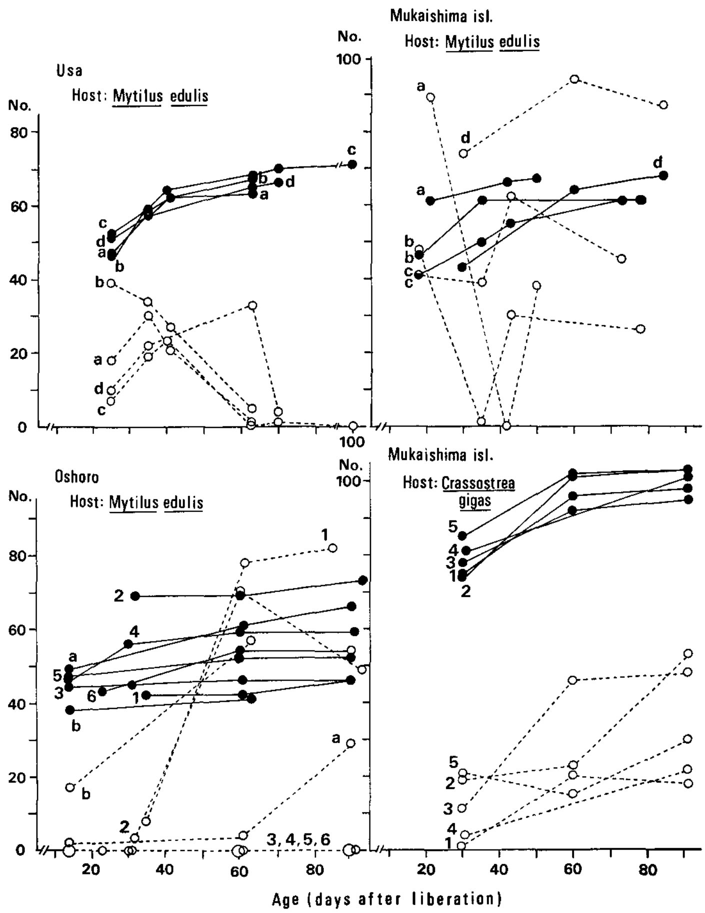

Fig. 20. Successive changes of number of marginal swellings (solid line) and cirri (dotted line) in several laboratory-reared specimens at 20°C from three localities. Each number in the figure shows the individual specimen.

gradually. (10) The black band is often present both on the abaxial side of the tentacular bulbs and the interradial region of the manubrium (Fig. 19, F), though it is a variable character and often indistinct or absent (Table 24). (11) The lateral cirri are either produced subsequently on one side or both sides of the tentacular bulbs and marginal warts (Fig. 19, C-E), or not produced anywhere and disappear gradually. It is also a variable character and after disappearance with the maturation of gonad it sometimes reappears afterwards with the age (Fig. 20; Table 24).

Going through the process of the above-summarized metamorphosis, the newly liberated medusa develops, matures, and degenerates, while the degree and the way of metamorphosis differs between the materials from northern and southern Japan. In the northern material the newly liberated medusa has usually four tentacles and begins to mature on the 14th day as a precocious medusa. With the maturation the cirri entirely or mostly disappear, while in some specimens they reappear afterwards with the age (Fig. 20). And several statocysts often disappear in the specimen near degeneration (Table 24, upper columns). In contrast with this, in the southern material the newly liberated medusa has usually two tentacles and the maturation begins on about the 30th day. The cirri usually do not disappear when matured and rather many cirri are produced on various marginal swellings (Fig. 19, C-E; Fig. 20). Although the morphology of mature medusa from Usa is almost similar to that from northern Japan (see Fig. 21) except for the character of cirrus, the material from Seto Inland Sea (cf. Table 24, Mukaishima Island), particularly the specimen whose host is an oyster, grows into the most-developed medusa with very elongated peduncle (up to 7.1 mm in length), numerous tentacles (up to 20 in number), a great number of marginal swellings (up to 103 in

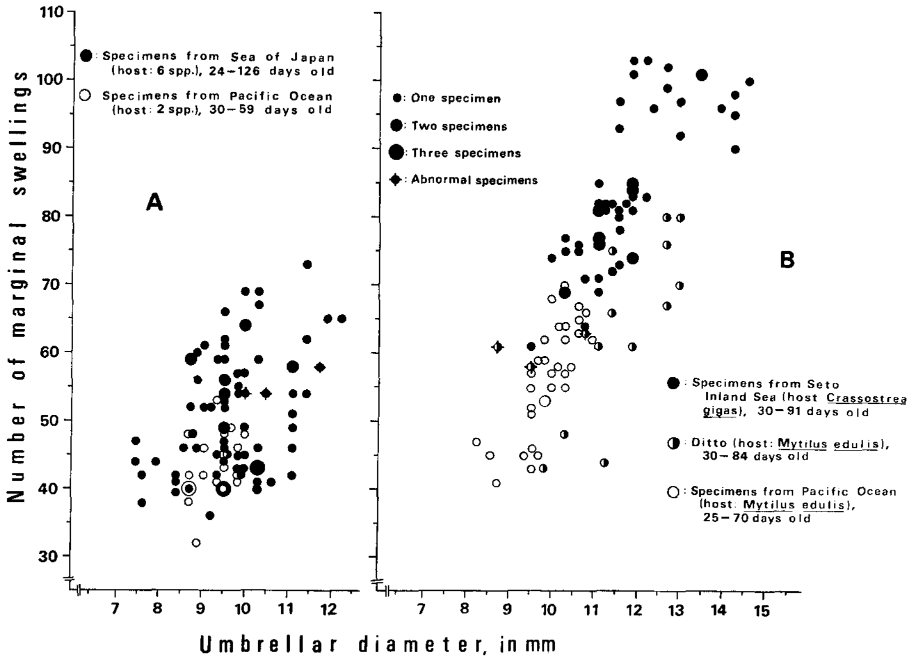

Fig. 21. Relationship between the umbrellar diameter and the number of marginal swellings of mature to spent medusa from northern Japan (A: specimens (○) from Akkeshi, Mori, and Kuroiwa, facing the Pacific Ocean and those (●) from Oshoro, Zenibako, and Utasutsu, facing the Sea of Japan) and southern Japan (B: specimens (○) from Usa, facing the Pacific Ocean and those (◐ ●) from the Inland Sea of Japan).

number); the size attains 14.6 mm in diameter and besides numerous lateral cirri several adaxial and marginal cirri are present and the number of cirri attains 98.

To show the above-mentioned morphological difference as well as the relationship between the umbrellar diameter and the number of marginal swellings between the materials from two Japanes regions, Fig. 21 and a table shown below are prepared, using numerous mature (♂♀) to spent specimens described in this chapter, namely 71 specimens which are of 24–126 days old and come from polyps associated with seven bivavle species collected from six localities in northern Japan (not included the specimens reared in the instant sea water of various salinities) and 53 specimens which are of 25–91 days old and come from polyps associated with two bivalve species from two localities in southern Japan. The number of specimens in Fig. 21 and the table are more than that of the individuals examined, because a number of same specimens were measured repeatedly, that is measured at their different ages.

No. of cirri in a medusa		0	1-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
No. of specimens from	North. Japan	63	14	9	4	2	3	1	2	2	2	0
	South. Japan	1	17	30	24	11	4	4	5	3	1	2

III. Gametes, Larvae, and Primary Polyp

A. Egg and Sperm

The egg size was examined in a large number of eggs spawned from many laboratory-reared mature medusae from both northern and southern Japan (Table 25). Almost all of these eggs were unfertilized within one day after discharge. The size of the discharged eggs were not different between the medusae from northern Japan (Oshoro, Mori, and Kuroiwa) and those from southern Japan (Mukaishima Is. and Usa). The egg was spherical in shape, though the size considerably varied as shown in Table 25. Of these eggs, a mature egg with an apparent germinal vesicle was 64–82 μm in diameter (Fig. 22; Plate X, P). The smaller eggs were probably immature ones or unhealthy ones probably lost the ability to fertilize. The size of egg was very small and the present egg may be classified in the smallest one among hydrozoans (see Tardent 1978, p. 174). As rare cases, elliptical eggs were found and the size was 66–90 x 58–72 μm in 14 eggs.

As to the morphology and size of sperm, no distinct difference was found in both the medusae from northern and southern Japan as was the same case in the egg. The head of sperm was cone-shaped and in the middle piece there were two small globules side by side (Fig. 22, B). The length of head and middle piece together was about 2.5 μm and the greatest width of middle piece was about 2.0 μm. The tail was 50–60 μm in length.

Table 25. Egg diameter of *Eutima* from various localities.

	Locality	Mukaishima Is.	Usa	Oshoro	Oshoro	Mori and Kuroiwa	Total (%)
	Host bivalve	*Mytilus edulis*	*Mytilus edulis*	*Mytilus edulis*	*Creno-mytilus grayanus*	*Mytilus edulis*	
	No. of medusae from which eggs are discharged	3	6	3	3	6	
Egg diameter, in μm	20		1	1		1	3 (0.1)
	22		0	0		0	0 (0)
	24		4	0		3	7 (0.3)
	26	2	4	1		4	11 (0.5)
	28	0	4	1	1	4	10 (0.5)
	30	0	0	1	1	1	3 (0.1)
	32	0	9	2	4	3	18 (0.9)
	34	0	6	6	5	12	29 (1.4)
	36	2	13	9	6	6	36 (1.7)
	38	2	4	1	1	7	15 (0.7)
	40	1	8	5	3	13	30 (1.4)
	42	3	11	6	11	13	44 (2.1)
	44	2	17	13	12	12	56 (2.7)
	46	1	4	1	5	6	17 (0.8)
	48	4	20	12	13	21	70 (3.4)
	50	2	19	16	12	23	72 (3.5)
	52	2	16	13	6	16	53 (2.6)
	54	1	12	7	8	12	40 (1.9)
	56	10	40	19	21	17	107 (5.1)
	58	17	50	13	25	39	144 (6.9)
	60	5	46	18	23	36	128 (6.2)
	62	6	32	4	11	23	76 (3.7)
Normal (mature) egg	64	4	119	56	37	72	288 (13.9)
	66	6	114	45	14	48	277 (10.9)
	68	8	111	30	10	29	188 (9.0)
	70	6	58	14	1	11	90 (4.3)
	72	1	82	35	3	45	166 (8.0)
	74		14	7	0	43	64 (3.1)
	76		3	0	0	28	31 (1.5)
	78		1	0	1	12	14 (0.7)
	80		0	17		14	31 (1.5)
	82		1	7		1	9 (0.4)
	84					1	1 (+)
Total no. of eggs (%)		85 (4.1)	823 (39.6)	360 (17.3)	234 (11.3)	576 (27.7)	2078 (99.8) (100)

B. Planula Larva

Using nine pairs of the laboratory-reared mature medusae mated between the specimens from the same locality or those from different localities, the fertilization was made and the planula larva was obtained (Table 26). Within two or three days after each pair began to be reared in one small container many planulae appeared, and no sexual isolation was present between the hydroid from southern Japan and that from northern Japan.

The planula larva swam actively and fast. By the movements of numerous epidermal cilia which were about 16 μm in length, the planula rotates clockwise when viewed from the direction of the proceeding. The planula (Fig. 22, D; Plate X, Q) was elliptic in shape and was 56–96 μm (mean 71 μm) in length and 40–64 μm (mean 52 μm) in greatest width in 78 specimens from several localities (Table 26). This size of planula was very small and the present planula may be classified in the smallest one among hydrozoans (see Tardent 1978, p. 228) as is the same case in the egg. The embryo just before planula (Fig. 22, C), which had no or very few cilia and nematocysts, was larger than the typical planula and was 72–106 μm (mean 84 μm) in length and 48–60 μm (mean 54 μm) in greatest width in 20 specimens from Oshoro. The planula usually survived for more than two weeks, but it decreased in size with the age and the number of cilia also decreased (Fig. 22, E, F). The old-age planula tended to sink to the bottom of the rearing container. The aged planula of 7–17 days old was 36–66 μm (mean 53 μm) in length and 28–50 μm (mean 41 μm) in greatest width in 42 specimens from several localities (Table 26).

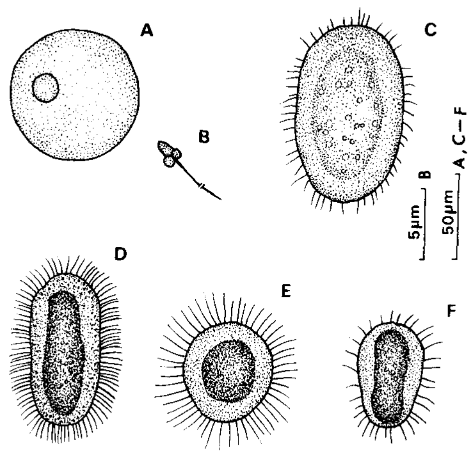

Fig. 22. Morphology of gametes and larvae. A: an unfertilized egg, B: a spermatozoon, C: an embryo just before planula about 20 hr. old, D: a typical planula about 5 days old, E, F: two aged planulae about 14 days old.

Table 26. Mating of mature medusae from some localities and the size of planulae appeared, in μm.

Female medusa Host (Locality)	×	Male medusa Host (Locality)	No. of pairs	Days for appearance of planula	Length (min.-mean-max.) × maximum width (ditto) of planulae, no. of planulae examined (age in days)
Mytilus edulis (Usa)	×	*Peronidia venulosa* (Zenibako)	1	3	—
Mytilus edulis (Oshoro)	×	*M. edulis* (Oshoro)	3	2	57-76-96×40-56-64, 17 (2-3)
Crenomytilus grayanus (Oshoro)	×	*C. grayanus* (Oshoro)	1	2-3	36-52-62×28-35-42, 4 (7)
Crenomytilus grayanus (Oshoro)	×	*Mytilus edulis* (Kuroiwa)	1	2-3	56-63-66×48-51-54, 11 (3) 36-50-60×28-33-40, 12 (10)
Mytilus edulis (Mori)	×	*M. coruscus* (Utasutsu)	1	2-3	60-70-88×48-52-58, 26 (3) 42-53-66×31-38-44, 12 (10)
Mytilus edulis (Kuroiwa)	×	*M. edulis* (Kuroiwa)	2	3	60-72-88×40-50-64, 24 (3-5) 40-50-62×32-42-50, 14 (17)

It was observed that many specimens were often gathered on a certain small area of the bottom of the container.

Some of the planulae could survive for about a month, but no planulae transformed into the primary polyps despite of manifold trials carried out many times. All the planulae, which did not attach to the rearing container without hosts or piecies of various host organs cut off, became completely destroyed without further differentiation. This fact may indicate that for the settlement of the larva a certain indispensable connection is established between the planula and the intact host bivalve. It is interesting here to note that (1) in some Eutimid hydroids which are possibly not commensal ones living in bivalves the planulae could attach to the rearing vessel and metamorphosed into the primary polyps (cf. VII. B) and that (2) the size of eggs of commensal hydroids belonging to *Eugymnanthea* is also very small (55–95 μm, Cerruti 1941), which might have a certain meaning for the reproductive strategy (See next section).

C. Primary Polyp

In order to observe the morphology of primary polyp and to verify the inference concerning the settlement of planula (see I. B. 2), four small specimens of *Mytilus edulis*, which were collected from Oshoro on October, 1981, were used as a host. These bivalves were separately kept in a small vessel, into which tens or hundreds of planulae of several days old were put. These planulae were obtained from seven laboratory-reared mature medusae (2♂+5♀), which come from two large specimens of *M. edulis* collected from Oshoro on June, 1981.

Within several days, as shown below, a small number of metamorphosing planulae or primary polyps were found to be attached to the very restricted body portions of the host, namely exclusively the small area of the mantle just beneath the labial palp.

Host size, in anterior-posterior axes (cm)	Days after addition of planulae	No. of planulae attached in each side of mantle cavity	Body portions to which planulae attached
3.5*	1	10, 14	mantle just beneath the labial palp (=**m**), **m** plus labial palp
3.0	1	1, 2	**m**, middle part of mantle
2.8	4	0, 4	–, **m**
2.7*	4	1, 6	**m**, **m**

The inference regarding the site for settlement of larva may be ascertained, though attachment to the labial palp and the other portion of mantle of the host were observed. The direction of water current within the mantle cavity of the host may be one of the primary factors to explain the above limited settling site for planula, so in this sense the planula passibly attached to the host. On the other hand, the inference concerning the number of planula invaded in a host at time is one not supported, because more than one planulae (3–24) invaded to one host. It is noticeable that several planulae were entangled in the pseudofaeces, but no planulae except the ones attached to the host were found in the rearing sea water. Accordingly there is a possibility that a number of planulae is eaten up by the host.

Ten primary polyps of several days old were measured, four were in living state and the others in preserved state, both picking up from the two hosts, asterisked in the above table, after narcotization. The morphology of primary polyp in well-extended condition is as follows.

Length from hypostome to pedal disk: 54–88 μm (mean 70 μm)
Width of hydrocaulus: 24–29 μm (mean 26 μm)
Diameter of pedal disk: 33–48 μm (mean 38 μm)
Number of tentacles: 5–7 (mean 5.6)

The primary polyp is solitary and very small, being as large as the planula. The hydrocaulus always sits upright in the edge of the ovoid pedal disk (Fig. 23, H). The latter period of hydranth formation could be observed in one specimen (Fig. 23, A-D; Plate X, R) after it was removed from the host in the stage of Fig. 23, A. In this specimen the tentacle was fully developed within two days thereafter, accompanying the development of tentacular web. This specimen survived for a month, and no further morphological change did not take place except degeneration of the pedal disk.

On the other hand, another, probably an abberant, morphological change of planula was observed in three specimens without hosts. They had no pedal disk,

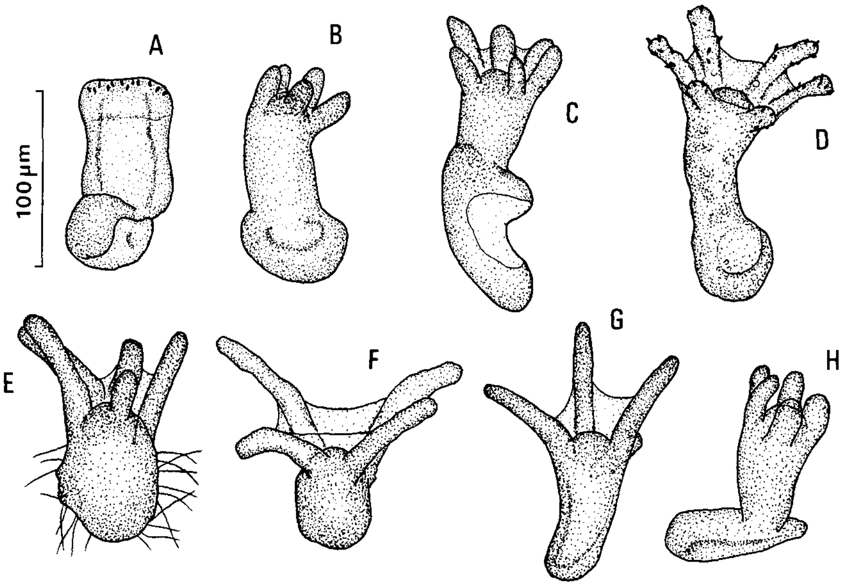

Fig. 23. Morphology of primary polyp. A-D: hydranth formation of the same specimen (A: metamorphosing planula within a day after attaching to the host by the pedal disk; B: five hours after A, tentacles slightly developed; C: 21 hours after A, note the presence of tentacular webs; D: 51 hours after A, fully developed primary polyp), E-G: three aberrant polyps without pedal disk, note in E the presence of cilia, H: primary polyp, note the position of hydrocaulus.

while two had four tentacles with webs (Fig. 23, F, G) and the other had not only five tentacles with webs but also many cilia by which it swam (Fig. 23, E).

Now that both the morphology of planula and its most probable settling site within the host has been revealed, host selection of planula among the bivalves belonging to Mytilidae will be able to clarify in the near future, expecting to make an explanation of the problem posed in VI. B.

IV. Nematocysts

All the examinations of nematocysts were made on the living specimens except for the newly liberated medusa from Akkeshi in which a frozen specimen was used. The constitution of nematocyst-kinds and their size (length x maximum width) in undischarged state were examined in different life stages and on their various body portions. The results are shown in Tables 27–31 together with the description already reported by the author (Kubota 1978a, '79b).

One kind of nematocysts, basitrichous isorhizes, was found in the polyp with or without medusa-buds. There were two types, stumpy and slender ones. And the latter was found on all of the body portions, while the former was not present on tentacles. The constitution and size of nematocysts were not different among the materials regardless of the difference of the locality and the host species (Table 27).

Table 27. Nematocysts of polyp. Size: length × maximum width; range (mean), number of nematocysts examined, in μm.

Locality	Host	No. of specimens examined	Basitrichous isorhizes	
			Stumpy type	Slender type
Oshoro[1]	*Mytilus edulis*	2	6.4-8.2×2.4-4.0 (7.0) 20 (3.0)	5.8-8.0×1.6-1.8 (6.9) 40 (1.7)
Akkeshi[2]	*Clinocardium californiense*	4	6.2-8.4×2.6-4.0 (7.4) 67 (3.1)	6.8-8.2×1.8-2.2 (7.4) 59 (2.0)
Mitsuhama	*Paphia schnelliana*	2	6.8-8.0×3.0-4.0 (7.4) 32 (3.4)	6.8-8.0×1.7-2.1 (7.4) 32 (1.8)
Mukaishima Is.	*Crassostrea gigas*	2	6.6-8.0×2.8-3.6 (7.3) 25 (3.3)	6.6-8.0×1.8-2.0 (7.4) 25 (1.9)
	4 species	10	6.2-8.4×2.4-4.0 (7.3) 144 (3.2)	5.8-8.2×1.6-2.2 (7.3) 156 (1.9)

1) Kubota 1978a. 2) Kubota 1979b.

In the newly liberated medusa three kinds of nematocysts were found. They were large, medium, and small types of atrichous isorhizes, stumpy and slender types of basitrichous isorhizes, and one type of merotrichous isorhizes (Table 28). The size of these nematocysts was not different among the materials examined even if the locality and the host differed as is the same case in the polyp. It should be mentioned here that the medium type of atrichous isorhizes in the specimen from Akkeshi was smaller than the others. This may be caused by the difficulty in separation of the medium and the small types because of the breakdown of the specimen examined by refrigeration.

In the aged medusa over a month-old from the mature medusa to the spent one, two or three kinds of nematocysts were found. In the specimens with cirri, three kinds of nematocysts such as large, medium, and small types of atrichous isorhizes, one (slender) type of basitrichous isorhizes, and one type of merotrichous isorhizes were present, while two kinds in the specimens without cirri because of the absence of merotrichous isorhizes which were exclusively found on the distal end of a cirrus (Table 29). The size of all these nematocysts was constant in these developmental stages regardless of the different age; and as is the same case in the polyp and the newly liberated medusa no distinct size difference was found among the materials examined even if the locality and the host were dissimilar. It is notable that in this stage the exumbrellar nematocysts disappeared and that basitrichous isorhizes on tentacles tended to be smaller than those on oral lips, differing from the case of

Table 28. Nematocysts of the youngest medusa. Size: length × maximum

Locality	Host	No. of specimens examined	On tentacles	
			Atrichous isorhizes Large type	Atrichous isorhizes Medium type
Oshoro[1]	*Mytilus edulis*	3	7.6-10.0×3.2-4.8 (8.7) 35 (4.1)	5.6-7.2×2.4-3.2 (6.2) 30 (2.6)
Akkeshi[2]	*Clinocardium californiense*	1	7.8-8.8 ×4.0-4.8 (8.2) 7 (4.3)	5.2-6.0×2.0-2.7 (5.5) 7[3] (2.3)
Mitsuhama	*Paphia schnelliana*	2	7.4-9.8 ×3.6-5.0 (8.7) 23 (4.2)	5.8-7.6×2.6-3.4 (6.7) 19 (2.9)
Mukaishima Is.	*Mytilus edulis*	1	8.2-10.8×3.4-4.8 (9.7) 25 (4.2)	6.4-8.0×2.0-3.4 (7.4) 25 (2.9)
	Crassostrea gigas	4	8.0-10.0×3.2-4.8 (9.3) 20 (4.3)	6.4-7.6×2.6-3.4 (7.0) 20 (3.0)
	4 species	11	7.4-10.8×3.2-5.0 (8.9) 110 (4.2)	5.6-8.0×2.0-3.4 (6.8) 94 (2.9)

1) Kubota 1978a. 2) Kubota 1979b. 3) Atrichous isorhizes, medium type and small type.

Table 29. Nematocysts of aged medusa from mature to spent one. Size:

Locality	Host	Age (days)	No. of specimens examined	Atrichous isorhizes Large type
Oshoro	*Mytilus edulis*	28	1[1]	8.0-10.0×3.6-4.4 (9.4) 15 (4.0)
		60-64	5	8.0-9.8 ×3.2-4.6 (8.8) 21 (3.8)
		90-93	5	8.1-10.2×3.2-4.4 (8.9) 19 (3.8)
Akkeshi	*Clinocardium californiense*	30	2[2]	7.6-9.0 ×3.2-4.2 (8.3) 10 (3.7)
Usa	*Mytilus edulis*	36-41	4	8.0-10.4×3.2-4.8 (9.1) 48 (3.9)
		63	2	8.4-10.0×3.6-4.8 (9.3) 31 (4.2)
Mukaishima Is.	*Mytilus edluis*	60	1	8.8-10.4×3.4-4.2 (9.5) 25 (3.8)
	Crassostrea gigas	59	2	8.8-10.6×4.0-4.8 (9.7) 24 (4.3)
		91	3	8.4-10.6×3.6-4.8 (9.5) 46 (4.2)
	3 species	28-93	25	7.6-10.6×3.2-4.8 (9.2) 239 (4.0)

1) Kubota 1978a. 2) Kubota 1979b.

width; range (mean), number of nematocysts examined, in μm.

	On oral lips	On exumbrella	On cirri	
Basitrichous isorhizes Slender type	Basitrichous isorhizes Slender type	Basitrichous isorhizes Stumpy type	Merotrichous isorhizes	Atrichous isorhizes Small type
6.4-8.8 ×2.0-2.6 (7.4) 30 (2.3)	6.6-8.4×2.0-2.4 (7.4) 35 (2.2)	8.4-11.2×4.8-5.8 (9.7) 35 (5.0)	8.8-12.2×2.4-4.0 (11.0) 35 (3.3)	4.2-4.8×1.8-2.4 (4.6) 15 (2.1)
5.6-8.8 ×1.8-2.6 (6.5) 19[4] (2.1)	—	8.8-10.4×4.4-5.0 (9.2) 10 (4.8)	9.6-11.4×3.0-3.4 (10.2) 10 (3.2)	—
6.8-9.2 ×2.2-3.0 (8.0) 25 (2.5)	6.8-8.6×2.4-2.4 (7.8) 10 (2.4)	8.0-9.6 ×4.8-5.6 (9.1) 10 (5.0)	9.8-11.6×3.2-4.0 (10.9) 26 (3.4)	4.2-5.6×1.8-2.2 (4.9) 21 (1.9)
7.4-10.8×2.2-2.8 (8.5) 25 (2.5)	7.6-8.8×2.4-2.6 (8.2) 25 (2.4)	9.2-10.8×4.8-5.8 (9.9) 25 (5.0)	10.2-12.0×3.2-4.0 (11.2) 30 (3.4)	4.2-6.6×1.6-2.6 (5.0) 20 (1.8)
7.4-9.2 ×2.4-2.8 (8.6) 25 (2.6)	—	8.8-11.2×5.0-6.4 (10.0) 20 (5.5)	10.4-12.2×3.2-4.4 (11.2) 20 (4.0)	3.6-5.0×1.6-2.4 (4.4) 26 (1.8)
6.4-10.8×2.0-3.0 (8.1) 105 (2.5)	6.6-8.8×2.0-2.6 (7.8) 70 (2.3)	8.0-11.2×4.4-6.4 (9.6) 100 (5.1)	8.8-12.2×2.4-4.4 (10.9) 121 (3.5)	3.6-6.6×1.6-2.6 (4.7) 82 (1.9)

4) Basitrichous isorhizes, slender type on tentacles and that on oral lips.

length×maximum width; range (mean), number of nematocysts examined, in μm.

On tentacles		On oral lips	On cirri	
Atrichous isorhizes Medium type	Basitrichous isorhizes Slender type	Basitrichous isorhizes Slender type	Merotrichous isorhizes	Atrichous isorhizes Small type
5.6-6.6×2.0-2.4 (5.9) 7 (2.2)	6.2-7.2×1.6-1.8 (6.6) 20 (1.8)	7.4-8.8×2.2-2.6 (8.2) 19 (2.4)	—	—
5.4-7.4×2.1-3.2 (6.1) 20 (2.5)	5.6-8.0×1.8-2.4 (6.4) 41 (2.1)	7.2-8.2×2.1-2.6 (7.9) 18 (2.4)	11.6-11.6×3.2-3.8 (11.6) 2 (3.5)	4.0-4.0×1.7-1.8 (4.0) 2 (1.8)
5.0-6.8×2.0-3.2 (5.8) 19 (2.3)	5.6-8.2×1.7-2.4 (6.5) 40 (2.0)	7.4-9.2×2.2-2.6 (8.4) 35 (2.4)	10.4-12.6×3.2-4.0 (11.3) 15 (3.4)	4.8-6.4×1.8-2.2 (5.4) 17 (1.8)
5.2-6.4×1.8-2.4 (5.9) 9 (2.2)	5.4-8.2×1.8-2.4 (6.3) 30 (2.0)	×	—	—
5.2-6.6×1.8-2.4 (5.8) 27 (2.1)	5.2-8.4×1.6-2.4 (6.6) 52 (1.8)	×	×	×
5.2-7.6×1.8-3.2 (6.0) 20 (2.1)	6.0-8.0×1.7-2.2 (6.6) 34 (1.9)	×	×	×
5.2-8.0×1.8-3.2 (6.7) 25 (2.4)	6.4-7.2×1.8-2.2 (6.7) 25 (1.8)	7.8-9.6×2.0-2.6 (8.5) 25 (2.3)	10.4-12.8×2.8-3.8 (11.8) 21 (3.4)	4.0-6.6×1.6-2.4 (4.8) 21 (1.8)
6.6-8.2×2.4-3.4 (7.3) 21 (2.8)	6.4-8.0×2.0-2.4 (7.0) 20 (2.2)	×	×	×
5.6-8.4×2.3-3.4 (7.0) 36 (2.7)	6.0-7.4×1.8-2.2 (6.6) 30 (2.0)	7.8-9.6×2.0-2.8 (8.6) 33 (2.5)	10.4-11.6×3.4-4.0 (10.9) 21 (3.8)	4.0-5.8×1.6-2.4 (4.4) 27 (1.8)
5.0-8.4×1.8-3.4 (6.3) 184 (2.4)	5.2-8.4×1.6-2.4 (6.6) 292 (2.0)	7.2-9.6×2.0-2.8 (8.3) 130 (2.4)	10.4-12.8×2.8-4.0 (11.4) 59 (3.5)	4.0-6.6×1.6-2.4 (4.7) 67 (1.8)

×: Not examined. —: Absent.

Table 30. Nematocysts of planula. Size: length×maximum width; range (mean), number of nematocysts examined, in μm.

Locality	Host	Age (days)	No. of specimens examined	Atrichous isorhizes
Oshoro	*Mytilus edulis*	2-3	4	5.0-7.2×1.6-2.4 (6.0) 54 (2.0)
	Crenomytilus grayanus	3	2	5.4-7.3×1.6-2.8 (6.3) 41 (2.0)
Kuroiwa	*Mytilus edulis*	5	2	4.8-6.4×1.6-2.4 (5.8) 40 (1.8)
	Mytilus edulis	17	2	5.0-6.6×1.6-2.8 (5.7) 13 (2.0)
2 species		2-17	10	4.8-7.3×1.6-2.8 (6.0) 148 (2.0)

the youngest medusa described above in which both were of the same size. And the medium type of atrichous isorhizes in the specimens from Mukaishima Island tended to be larger than the others, and the large type of atrichous isorhizes in the specimen from Akkeshi tended to be shorter.

It was observed that in one nematocyst knob of the cirri 10–19 merotrichous isorhizes were contained in the aged medusae over one-month-old as well as the newly liberated medusa. The possession of this kind of nematocyst is considered to be one of the diagnostic characters of Thecata-Leptomedusae as was pointed out by Werner (1965).

In planula only one kind of nematocysts, atrichous isorhizes, was found (Table 30). No distinct size difference of the nematocyst was found among the specimens of different ages and those from different localities and hosts, though in some specimens a larger and a smaller nematocysts were found.

It is found that in the medusa from the newly liberated one to spent one the following nematocysts were nearly the same in size and structure: each of three types of atrichous isorhizes on tentacles and cirri (Fig. 24, Aa-C), merotrichous isorhizes on cirri (Fig. 24, Dd), and basitrichous isorhizes on tentacles and oral lips (though nematocysts on tentacles of the mature to spent medusa tends to be shorter). Of these nematocysts in medusa, basitrichous isorhizes are identical with the slender type of basitrichous isorhizes in polyp in size and structure (Fig. 24, Ee), and the medium type of atrichous isorhizes is nearly the same as atrichous isorhizes of planula in size and structure (Fig. 24, B). The stumpy type of basitrichous isorhizes in the newly liberated medusa (Fig. 24, Gg) and that of those in polyp (Fig. 24, Ff) is the same in structure, but different in size.

From the facts described above, the constitution of nematocysts in the present hydroid is clearly different in the life stage (Table 31). The complexity of the constitution is appreciated in the following order: planula, polyp, and medusa.

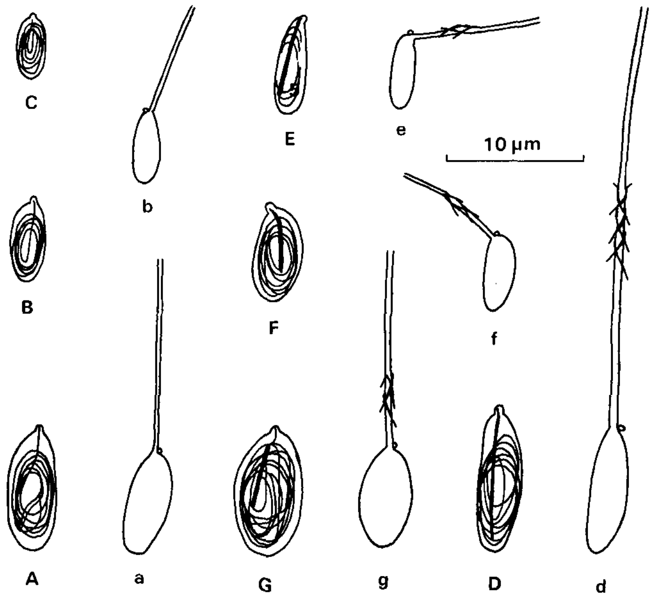

Fig. 24. Morphology of nematocysts (from Kubota 1978a). Capital letters signify undischarged state of nematocysts and small ones their discharged state. A-C: atrichous isorhizes (A: large type, B: medium type, C: small type), D: merotrichous isorhiza, E-G: basitrichous isorhizes (E: slender type, F, G: stumpy type).

Table 31. Distribution of nematocyst kinds and types among different developmental stages of *Eutima*.

Nematocyst kind	Nematocyst type	Planula	Polyp	Youngest medusa	Mature medusa
Atrichous isorhizes	Small type	+		+	+
	Medium type			+	+
	Large type			+	+
Basitrichous isorhizes	Slender type		+	+	+
	Stumpy type		+	+	
Merotrichous isorhizes	—			+	±

In comparison with the polyp and the planula the medusa has various kinds and types of nematocysts in proportion to the complication of body structure. It is noteworthy that in the medusa the constitution of nematocysts is different among the body portions; two kinds were found on tentacles or cirri, while only one kind on oral lips or exumbrella (Tables 28, 29). Although the function of each nematocyst of the present hydroid has been fully unknown, the slender type of basitrichous isorhizes, which is found in both the tentacle and the oral lip of medusa as well as in whole body of polyp, is possibly equipped for paralysis of the prey.

On the other hand, it is noticeable from the phylogenetic point of view that the planula has only the primitive nematocysts as was already pointed out by Werner (1968) and that a diagnostic nematocyst merotrichous isorhizes is found only in the medusan generation.

V. Taxonomy

Owing to the complicated life history contrary to the simple morphology of the present Eutimid hydroid and its related ones, the taxonomic status of the present hydroid has been remained somewhat problematical. In an author's previous paper dealing with a material from Oshoro (Kubota 1978a), a discussion on the complex taxonomic situation in the commensal hydroids belonging to the genera *Eugymnanthea* and *Eutima* was given in detail, in which the hydroid was identified with *Eugymnanthea cirrhifera* Kakinuma but the generic status was transferred to *Eutima*, mainly based on the morphology of mature medusa. However, the taxonomic relationship of the present species with the other two species previously described in Japan, *Eutima japonica* Uchida, 1925 and *Eugymnanthea* (=*Ostreohydra*) *japonica* (Yamada, 1950), has been unsolved.

Considering the present investigations on the life-histories of the Japanese commensal hydroids associated with various pelecypods from various localities, they are all assignable to a single species. The difference in the degree of growth of medusa among the specimens (see II) is conceivable as a variation based on the following observations: (1) Regardless of the host difference all the materials have a similar process of metamorphosis and one of the major differences, the number of cirri in the medusa, is not recognizable as a specific character, because the presence of cirri is variable among individuals on the same developmental stage as well as those on different developmental stages, moreover the number of cirri can be altered by the rearing condition, i.e. salinity or water temperature (see Tables 19–22); (2) The difference in the number of some other morphological characters than the cirri of medusa (Te, Ms, St, Stl) as well as the length of peduncle generally correlates with the difference of body size; (3) Fertilization easily takes place among different populations even if their hosts are different.

Judging from the morphology and life-history as well as the distribution and host preference of the Japanese commensal hydroids examined (cf. VI), it is highly possible that *Eutima cirrhifera* (Kakinuma) is synonymous with *Eugymnanthea japonica* (Yamada) (so-called polyp species) and *Eutima japonica* Uchida (medusa species). However, there is a suspicion in this understanding, because the small-sized mature medusa of *Eutima japonica* from Japan closely resembles *Eutima commensalis* Santhakumari from India. The polyp and the medusa of Indian *E. commensalis* have not been connected by rearing directly, and in India many other *Eutima*-species (medusa species) have been recorded (Kramp 1961, '65, '68). Accordingly further faunistic survey will be needful both in Japan and India. Although the above-mentioned problem still remains unsettled, it would be better for the present Japanese Eutimid commensal hydroid to nominate *Eutima japonica* Uchida hereafter. This taxonomic treatment, however, is conventional and the hydroid taxonomy is not always sufficient in this manner owing to the complicated nature of this animal, therefore a special discussion is prepared (VII. A).

VI. Distribution and Host Preference at Japanese Coasts

At various Japanese coasts from Shikoku to Hokkaido, facing the Pacific Ocean, Sea of Japan, or Seto Inland Sea, occurrence of the commensal hydroids living in bivalves was surveyed for about four years (cf. Table 1). Because of its intimate association with a common mussel, *Mytilus edulis*, this bivalve was collected in large quantities from almost all of the coasts surveyed. Besides *Mytilus edulis* other various kinds of bivalves were collected as many as possible at the same time in order to reveal the host preference of the hydroid. This collection and investigation were made most intensively at Oshoro, Hokkaido, where the commensal polyp is found throughout the year (see I. B). The identification of a hydroid within each host bivalve from each locality was made by its rearing from polyp to mature medusa as a general rule (see Table 2). In the case that this examination was not fully possible, at least the polyp with a well-developed medusa-bud near or just before liberation was observed to identify a material. This method was adopted for the precise identification of each material, because the distinction of species or genera is usually difficult in the polypoid generation (cf. VII). In addition to the distributional records recently obtained by the author, all the former records, particularly those regarding the planktonic mature medusa reported by Uchida (1925) and Yamazi (1958) from several localities in Japan (see II. C) were included in consideration.

A. Distribution of *Eutima japonica* Uchida

Eutima japonica was, in general, commonly distributed from southern to northern Japan (Fig. 25). It occurred even in such localities in both Akkeshi Bay and Uchiura Bay, Hokkaido where the effect of the cold current (Oyashio) is remarkable (Fig. 25, D-G). Going into particulars, the following distributional difference was noticed. This species was distributed commonly at the coasts facing the Pacific Ocean and Seto Inland Sea, while the occurrence records were scarce at the coasts facing Sea of Japan, which may be related to the ecological and/or historical reason. And the following tendency was experienced that occurrence of the species is more frequently at the coasts inside a bay or within an inland sea (Fig. 25, B-E, G, R, U-Z) than those outside a bay or those facing open waters (Fig. 25, A, F, I, K, O, R).

B. Host Preference of *Eutima japonica* Uchida

The polyp of *Eutima japonica* was certainly commensal with 11 species of bivalves of different lineage, of different shell size and space of mantle cavity, and of various modes of life. And it may be safely said that *E. japonica* was associated

Table 32. The bivalve species and their sizes examined at various (11) localities shows the number of bivalves

Locality and bivalve species	Part of shell measured*	No. of bivalves					
		0.1–0.9	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9
Zenibako							
Gomphina melanaegis	L			1	13	85	4
Mactra chinensis	L			4	6		2
Pseudocardium sachalinensis	L			5	17	5	1
Peronidia venulosa	L				5	7	6
Oshoro							
Acila insignis	L	4	17	2			
Arca boucardi	L			6	19	20	8
Mytilus edulis	A	28	147 (2)	592 (55)	1011 (217)	737 (271)	210 (117)
M. coruscus	A			5	17	124	207
Crenomytilus grayanus	A	3	10	9 (2)	2	2 (1)	3 (2)
Septifer virgatus	A			88	496 (2)	216 (1)	3
Modiolus modiolus	A		1	2	8	24	37
Chlamys swifti	H					2	3
C. farreri	H				1	2	3
Patinopecten yessoensis	H						
Crassostrea gigas	H						
Clinocardium buellowi	L			1			
Ruditapes philippinarum	L		6	124	423	200	1
Saxidomus purpuratus	L						
Protothaca euglypta	L		42	204	20		
Peronidia venulosa	L						
Heteromacoma irus	L		1	8	4	1	
Agriodesma naviculum	L					1	1
Utasutsu							
Mytilus edulis	A			5 (4)	27 (23)	4 (3)	1 (1)
M. coruscus	A			2	23 (1)	11	1
Septifer virgatus	A			4	30	6	
Mori							
Mytilus edulis	A			9	34	28 (1)	22
Kuroiwa							
Mytilus edulis	A			4 (1)	43 (16)	17 (1)	4 (2)
Akkeshi							
Mytilus edulis	A			39	269	25	1
Musculus laevigatus	A		1	4	4	2	
Chlamys swifti	H						
Patinopecten yessoensis	H						
Crassostrea gigas	H						
Clinocardium californiense	L					5	22 (1)
C. buellowi	L		1	3	4	1	
C. nuttalli	L						
Ruditapes philippinarum	L		2	25	46	85	114
Protothaca euglypta	L		12	10	2		
Mya arenaria	L			1	3	1	2
Agriodesma naviculum	L			2	6	4	4

in Japan where commensal polyps were found. The number in parenthesis associated with polyps.

distributed in size ranges between 0.1 and 16.9 cm											
6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	Total no. of bivalves examined
1											104
5	3										20
2		1	1								32
11	10 (1)										39 (1)
											23
2											55
41 (21)	6 (4)	1 (1)									2773 (688)
152	77	48	20	18	9	5	10	5	1	1	669
1 (1)	5 (5)	5 (4)	8 (7)	13 (13)	15 (14)	11 (11)	12 (11)	2 (2)			101 (73)
											803 (3)
55	32	52	72	75	26	1					385
1	2 (1)	1									9 (1)
4	8	2	1								21
1	7	4	1			1	1				15
3	16	28	31	39	37	15	9		1		179
											1
											754
	1	1									2
											266
	25	2									27
											14
											2
											37 (31)
											37 (1)
											40
5											98 (1)
3	1										72 (20)
											334
											11
			3								3
1	1	1	4	5	22	19	19	5			77
	1	5	9	11	13	9	3	1	1		53
9											36 (1)
											9
	2										2
34											306
											24
9	22	4									42
4		1									21

Table 32

Localiity and bivalve species	Part of shell measured*	No. of bivalves					
		0.1–0.9	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9
Enoshima Is.							
Mytilus edulis	A			9	33 (7)	82 (14)	28 (6)
Usa							
Mytilus edulis	A				2	3	3 (1)
Septifer virgatus	A		76	227 (1)			
Musculista senhousia	A		48	12			
Crassostrea gigas	H			2	25	95 (1)	63
Ruditapes philippinarum	L		22	159	89	126	4
Coecella chinensis	L		9 (2)	6 (1)			
Mukaishima Is.							
Barbatia virescens	L			4	21 (1)	9 (1)	2
Mytilus edulis	A		11	76 (2)	74 (2)	57 (6)	34 (1)
Crassostrea gigas	H				21	117 (1)	54
Ruditapes philippinarum	L		4	214	42	2	
Paphia vernicosa	L			4	40	24	3
Protothaca jedoensis	L		10	27	41	33	11
Coecella chinensis	L		10	28	2		
Mitsuhama							
Barbatia virescens	L			6	12		
Mytilus edulis	A	8	81	54	89 (6)	91 (11)	25 (8)
M. coruscus	A		1	2	25	27	21
Septifer virgatus	A		8	12	2		
Modiolus auriculatus	A			27 (1)	44	3 (1)	
Crassostrea gigas	H			1	20	17	2
Paphia schnelliana	L						
P. euglypta	L						
Meretrix lusoria	L						1
Nuwajima Is.							
Mytilus edulis	A		5	22	45 (1)	65 (1)	28

* A: maximum anterior-posterior

with 12 bivalve species of 11 genera of eight families (Tables 32, 34; Fig. 26), with the proviso that three hydroids from Usa, of which polyps were associated with *Septifer virgatus*, *Crassostrea gigas*, and *Coecella chinensis*, respectively, belong to the same species. These polyps degenerated without budding of any medusa-buds, therefore their taxonomic status remains uncertain.

Of these 12 bivalve species examined the polyp was intimately associated with the bivalves belonging to the family Mytilidae both in northern and southern Japan (see Tables 32, 34); namely besides *Mytilus edulis* with which the polyp was frequently associated, the polyp was found in such bivalves as *Crenomytilus grayanus*, *Mytilus coruscus*, and *Septifer virgatus* in northern Japan, and in *Septifer virgatus*

(*Continued*)

distributed in size ranges between 0.1 and 16.9 cm											Total no. of bivalves examined
6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	
1											153 (27)
											8 (1)
											303 (1)
											60
17	2		1								205 (1)
											400
											15 (3)
											36 (2)
12	3 (1)										267 (12)
7											199 (1)
											262
2											73
											122
											40
											18
4 (1)	1 (1)										353 (27)
5	1										82
											22
											74 (2)
											40
2	24 (2)	34	14	3							77 (2)
1	2										3
4	3										8
1											166 (2)

axis, L: shell length, H: shell height.

and *Modiolus auriculatus* in southern Japan. And the bivalves belonging to other families than Mytilidae with which association of polyp was found were as follows: in northern Japan *Chlamys swifti* (Pectinidae) from Oshoro, *Peronidia venulosa* (Tellinidae) from Zenibako, and *Clinocardium californiense* (Cardiidae) from Akkeshi, and in southern Japan *Crassostrea gigas* (Ostreidae) from Mukaishima Island and Usa, *Barbatia virescens* (Arcidae) from Mukaishima Island, *Paphia schnelliana* (Veneridae) from Mitsuhama, and *Coecella chinensis* (Mesodesmatiidae) from Usa. Consequently the polyp was commensal with seven bivalve species in northern Japan and with seven species in southern Japan; and in only two species, *Mytilus edulis* and *Septifer virgatus*, the commensal hydroid was found in both the

Table 33. The bivalve species and their sizes examined at various

Locality	Bivalve species	Part of shell measured*	No. of bivalves		
			1.0-1.9	2.0-2.9	3.0-3.9
Teuri Is.	*Mytilus edulis*	A	10	114	144
	M. coruscus	A			3
	Septifer virgatus	A		13	5
Yagishiri Is.	*Mytilus edulis*	A	6	37	105
	Septifer virgatus	A		21	42
Off Ishikari	*Mactra chinensis*	L			
	Pseudocardium sachalinensis	L			
	Peronidia venulosa	L			
Tarukawa	*Gomphina melanaegis*	L			20
	Mactra chinensis	L			1
	Pseudocardium sachalinensis	L			4
	Peronidia venulosa	L			1
Muroran	*Mytilus edulis*	A		5	25
	Septifer virgatus	A			8
	Modiolus modiolus	A			2
	Crassostrea gigas	H			1
Asamushi	*Mytilus edulis*	A			5
	M. coruscus	A			
	Septifer virgatus	A			
	Modiolus modiolus	A			
	Chlamys farreri	H			
	Saxidomus purpuratus	L			
	Protothaca jedoensis	L		1	5
	P. euglypta	L		4	5
Fukaura	*Mytilus coruscus*	A			1
	Septifer virgatus	A	3	16	26
	Modiolus auriculatus	A	1	3	1
	Lithophaga curta	A	1	7	6
	Crassostrea gigas	H			
Sasagawanagaru	*Septifer virgatus*	A		23	91
Ogi	*Mytilus edulis*	A		23	27
Oozakai	*Mytilus edulis*	A	1	20	56
Miyazu	*Mytilus edulis*	A	2	17	31
Amanohashidate	*Mytilus edulis*	A		3	13
Amino	*Septifer virgatus*	A	2	14	3
Kumihama	*Mytilus edulis*	A	1	10	21
Yokosuka	*Mytilus edulis*	A	10	31	57
Kannonzaki	*Mytilus edulis*	A			4
Jôgashima Is.	*Mytilus edulis*	A	7	24	61
Shirahama	*Mytilus edulis*	A		8	36
	M. coruscus	A			
	Septifer virgatus	A		1	56
	S. bilocularis	A		39	15
	Modiolus auriculatus	A		3	23
Ushimado	*Mytilus edulis*	A		12	90

* A: maximum anterior-posterior

(19) localities in Japan where no commensal polyps were found.

distributed in size ranges between 1.0 and 13.9 cm										Total no. of bivalves examined
4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	
22	1	2								293
3	17	24	22	27	19	5	1			121
1										19
42	2	1								193
13										76
		11	11	1						23
			3	5						8
			2	14	7					23
195	168	5	1							389
	1									2
1	2									7
										1
56	55	29	3							173
2										10
6	2	1								11
2			1	1	1	1				7
25	82	51	15	3						181
	1	1	4	2	5	5				18
4	1									5
		4	7	17	5					33
	3		5	13	3					24
		1	5	3						9
3	2									11
										9
1	1			1	1	7	9	3	1	25
12	1	1								59
										5
										14
	4	1	1	4	3	10	6	5	3	37
3										117
16	10	3								79
35	2									114
28	4									82
21	13	2								52
1										20
26	7									65
21	12	16								147
21	11	6	2							56
78	52	15	8							245
24	3									71
	1	1	1	1						4
62										119
										54
3										29
65	16									183

axis, L: shell length, H: shell height.

Table 34. Association of Eutimid ployp with each of 34 bivalve species

Family	Species	Mode of life[1)]	Northern Japan		
			Ishikari Bay[2)]	Suttsu Bay[3)]	Uchiura Bay[4)]
Nuculidae	*Acila insignis*	B	23 (0)		
Arcidae	*Barbatia virescens*	A			
	Arca boucardi	A	55 (0)		
Mytilidae	*Mytilus edulis*	A	2773 (688)	37 (31)	343 (21)
	M. coruscus	A	699 (0)	37 (1)	
	Crenomytilus grayanus	A	101 (73)		
	Septifer virgatus	A	803 (3)	40 (0)	10 (0)
	Modiolus auriculatus	A			
	M. modiolus	(B)	385 (0)		11 (0)
	Musculus laevigatus	A			
	Musculista senhousia	A			
Pectinidae	*Chlamys swifti*	A	9 (1)		
	C. farreri	A	21 (0)		
	Patinopecten yessoensis	(B)	15 (0)		
Ostreidae	*Crassostrea gigas*	A	179 (0)		7 (0)
Cardiidae	*Clinocardium californiense*	(B)			
	C. buellowi	(B)	1 (0)		
	C. nuttalli	(B)			
Veneridae	*Ruditapes philippinarum*	B	754 (0)		
	Gomphina melanaegis	B	493 (0)		
	Paphia vernicosa	B			
	P. schnelliana	B			
	P. euglypta	B			
	Meretrix lusoria	B			
	Saxidomus purpuratus	B	2 (0)		
	Protothaca jedoensis	B			
	P. euglypta	B	266 (0)		
Mesodesmatiidae	*Coecella chinensis*	B			
Mactridae	*Mactra chinensis*	B	45 (0)		
	Pseudocardium sachalinensis	B	47 (0)		
Tellinidae	*Peronidia venulosa*	B	90 (1)		
	Heteromacoma irus	B	14 (0)		
Myidae	*Mya arenaria*	B			
Lysiidae	*Agriodesma naviculum*	A	2 (0)		
	TNB (TNBP)[10)]		6777 (766)	114 (32)	371 (21)
	NBS (NBSP)[11)]		21 (5)	3 (2)	4 (1)

1) A: attaching type, B: burrowing type, (B): semi-burrowing type. 2) Off
5) Akkeshi. 6) Usa. 7) Mukaishima Is., Nuwajima Is., Mitsuhama, Ushimado.
surveyed, NRP: number of regions in which polyps were found. 10) TNB: total
11) NBS: number of bivalve species examined, NBSP: number of bivalve species

collected from seven regions in Japan where polyps were found.

	Southern Japan				
Akkeshi Bay[5]	Tosa Bay[6]	Seto Inland Sea[7]	Sea of Sagami-Nada[8]	NR(NRP)[9]	TNB (TNBP)[10]
				1 (0)	23 (0)
		54 (2)		1 (1)	54 (2)
				1 (0)	55 (0)
334 (0)	8 (1)	969 (41)	601 (27)	7 (6)	5065 (809)
		82 (0)		3 (1)	818 (1)
				1 (1)	101 (73)
	303 (1)	22 (0)		5 (2)	1178 (4)
		74 (2)		1 (1)	74 (2)
				2 (0)	396 (0)
11 (0)				1 (0)	11 (0)
	60 (0)			1 (0)	60 (0)
3 (0)				2 (1)	12 (1)
				1 (0)	21 (0)
77 (0)				2 (0)	92 (0)
53 (0)	205 (1)	239 (1)		5 (2)	683 (2)
36 (1)				1 (1)	36 (1)
9 (0)				2 (0)	10 (0)
2 (0)				1 (0)	2 (0)
306 (0)	400 (0)	262 (0)		4 (0)	1722 (0)
				1 (0)	493 (0)
		73 (0)		1 (0)	73 (0)
		77 (2)		1 (1)	77 (2)
		3 (0)		1 (0)	3 (0)
		8 (0)		1 (0)	8 (0)
				1 (0)	2 (0)
		122 (0)		1 (0)	122 (0)
24 (0)				2 (0)	290 (0)
	15 (3)	40 (0)		2 (1)	55 (3)
				1 (0)	45 (0)
				1 (0)	47 (0)
				1 (1)	90 (1)
				1 (0)	14 (0)
42 (0)				1 (0)	42 (0)
21 (0)				2 (0)	23 (0)
918 (1)	991 (6)	2025 (48)	601 (27)	7 (7)	11797 (901)
12 (1)	6 (4)	13 (5)	1 (1)	34 (12)	—

Ishikari, Tarukawa, Zenibako, Oshoro. 3) Utasutsu. 4) Muroran, Kuroiwa, Mori.
8) Yokosuka, Kannonzaki, Jôgashima Is., Enoshima Is. 9) NR: number of regions
number of bivalves examined, TNBP: total number of bivalves with polyps.
associated with polyps.

areas. It is noticeable that more than half the number of bivalve species associated with polyps, seven in number, inhabited the intertidal region of a coast*.

The relationship between the association frequency of polyp and the mode of life of the host bivalves was surveyed. The mode of life of bivalves examined could be grossly classified into two types, one is attached to various substrata by a byssus or a shell side and the other is buried into the bottom to different depths, though some were of an intermediate type between the two. Of 14 bivalve species of attaching type, 57% were associated with polyps, and in a large number of specimens 9% were with polyps while of 22 species of burrowing type, 18% were associated with polyps and in a large number of specimens only 0.2% were with polyps (Table 35). Accordingly the polyp was much more frequently commensal with the bivalves of attaching type than those of burrowing type. It is noticeable that of these bivalves of burrowing type the commensal polyp was usually associated with the species of which habitat was on or near the surface of the bottom of the sea (*Clinocardium*, *Phaphia*, and *Peronidia*).

At the most intensively surveyed locality, Oshoro, examining a large number of specimens of many bivalve species at all seasons, the commensal polyp was also exclusively found in the bivalves of Mytilidae (see Tables 32, 34). At Oshoro five Mytilid bivalves were commonly found and the host specificity of the commensal polyp with these bivalves was especially investigated in detail. As a result, the intimacy of association of the commensal polyp with the bivalves was different with each other, and it decreased in the following order: *Crenomytilus grayanus*, *Mytilus edulis*, *Septifer virgatus*, and *Mytilus coruscus* or *Modiolus modiolus difficilis* (Table 36). This marked host preference to the above two Mytilid species was further confirmed by the following facts: (1) in several limited habitats in Oshoro Bay where very few number of *Crenomytilus grayanus* were mingled with a mass of *Modiolus*, the polyp was exclusively associated with the former even if it was immature and small; (2) in some *Mytilus edulis* which were found in the subtidal zone attaching to a rock wall very sporadically, the high frequency of association of polyp was observed. The most noticeable fact is that no polyps

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* After the present manuscript had been completed it was kindly informed by Mr. K. Konno that a commensal polyp occurred from Usa associating with an unrecorded host. Fifteen preserved specimens of *Barbatia virescens*, which were collected on February 4th, 1981 by him, were sent to the author. The polyp was found in one specimen out of 15 ones. An identification of this hydroid is, however, difficult because all the polyps, which attached to one side of the mantle of the host and ca. 30 in number, had no medusa-buds. But by this information it is clarified that five bivalve species were associated with polyps at Usa, that is the case of the most frequent association in terms of the number of host species recorded at a locality (cf. Tables 1, 34).

Further distribution of *Eutima japonica* is recorded at Otsuchi (Fig. 25, Z) through the courtesy of Dr. Takeshi Kajihara, who found commensal ployps in the mantle cavity of *Mytilus eduis* in August, 1981. Many polypoid specimens bore well-developed medusa-buds, whose morphology indicated that they belong to the present species. According to him, similar polyps were also infected in *Septifer virgatus* from Otsuchi.

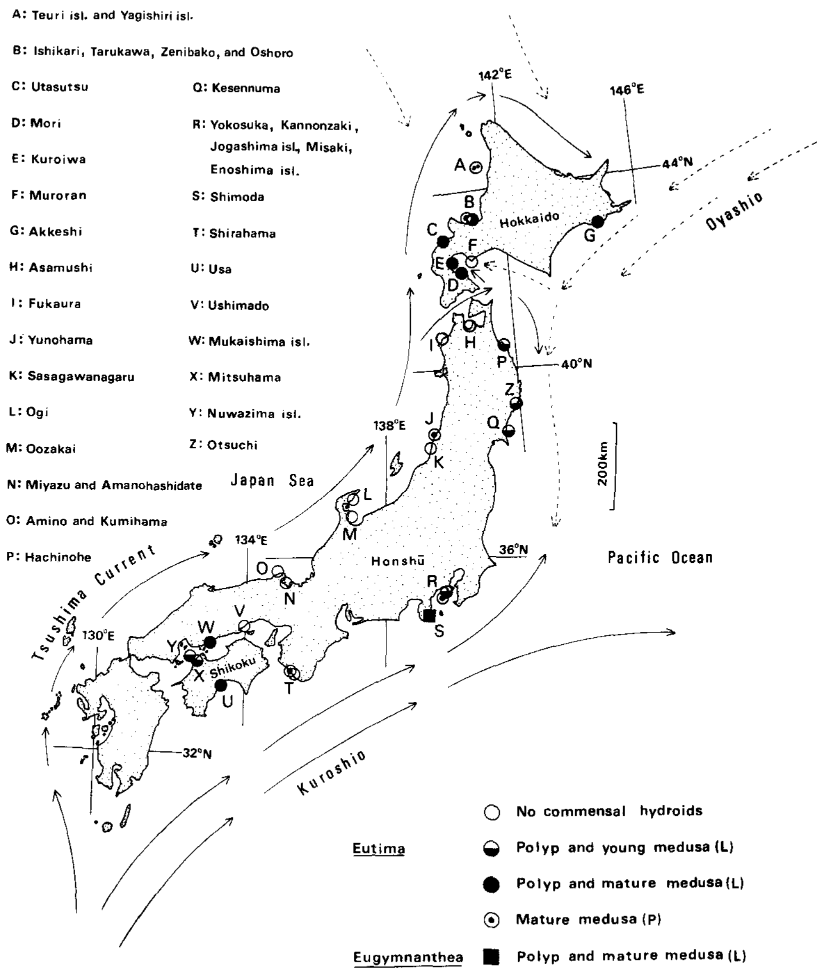

Fig. 25. Distribution of the commensal hydroids belonging to the genera of *Eutima* (circle) and *Eugymnanthea* (square) in Japan. L: medusae were obtained by laboratory rearing, P: medusae were found among plankton samples. These data are compiled from the following references: Uchida 1925, '64; Yamada 1950; Yamazi 1958; Kakinuma 1964; Kubota 1978a, '79a, b, and present work.

were found in *Mytilus coruscus* despite of its similar mode of life as well as the body structure to *Mytilus edulis* or *Crenomytilus grayanus*. As is shown in Table 36, *M. coruscus* was found attaching to the substrata within the depth of at least 5 m, overlapping with the habitat of the two bivalve species associated with polyps, moreover it is a large bivalve and sometimes grew larger than *Crenomytilus* in this

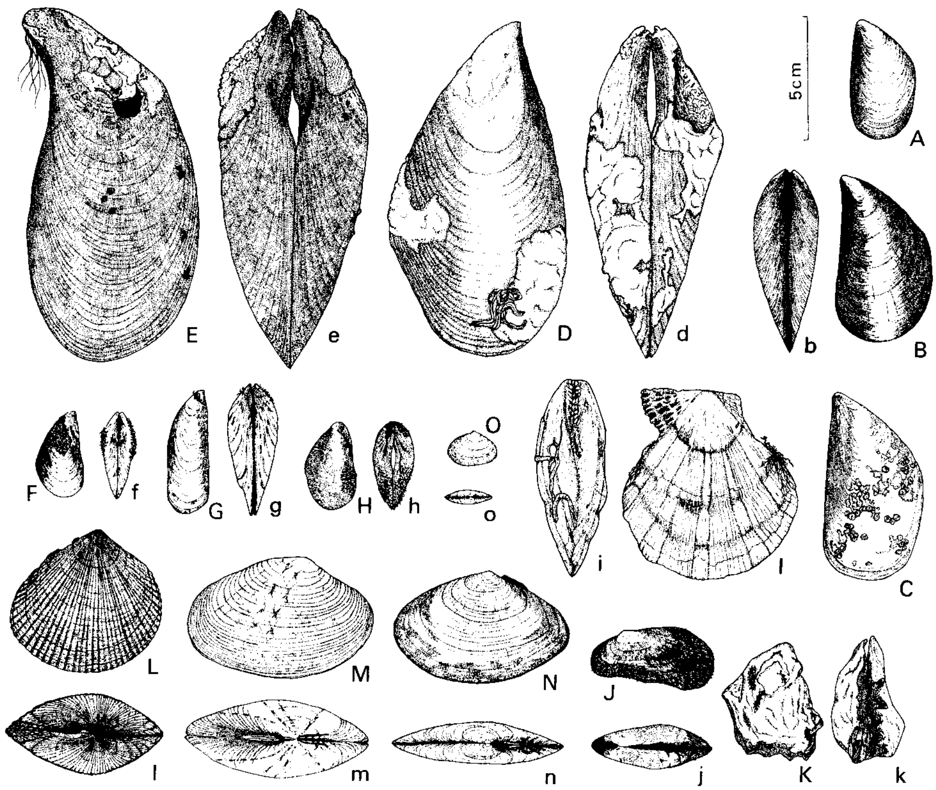

Fig. 26. Shells of 12 bivalve species associated with commensal polyps. Capital letters indicate lateral view and small letters dorsal or ventral view except for i, k. A: *Mytilus edulis* on the intertidal wave cut bench, B(b): *M. edulis* on buoy or rope, C: *M. edulis* in the subtidal region, D(d): *Mytilus coruscus*, E(e): *Crenomytilus grayanus*, F(f): a young shell of *C. grayanus*, G(g): *Septifer virgatus*, H(h): *Modiolus auriculatus*, I(i): *Chlamys swifti*, J(j): *Barbatia virescens*, K(k): *Crassostrea gigas*, L(l): *Clinocardium californiense*, M(m): *Paphia schnelliana*, N(n): *Peronidia venulosa*, O(o): *Coecella chinensis* (A-G, I: from Oshoro, H, M: from Mitsuhama, J, O: from Mukaishima Island, K: from Usa, L: from Akkeshi, N: from Zenibako).

locality. And even with *Septifer*, which exclusively inhabited the upper intertidal zone and was small and slender, the polyp was associated, though the association rate was very low. Therefore, *Mytilus coruscus* seemed to be a suitalbe host, but complete absence of polyp within it gives a riddle to us. In not only Oshoro but also in all the other localities surveyed, no polyp was commensal with *Mytilus coruscus* except only one small specimen which was collected in the intertidal region of Utasutsu near Oshoro, Hokkaido (cf. Tables 32, 34; Fig. 25, C). For a certain biological meaning of *Eutima japonica* as a symbiont and/or of *Mytilus coruscus* as

Table 35. Relationship between the mode of life of bivalves and the association rate of polyp.

Mode of life of bivalves	No. of bivalve species examined (no. with polyp): association rate (%)	No. of bivalve specimens examined in Japan (no. with polyp): association rate (%)	No. of bivalve specimens examined at the localities where polyp was found (no. with polyp): association rate (%)
Attaching type	14 (8): 57	10075 (894): 8.9	7334 (894): 12.2
Burrowing type	22 (4): 18	3660 (7): 0.2	3178 (7): 0.2
Total	36 (12): 33	13735 (901): 6.6	10512 (901): 8.6

Table 36. Comparison of association rate of polyp among the five Mytilid bivalves from Oshoro.

Bivalve species	Habitat of bivalve	Depth in which bivalves were collected (m)	Maximum shell size (cm)[1]	No. of bivalves examined (no. with polyp)	Association rate (%)
Septifer virgatus	Upper region of intertidal wave cut bench	—	5.0	803 (3)	0.4
Mytilus edulis	Mostly intertidal wave cut bench, frequently fishing ropes or buoys, rarely subtidal rock wall	2	8.2	2773 (688)	24.8
Modiolus modiolus	Mostly muddy bottom, frequently subtidal wave cut bench	4	12.3	385 (0)	0
Mytilus coruscus	Mostly subtidal rock wall, frequently intertidal wave cut bench	5	16.5	699 (0)	0
Crenomytilus grayanus	Subtidal rock wall	15	14.3	101 (73)	72.3

1) Maximum anterior-posterior axis.

a host, the commensal relationship between these two organisms may be difficult to come into existence.

On the other hand, it is noteworthy that no commensal polyp was found in northern *Modiolus* (*M. modiolus*), while it was found in southern one (*M. auriculatus*) (see Tables 32, 34). Accordingly the host preference seems to be appreciated in the bivalves of the genus *Modiolus*, though not so apparent as the case of the genus *Mytilus*. The northern *Modiolus* usually inhabited the muddy or sandy bottom, nearly all of its body buried, while the southern one attached to the rock in a tide pool. This difference in the mode of life of these two *Modiolus* species may be one of the reasons why the difference of host preference appeared.

The host preference of the commensal polyp of *Eutima japonica* is summarized as follows. The polyp has a distinct host preference to the bivalves of Mytilidae, among which it has the most intimated association with *Crenomytilus grayanus* and *Mytilus edulis* in the next place. Notwithstanding this it has an ability to associate with other various bivalves of different lineage, and among which the polyp is more frequently associated with the bivalves of attaching type than those of burrowing type.

The above-described mode of association of the present hydroid with bivalves indicates that the present hydroid is a generalist. If an organism evolves from a generalist to a specialist, the present hydroid which seems to appear at a time not far before present will diversify further, utilizing effectively the unique ecological niche which is still vacant to a greater degree.

C. Considerations on the Distribution of Japanese Commensal Hydroids Living in Bivalves

Eutima japonica is known only from Japan at present (see Fig. 25), and in various localities it is intimately associated with *Mytilus edulis*. However, one mature medusan specimen was collected in the central part of the north Pacific (39°43′N, 167°55′W) in 1934, far away from Japanese coasts (Kramp 1965), where this specimen which may be liberated from the polyp at a certain Japanese coast was carried by the warm current Kuroshio. On the other hand, according to Drs. A. Inaba and T. Hoshino, Hiroshima University, the commensal polyp has been found in *Mytilus edulis* at Mukaishima Is. since 1950's (personal communication). But this wide-spread host is said to be an immigrant bivalve from foreign countries. Therefore a question is raised whether *E. japonica* is a true endemic species or an immigrant one. In Japan *Mytilus edulis* was for the first time recorded at Kobe, southern Japan in 1935, and on and after that year it spread out all over the Japanese waters, though a part of the populations in Hokkaido, i.e. those in the northeastern coasts, is said to be indigenous (Habe and Ito 1965; Habe 1977, etc.). There is another report that the year of immigration of *M. edulis* is just after the Great Earthquake of 1923, and thereafter the mussel spread the Japanese coasts except Hokkaido area (Arakawa 1980). Recently Ho (1980) suggested a very recent immigration of *M. edulis* into Japan from both Europe and North America based on his study on parasitic copepods in marine mussels. But neither commensal polyps living in bivalves nor Eutimid medusae have been recorded in the Pacific coasts of the United States. Accordingly it is likely that *Eutima japonica* was transported into Japan from Europe together with the host by harboring it.

In this connection the author may add that the surprising occurrence of *Eugymnanthea inquilina* at Shimoda, central Japan (see Fig. 25, S), associating with *Mytilus edulis* (Kubota 1979a, former identification of its host as *M. coruscus* is erroneous). As mentioned in the beginning of the present paper, this species was at first discovered in Italy in 1935 and has not been reported in other waters than the Mediterranean, restricted to the sea around Italy (cf. Morri 1981). And still now it is distributed there: Dr. Ferdinando Boero, Genova University, recently found it in *Mytilus galloprovincialis* from La Spezia near Genova (14-VIII-'80), and thanks to his generosity the author could observe the morphology; and the nematocyst equipment, which has been unknown, was the same as that of Japanese *Eugymanthea* as follows: Polyp (in six preserved specimens, three with a medusa-bud and the other without it) basitrichous isorhizes 6.6–7.8–8.8, 0.56 x 1.6–2.0–2.4 μm, 0.26, 42 (on tentacle), 6.6–7.5–8.2, 0.44 x 1.6–1.9–2.4 μm, 0.26, 17 (on hydrocaulus); Medusa-bud (in three preserved female ones, in the well-developed stage) basitrichous isorhizes 6.4–7.1–7.6, 0.31 x 3.0–3.4–4.0 μm, 0.29, 24 (on exumbrella).

Although the birthplace of *Eugymnanthea inqulina* is unknown, it is likely that this Mediterranean hydroid immigrated to Japan together with the host *Mytilus galloprovincialis* which is said to be synonymous with *M. edulis* or a subspecies of *M. edulis*, and it is unlikely that the opposite case would happen. If this would be true, the morphological change of European *Eugymnanthea* under the environment of the Japanese waters for a short time is noticeable from the evolutionary point of view. However, it is possible that *Eugy. inquilina* survived in both the sides of the former Thethys Sea. Further studies on the morphology and distribution of this hydroid will reveal this biological aspect.

Compared with a wide distribution of *Eutima japonica*, in Japanese waters the distribution of *Eugymnanthea inquilina* was restricted, and it occurred for the present only at one place, Shimoda, Sagami Bay, central Japan. In this water *Eutima japonica* was also found (Fig. 25, R), therefore both species are distributed sympatrically there. The restricted distribution of *Eugymnanthea* seems to be mainly attributable to the following reason: the primary capacity to spread the species by itself (by the planktonic medusa) is very weak because of its short-living medusa in comparison with *Eutima* which has a well-developed and long-living medusa, therefore *Eugymnanthea* is defeated in competition. It is important to clarify the host preference of Japanese *Eugymnanthea*, which has not yet investigated, while in Italian *Eugymnanthea* it was relatively well studied by Crowell (1957). According to his observation, *Eugy. inquilina* was frequently associated with several kinds of bivalves of both attaching and burrowing types, and no distinct host specificity was found.

Returning to the context mentioned above, in 1922 *Eutima japonica* was collected from Japan in the coasts of both Sea of Japan and the Pacific Ocean (Yunohama and Misaki) by Uchida (1925) (Fig. 25, J, R). Therefore it was already distributed in our country before the immigration of European *Mytilus edulis*. Hence it is very likely that *E. japonica* is not an immigrant species but an endemic one. Because of its ability to associate with various kinds of bivalves, especially with Mytilid ones, *E. japonica* would become to be commensal with European *Mytilus* with its spread and settlement in Japanese waters. The original host of *E. japonica* is, for the present, uncertain, though it seems that *Crenomytilus grayanus* is one of the highest possibilities.

VII. Systematic Considerations on Commensal Hydroids Associated with Bivalves and Their Phylogeny and Evolution

At the present time at least four species of the commensal hydroids associated with bivalves are recognized in the world. They are three species of the genus *Eutima*, *E. japonica* Uchida, 1925, *E. commensalis* Santhakumari, 1970, and *E. sapinhoa* Narchi and Hebling, 1975, and one species of *Eugymnanthea* which is divided into two subspecies, *E. inquilina inquilina* Palombi, 1935 and *E. inquilina japonica* Kubota, 1979. Besides these there are two uncertain species, *Eugymnanthea ostrearum* Mattox and Crowell, 1951 and *Eugy.* sp. Ramachandra Raju *et al.*, 1974. The generic status of the former is here tentatively assigned to *Eutima* instead of *Eugymnanthea* because its newly liberated medusa or slightly developed medusa is immature (see Kubota 1978a). However, the assignment of the genus *Eugymnanthea* for the latter is inappropriate from the life-historical point of view. How do we treat such a troublesome case? A solution will be shown later in this chapter.

Every species of these commensal hydroids has both polypoid and medusan generations, and the life-history has been clarified by rearing in laboratory and/or field work. The morphology and some biological notes in such life stages as polyp, newly liberated medusa, and mature medusa of these five species are summarized in Tables 37 and 38. The morphological comparison among them in these life stages was already made and a general discussion on the peculiar morphology of polyp was given in a previous paper (Kubota 1978a).

A. Grouping of Commensal Hydroids Living in Bivalves from the Life-Historical Point of View, with a Proposal of a New Species-Designation

Because of the Athecata-like morphology of the polyp in the outward appearance, particularly of the solitary form without periderm, the commensal hydroids living in bivalves are considered as the most specialized group in Thecata-Leptomedusae, and it comes to my conclusion at present that all of them belong to Eutimidae while these have been treated under different families by former workers. The commensal hydroids can be divided into three groups based on the combination of morphology of polyp and medusa as follows:

Group I: *Eutima japonica, Eutima sapinhoa, Eutima ostrearum*......with ordinary polyp and ordinary medusa

Group II: *Eutima commensalis*......with extraordinary polyp and ordinary medusa

Group III: *Eugymnanthea inquilina inqulina, Eugymnanthea inquilina japonica*......with ordianry polyp and extraordinary medusa

The polyps of group I and the polyps of group III are of similar morphology and distinct separation is difficult with each other, though *E. sapinhoa* tends to have more tentacles than the others (Table 37). The common characteristics in these polyps are: (1) an unbranched solitary body with a pedal disk of sucker type; (2) complete absence of periderm on whole body portions, while only a medusa-bud is covered with a thin membrane; (3) presence of a membraneous web on the base of tentacles. Of these three characteristics the former two are specialized ones among the thecate hydroids, and they are exclusively found in the commensal hydroids living in bivalves. They could be considered as secondary modified characters (derived ones) evolved correlating with the commensal life within the mantle cavity of bivalves. As to the other character, the intertentacular web, it is rather commonly found in many genera of the thecate hydroids with medusan generation such as *Aequorea* (Aequoreidae), *Eucheilota* (Lovenellidae), *Gastroblasta* (Campanulariidae), *Eutonina* (Eutimidae), *Helgicirrha* and *Eirene* (Eirenidae), *Hydrodendron*, *Hydranthea*, and *Campalecium* (Haleciidae), etc. (see Russell 1953, Millard 1975, etc.). Accordingly this web could be considered as a primitive character in Thecata. Another possibly primitive character of the Thecata-Leptomedusae is the nematocysts of a small (slender) type of microbasic mastigophores or basitrichous isorhizes. This can be said by the fact that this nematocyst is distributed in all the thecate hydroids, both in polypoid and medusan generations (see Itô and Inoue 1962, Kubota 1976, '78a, etc.), though it was also found in some athecate hydroids and not yet fully examined in some commensal hydroids associated with bivalves.

In contrast with these ordinary polyps of groups I and III, the polyp of group II is a peculiar one. Instead of possessing the pedal disk of a sucker type, it has a root-like pedal disk which penetrated into the host tissue. This solitary polyp with a root-like pedal disk usually buds a number of daughter zooids and becomes a branched polyp consisting of 39 zooids at maximum (see Santhakumari and Nair 1969). It is noticeable that the original hosts of this polyp are wood-boring bivalves and they are different from hosts of the polyps of groups I and III in the mode of life as well as the body structure.

On the other hand, from the polyps of groups I and II immature small medusae are liberated, and after metamorphosis they become a mature form with the characteristics of the genus *Eutima* (Talbe 38). Of these mature medusae, *E. japonica* is the largest one with the largest number of tentacles and the most elongated peduncle, while *E. sapinhoa* is the smallest medusa with the smallest number of tentacles. As to the characteristic of the lateral cirri, *E. commensalis* of the group II has the cirri in every developmental stage, while *E. sapinhoa* has no cirri in every stage. *E. japonica* invariably possesses numerous cirri in very young stage, but in the mature stage two forms are recognized as to the presence of cirri (though they are not clearly discriminated, see II): one is the form without cirri (if present the number is small) found in the specimens from northern Japan and the other is the one with many cirri (though some had a small number of cirri) found in the specimens from southern Japan. Accordingly *E. japonica* is the medusa with or without cirri and it is the intermediate form between *E. sapinhoa* without cirri and *E. commensalis* with cirri in terms of the cirri. *E. ostrearum* is possibly of

Table 37. Morphology and some biological notes of polyp in six

Species	Nation (Host)	Body length (mm)	Body width (mm)	No. of tentacles	No. of polyp per host
Eutima ostrearum	Puerto Rico (*Crassostrea rhizophorae*)	up to 3.8 mean 1.5	up to 0.35	up to 35 mean 30	up to 210
Eutima commensalis	India (*Nausitora hedleyi*)	0.23-1.2[2] up to 4.1[3]	0.04-0.13	6-20	up to 80
Eutima sapinhoa	Brazil(*Tivela mactroides*)	0.23-2.3	mean 0.35	8-44 mean 40	—
Eutima japonica	Japan (7 spp.)[4]	0.25-7.8	0.10-0.40	8-31	up to 2043[5]
Eugymnanthea inquilina inquilina	Italy (*Tapes decussatus*)	0.50-0.90 mean 0.75	mean 0.25	20-30	—
	Italy (*Mytilus galloprovincialis*)	0.2-3.5 mean 2.0	—	10-30	—
E. i. japonica	Japan (*Mytilus edulis*)	0.10-1.5	0.04-0.16	12-27	up to 669

1) M: mantle, LP: labial palp, G: gill, F: foot, VM: visceral mass. 2) In single zooid. Oshoro, while in *Crenomytilus grayanus* several ten thousand polyps were associated. 6) See

Table 38. Morphology of the youngest medusa and mature medusa in six

Species (Nation)	Age (days)	W (mm)	H (mm)	Te
Eutima ostrearum (Puerto Rico)	1-8	within 3.0	3.0	4
Eutima commensalis (India)	1	0.44-0.50	0.41-0.44	2
	ca. 1[1]	0.41-0.59[2]	0.32-0.53[2]	0-2
	mature[1]	5.3-5.9[2]	3.2-3.5[2]	8
Eutima sapinhoa (Brazil)	1	0.9-3.0	0.7-2.9	4
	25	4.0	4.0	4
Eutima japonica (Japan)	1[4]	0.84-3.0	0.56-2.0	usually 2 or 4
	20-42[5]	7.5-12.2	4.8-8.3	usually 8
	14-126[6]	7.5-14.6	4.8-9.5	8-20
Eugymnanthea inquilina inquilina (Italy)	1	0.55 or more	0.55	0
	1	—	1.2	0
	1	0.88-2.0	1.1-1.4	0
E. i. japonica (Japan)	1	0.78-1.2	0.52-0.80	0

1) Plankton. 2) Preserved state. 3) At the age of half a day.

the form without cirri, because no cirri were found in the youngest or immature medusa slightly developed.

In contrast with the well-developed medusae of groups I and II, the mature commensal hydroids belonging to the genera, *Eutima* and *Eugymnanthea*.

Body portions of bivalves to which polyp attached[1]					Seasonal occurrence of polyp	Time of medusa-bud formation	No. of host species	Author
M	LP	G	F	VM				
+	+	+	+		Jan. – Dec.	—	1	Mattox and Crowell (1951)
		+			Nov. – May	Nov. – Apr.	3	Santhakumari and Nair (1969)
+	+	+	+	+	Jan. – Dec.	—	1	Narchi and Hebling (1975)
+	+	+	+	+	Jan. – Dec.	Jan. – Dec.[6]	12	Kubota (present work)
+	+	+	+	+	Jan. – Dec.	Apr. – Jun., Oct. – Nov.	1	Palombi (1935)
+	+		+	+	Jan. – Dec.	July – Nov.	5	Cerruti (1941), Crowell (1957)
+	+	+	+	+	at least Aug.	at least Aug.	1	Kubota (1979b)

3) Colony height. 4) See Table 3. 5) In *Mytilus edulis* from the intertidal region of Table 12.

commensal hydroids belonging to the genera, *Eutima* and *Eugymnanthea*.

Ms	C	Tb or Mw with cirri	No. of cirri on 1Tb, 1Mw	St	Stl	Stl/St	Author
8-16	0	0, 0	0, 0	8	—	2-6	Mattox and Crowell (1951)
8	8	2, 2	2, 2	8	8?	1?	Santhakumari and Nair (1969)
8	8	2, 2	2, 2	8	—	—	Santhakumari (1970)
56	80	8, 32	2, 2	8	—	—	
16-24	0	0, 0	0, 0	0-8	—	6-8[3]	Narchi and Hebling (1975)
32	0	0, 0	0, 0	8	—	—	
8	12-52	4, 0- 4	2-9, 0-6	8	8-35	1-7	Kubota (1978a, 1979b, present work)
32-85	0-74	0-9, 0-31	up to 5, 3	8	45-105	4-15	
32-103	0-98	0-15, 0-54	up to 5, 3	4-21	28-300	up to 20	
4	0	0, 0	0, 0	8	—	—	Palombi (1935)
8	0	0, 0	0, 0	8	—	1-4 mostly 3	Cerruti (1941)
8	0	0, 0	0, 0	8	—	up to 3	Uchida (1964)
4-8	0	0, 0	0, 0	4-8	4-8	1	Kubota (1979a)

4) See Table 13. 5) See Table 23. 6) See Table 24.

medusae of group III are very tiny and degenerated. They are ephemeral, short-living medusae, and already mature when liberated from the polyp. They entirely lack the tentacles and the manubrium, and if the manubrium is found it appears as a mere trace; moreover the marginal warts or the statocysts are variable in number and their arrangement is sometimes irregular. The noticeable fact is that these peculiar medusae occasionally do not detach from their polyps and degenerate on them after discharge of the gametes under a certain environmental condition.

Consequently in the groups I and II their medusae are of similar morphology despite of the clear difference of the polyps. On the contrary, in the groups I and III their polyps are of similar morphology, but the medusae are apparently different (Fig. 27). This discrepancy has been well known among the hydroid workers for a long time and makes the hydroid taxonomy difficult (see Boero 1980, etc.).

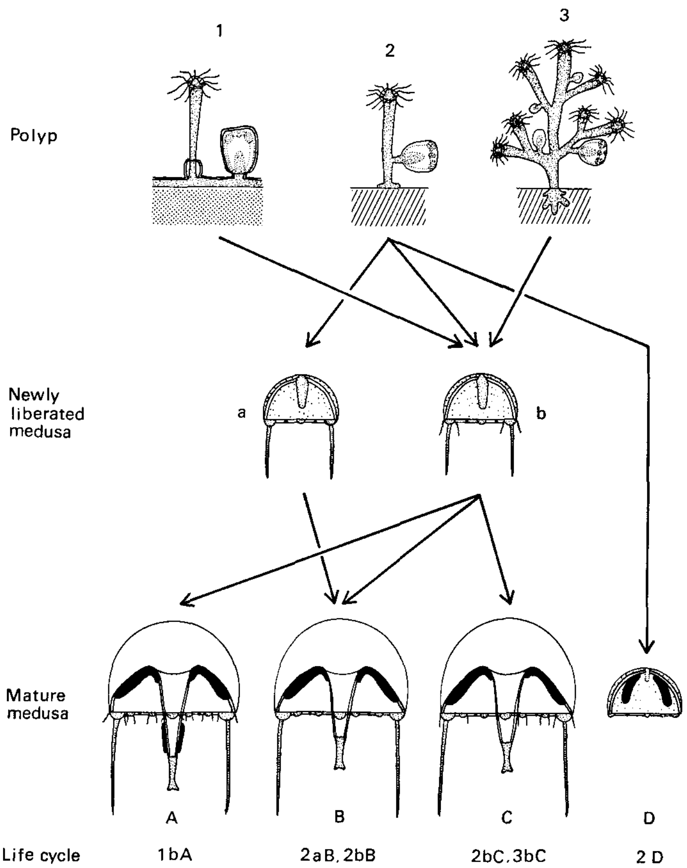

Fig. 27. Schematic illustration of the life-histories of the commensal hydroids associated with bivalves (2aB-2D) and the hydroids of their ancestral type (1bA). 1bA: *Eutima mira*, *E. gracilis*, *E. gegenbauri*; 2aB: *E. sapinhoa* (Group I); 2bB and 2bC: *E. japonica* (I); 3bC: *E. commensalis* (II); 2D: *Eugymnanthea inquilina* (III).

In this connection the author may make special mention of that he has been struggling for a better solution to settle a confused hydroid taxonomy (Kubota 1978a, b, '79a, b, '81). A newly discovered hydroid, in principle, must not be designated as a new species unless its life-history is undoubtfully clarified by both laboratory and field works. However, dual classification system has been often adopted for convenience' sake. As a natural course of event we often encounter a difficulty in assigning a reasonable scientific name for a certain hydroid due to the above-mentioned morphological inconsistency (see Fig. 27). In the case that both the polyp and medusa are clearly different when compared the two materials, these two are very likely two separate species. Then if only one generation (polyp or medusa) is different in the given two materials, how do we taxonomically treat these two materials? Hydroids usually show a morphological plasticity as plants do, therefore a deliberate attitude should be taken for its taxonomic treatment. Keeping these in mind, for avoiding the confusion of hydroid classification the author will propose here a practicable treatment as a step for the complete nomenclature. It is a new species-designation coupling the polypoid and medusan names like *Clytia edwardsi* (polyp species) - *Phialidium haemisphaericum* (medusa species). According to this manner all the commensal hydroids living in bivalves can be designated as follows: *Eugymnanthea inquilina* - *Eugymnanthea inquilina inquilina* (the hydroid from Italy), *Eugy. inquilina* - *Eugy. inquilina japonica* (that from Japan), *Eugy. inquilina* - *Eutima japonica* (that from Japan), *Eugy. 'inquilina'* - *Eutima sapinhoa* (that from Brazil), *Eugy. inquilina* - '*Eutima ostrearum*' (that from Puerto Rico), '*Eutima commensalis*' - *Eutima japonica* (that from India). This designation, partly succeeding the former conventional nomenclature, is able to be used in every case of the taxonomic research of the hydroid even if one generation is unknown or absent: *Eutima commensalis* - ? (the polyp from India) or ? - *Eutima japonica* (the medusa from India).

B. Ancestral Type of Commensal Hydroids Associated with Bivalves

The commensal hydroids of the groups I and II belong to the genus *Eutima*. In this genus many (more than 10) planktonic medusae have been allocated as separate species after the description of the type-species, *E. mira* McCrady, in the 19th century (see Kramp 1961 and '68, Santhakumari 1970, etc.). Among these medusan species, however, in only such three species as *E. mira* McCrady, 1857, *E. gracilis* (Forbes & Goodsir, 1853), and *E.* (*Octorchis*) *gegenbauri* (Haeckel, 1864), their polyp generations have been revealed by rearing, though in the type-species the fully grown polyp with gonangium has been unknown (see Brooks 1884 and '86, Russell 1949 and '70). As mentioned by the author (Kubota 1978a, p.142) the polyps of these three Eutimid medusae bear some common characteristics (Fig. 27, 1): (1) not solitary, but a colonial polyp with a stolon; (2) presence of a periderm on the lower part of hydrocaulus and a medusa-bud is protected by a gonotheca; (3) presence of intertentacular web. These characteristics were usually found in the thecate-polyp, though the periderm shows a tendency of reduction.

Accordingly their morphology is clearly different from that of the commensal hydroids living in bivalves, but the following features make them closely resemble with each other: (1) a naked hydranth with an intertentacular web and a general form of a single polyp; (2) the general external morphology and the nematocyst equipment in both the newly liberated medusa and the mature medusa (see Weill 1934, Russell 1938, Kubota 1978a). It is possible that they are of the morphology similar to that of the ancestor of the commensal hydroids associated with bivalves.

Many *Eutima*-species of which life-history has been unknown might have either an ancestral type of polyp like *E. mira*, *E. gracilis*, and *E. gegenbauri*, spending rather a free-living life or a specialized polyp like a bivalve-inhabiting polyp belonging to *Eutima* and *Eugymnanthea*, spending a commensal life.

C. Phylogeny and Evolution of Commensal Hydroids Associated with Bivalves.

Among the Eutimid polyps which were of ordinary Thecata-morphology and spent an epizoic life on the exterior surface of various substrata (Fig. 28, *1*), some settled down in a unique ecological niche, "within the mantle cavity of bivalves" (Fig. 28, *3*), which had been unexplored by any other hydroids of different lineage. Associating with various free-living bivalves or some wood-boring ones, they adapted themselves to the commensal life by modifying their body structure functionally after overcoming a danger of ingestion by the host. The hydrorhiza evolved from

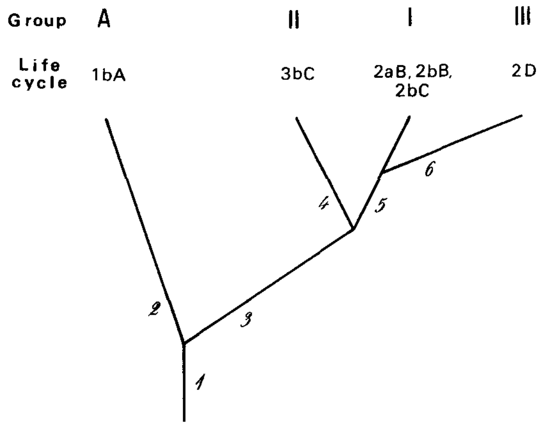

Fig. 28. Phylogenetic tree of the commensal hydroids associated with bivalves (I-III) and the hydroids of their ancestral type (A). *1*: with the morphology of typical Thecata-Leptomedusae (ancestor of Eutimid hydroid), *2*: periderm of polyp slightly reduced (direct descendant), *3*: commensal life with bivalves leads to the polyp reduction of periderm and stolon (ancestor of commensal Eutimid hydroid), *4*: evolution of a branched polyp with the pedal disk of root type, *5*: evolution of an unbranched polyp with the pedal disk of sucker type, *6*: medusan generation reduced to a short-living medusoid (as to Life cycle see Fig. 27).

a stolon to a pedal disk of sucker type (Fig. 28, *5*) or root type (Fig. 28, *4*), by which settlement to the host was ensured. For the sake of the protection by the host or some unknown reasons for a commensal life, the polyp took off the periderm completely. It is interesting here to note that (1) a nemertinean *Malacobdella* living in the mantle cavity of *Pseudocardium* has also a well-developed sucker and that (2) the carapace of most commensal pinnotherid crabs is not hard but soft. The polyp evolved in such a manner, but some primitive or ancestral features, the intertentacular web and a certain kind of nematocyst, were still present in the body.

Compared with the evolution of the polypoid generation, the medusan generation of the commensal hydroids living in bivalves has not been much changed. The immature medusa liberated from the polyp grows into the well-developed leptomedusa after metamorphosis (Fig. 28, *3–5*) as taking the similar process to the ancestral hydroid (Fig. 28, *1*) and its direct descendant (Fig. 28, *2*). In order to carry out its duty as a sexual generation, the medusa spends a relatively long planktonic life, exchanging a gene combination, during which it spreads the distribution of the species. Among these ordinary commensal hydroids which still (?) belong to the genus *Eutima*, some were specialized even in the medusan generation in order to spend a whole life near the host bivalves (by the reduction of the medusan generation). To this branch the genus *Eugymnanthea* belongs and it could be conceivable as the most advanced commensal hydroids with bivalves.

Summary

1. The life-history of the Japanese commensal hydroids associated with bivalves and their biological aspects such as nematocyst equipment, host preference, distribution, local variation were investigated from the systematic point of view during 1977 to 1981.

2. About 14000 specimens of 36 bivalve species collected from various localities were examined, and many hydroid specimens associated with 50 specimens of nine bivalve species were reared from polyp to mature medusa in laboratory, often covering all the life-span of medusa, and furthermore the rearing was extended to planula larva and primary polyp.

3. The polyp, under 8 mm in length, is usually solitary, with a sucker and 8–31 tentacles with intertentacular web, showing a wide variation on its morphology and size. The commensal life of polyp within a mantle cavity of *Mytilus edulis* was surveyed for a year at Oshoro, Hokkaido. The association rate was 25% on the average and polyps were often found on all the soft body portions of the host (587 polyps per host on the average). Both the daughter polyp and medusa-bud were produced actively in summer to autumn, but the asexual reproduction was scarcely observed in winter to spring. The time and place of the settlement of the hydroid as a new generation were clarified, and the whole life of the hydroid correlated with that of host was considered. Moreover, both the advantages and disadvantages of the commensal life between the hydroids and bivalves were reviewed.

4. The newly liberated medusa is about 1–2 mm in diameter, with eight marginal swellings, eight statocysts, and many (up to 52) cirri. The morphology is nearly stable regardless of the different locality or host, though the tentacles of medusa in southern population are usually two in number while four in northern one. The metamorphosis of medusa proceeds regularly, but the young medusa from northern Japan developed rapidly and grew up to a precocious and small (ca. 8 or 9 mm in diameter) mature medusa without or with a small number of cirri (up to 18) within at least a month after liberation. Compared with this in the southern medusa the maturation occurred later and sometimes grew into a larger medusa (up to 14.6 mm in diameter) with markedly elongated peduncle (up to 7.1 mm), much more marginal swellings (up to 103), and with many cirri (up to 98). The smaller northern mature medusa, however, grew further (up to 12.2 mm in diameter, with up to 73 marginal swellings) and a number of cirri (up to 82) reappeared in some specimens, moreover many cirri (up to 69) remained in the mature medusa reared at a high temperature (25°C) or a high salinity (40‰). Accordingly a clear distinction is difficult to find between the populations. The medusa usually survived for two to three months, and in some senile specimens near degeneration conspicuous morphological changes often occurred and they had up to 20 tentacles and 21 statocysts.

5. The egg is usually 64–82 μm in diameter and the typical planula is 56–96 μm in length and 40–64 μm in width, and they are markedly small among the hydrozoans. The planula metamorphosed into the primary polyp usually on the mantle just beneath the labial palp of *Mytilus edulis*. The primary polyp is 54–88 μm in length and had 5–7 tentacles with webs.

6. The nematocyst constitution and size in every material are nearly immutable regardless of the difference of the locality and the host. The nematocyst equipment is different among the life stages, and it becomes more complicated in the following order: planula (atrichous isorhizes of one type), polyp (basitrichous isorhizes of two types), and medusa (atrichous, basitrichous, and merotrichous isorhizes are found and the former two are divided into several types). The distribution of nematocysts is different in proportion to the body portions: in medusa atrichous and basitrichous isorhizes are found on tentacles, atrichous and merotrichous isorhizes are on cirri, and basitrichous isorhizes are on oral lips or exumbrella.

7. The taxonomic status of the present Japanese hydroid is concluded to be *Eutima japonica* Uchida, 1925 and with which *Ostreohydra japonica* Yamada, 1950 and *Eutima cirrhifera* (Kakinuma, 1964) are synonymous judging from various biological aspects.

8. *Eutima japonica* Uchida is commonly distributed through Japan, associated with 12 bivalve species of different lineage. It is usually commensal with the bivalves of which mode of life is of the attaching type, while rarely with the bivalves of the burrowing type; and the most frequent association is found in the bivalves belonging to the Mytilidae. *E. japonica* is very likely an endemic species,

while the other Japanese commensal hydroid *Eugymnanthea inquilina japonica* Kubota, 1979, which has been recorded only at Shimoda, central Japan, might be an immigrant species from Europe.

9. All the known commensal hydroids living in bivalves in the world are divisible into three groups from the life-historical point of view and their morphological characteristics are reviewed. The ancestral type of the commensal hydroids, which may spend a free-living life and has the ordinary morphology characteristic of Thecata-Leptomedusae, is inferred; and the phylogeny and evolution of the commensal hydroids associated with bivalves is considered.

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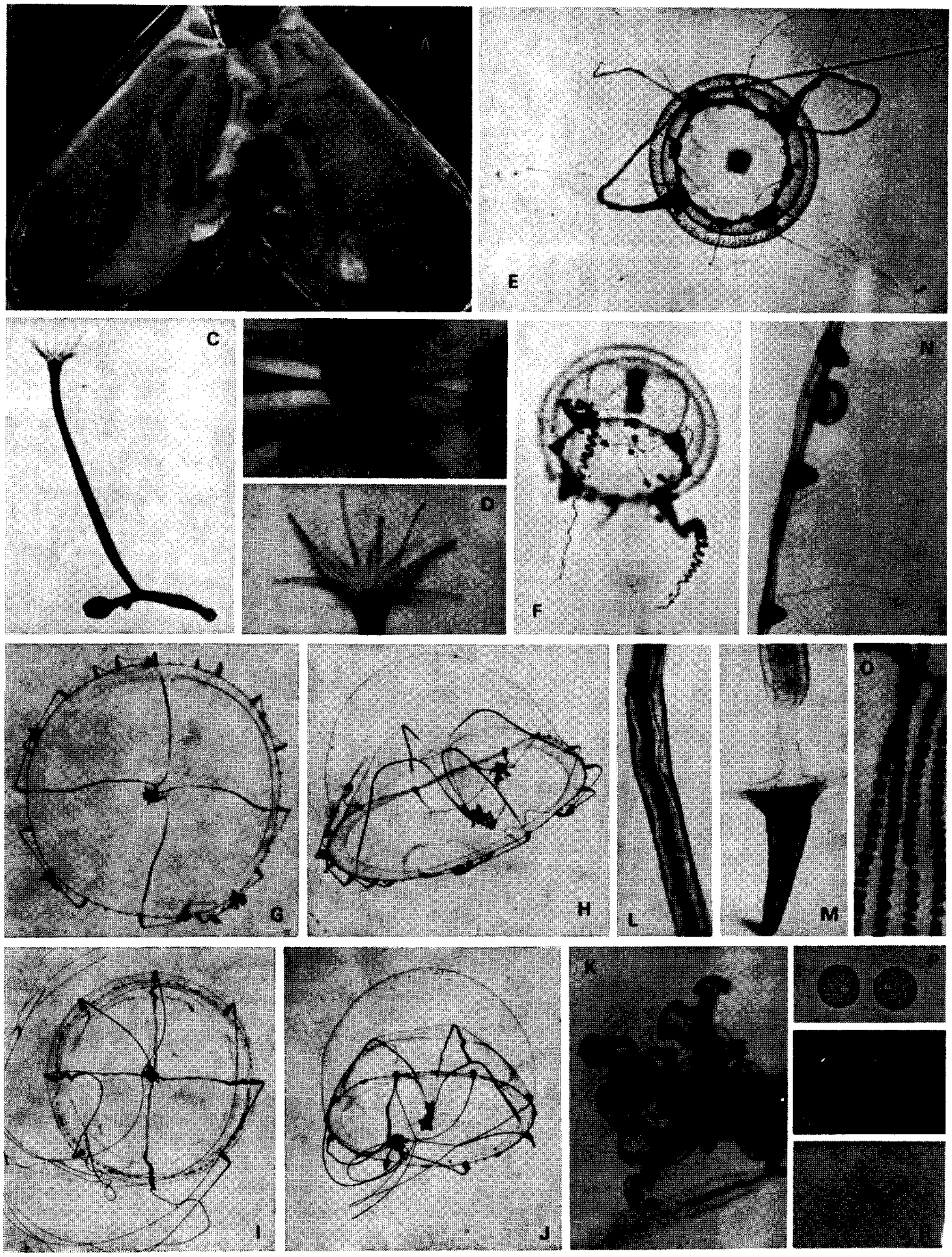
Explanation of Plate X

A: A specimen of *Mytilus edulis* from Oshoro (collected on November 28, 1980), associated with a number of polyps on its various body portions.
B: A body portion of the above host attached by many commensal polyps.
C: A polyp bearing two medusa-buds of different growths, 3.8 mm in length and 0.2 mm in width (host: *Mytilus edulis* from Mukaishima Is.).
D: An upper portion of the above polyp, showing a tentacular web.
E, F: A youngest medusa within one day old after liberation; W=1.1 mm, H=0.78 mm; E: oral view, F: side view (host: *Mytilus edulis* from Mukaishima Is.). Note two tentacles.
G, H: A medusa reared in laboratory (No. b) about two and a half months old; W=12.5 mm; G: aboral view, H: side view (host: *Mytilus edulis* from Mukaishima Is.). Note 19 tentacles and an elongated peduncle.
I, J: A medusa reared in laboratory (No. 9) about two months old; W=10.5 mm, Te=8; I: aboral view, J: side view (host: *Mytilus edulis* from Usa).
K: Folded oral lips of a male mature medusa reared in laboratory, 30 days old (host: *Mytilus edulis* from Kuroiwa).
L: A portion of gonad of the above male medusa from Kuroiwa.
M: A distal portion of gonad and a tentacular bulb of a male medusa reared in laboratory, 89 days old (host: *Crenomytilus grayanus* from Oshoro).
N: A portion of umbrellar margin of the above medusa from Oshoro, showing a statocyst containing many statoliths and marginal warts without or with a lateral cirrus.
O: A portion of tentacles of the above medusa from Oshoro.
P: Unfertilized eggs discharged from the mature medusa reared in laboratory, 45 days old from Usa (the same specimen shown in I and J).
Q: A planula larva appeared three days after mating of one pair of medusae reared in laboratory (host: *Crenomytilus grayanus* from Oshoro).
R: A primary polyp with six tentacles (the specimen shown in Fig. 23, D). Note the tentacular web.



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