STUDIES ON THE EARLY LIFE HISTORY OF WALLEYE POLLOCK *THERAGRA CHALCOGRAMMA* IN FUNKA BAY AND VICINITY, HOKKAIDO*

By

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Contents

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I. Introduction

Walleye pollock, *Theragra chalcogramma*, is a commercially important species in Japan and the annual hervest is approximately 1,500,000 tons. This species is widely distributed in the northern North Pacific and the spawning grounds have been reported from the seas adjacent to Hokkaido Island (Tomabechi *et al.*, 1952; Ito *et al.*, 1955; Ito and Kurahashi, 1955; Ishigaki *et al.*, 1960; Tanaka, 1970; Zver'kova, 1978), the Kamchatka Peninsula (Zver'kova, 1969), the Bering Sea (Maeda, 1972; Serobaba, 1974; Nishiyama and Haryu, 1981), Kodiak Island, the western Gulf of Alaska (Hughes and Hirschhorn, 1979), and in the Sea of Japan from Toyama to Niigata (Ogata, 1956).

In Hokkaido, Funka (Uchiura) Bay and vicinity is one of the primary spawning grounds of walleye pollock in Japan. Stocks in this area support a bottom gill net commercial fishery from October to March during the spawning season (Hakodate Fish. Exp. St., Muroran branch, 1980). Large annual hervest fluctuations of this fish are considered correlated with larval mortality, rather than spawning stock size (parental stock) and the mortality of the fish larvae during the first feeding stage is largely affected by the existing amount and quality of food available (ref. Hjort, 1914, 1926). Marr (1956) stated that there are 3 types of early survival curves: (1) the "critical period" type, with catastrophic mortalities restricted to a brief period, (2) survival rate increases constantly, and (3) survival rate is kept at a constant level. The concept of the "critical period" is widely accepted, but there is no supportive evidence (Sekiguchi, 1975).

Shelbourne (1957) reported that larval mortality of North Sea plaice *Pleuronectes platessa* was related to feeding conditions. In support of this concept, feeding of marine fish larvae has been studied by many investigators (Sysoeva and Degtereva, 1965; Watanabe, 1970; Last, 1978; Coombs *et al.*, 1981; etc.). It was shown that, for the northern anchovy *Engraulis mordax* in California, the size of anchovy in the recruitment year class was closely related to the standing crop of phytoplankton (Lasker *et al.*, 1970; Lasker, 1978).

In Funka Bay and vicinity, the location of fishing grounds for walleye pollock spawners shifts to a certain extent each year associated with the hydrographic conditions (Hakodate Fish. Exp. St., Muroran Branch, 1980). Transport process of walleye pollock eggs and resultant distribution in Funka Bay have been observed by Ito *et al.* (1955), Ito and Kurahashi (1955), Kamba (1977), and Nakatani and Maeda (1981). Several workers, such as Yusa (1954), Hamai *et al.* (1971), Fukuchi (1976), and Nakatani and Maeda (1984), have conducted rearing experiments with artificially fertilized eggs and found that water temperature for maximum hatching was 2.0°~4.0°C. Kamba (1977) and Nakatani and Maeda (1983) found that walleye pollock larvae initiate feeding mainly on copepod nauplii and larval copepodids.

In an attempt to understand the causative factors of walleye pollock population size fluctuations in the fishing grounds of Funka Bay and vicinity, larval transport by ocean currents and availability of food organisms for the larvae were investigated in this study.

II. Materials and Methods

In the years from 1977 to 1983, sampling surveys of Funka Bay and vicinity were made by the R/V "Ushio Maru" of Hokkaido University (Fig. 1, Table 1). Samples of walleye pollock eggs, larvae, and the larval food organisms were collected by vertical hauls from the sea bottom to the surface with a NORPAC net (mouth diameter = 45 cm, length = 180 cm, mesh = 0.33 mm). Samplings were also made by horizontal tows with MOTODA closing nets (MTD net; Motoda, 1971; mouth diameter = 56 cm, length = 200 cm, mesh size = 0.33 mm) for 5~10 minutes at a towing speed of 2 knots at 6 layers (10, 20, 30, 40, 60, and 80 m depth). Because of probability of net avoidance by walleye pollock larvae, a larval net (mouth diameter = 1.3 m, length = 4.5 m, mesh size = 0.62 mm) was towed from the sea bottom to the surface and at 4 layers (10, 30, 50, and 70 m) for 5~10 minutes at 3 knots in April. Square midwater trawl net (2.0×2.5 m; Fac. Fish., Hokkaido Univ., 1968) was towed for 10~15 minutes at the layer which coincided with echo-gram showing the larval images from an echo sounder (10~50 m depth) at 3 knots in May and otter trawl net (4.4×5.6 m) was towed at several depths (10~300 m) for 10~15 minutes at 3 knots from June to August. Copepod nauplii, which are the food for walleye pollock larvae at the stage of initial feeding, were collected by vertical hauls from the sea bottom to the surface with a NORPAC net (mouth diameter = 45 cm, length = 180 cm, mesh size = 0.10 mm) and with a Van Dorn water sampler at 10 m intervals from 10 m to 80 m depth. The samples were immediately preserved in 5% formaldehide solution on board. Salinity and temperatume were observed by Nansen bottle samplers with reversing thermometers at several depths.

Eggs and larvae of walleye pollock and zooplankton were sorted in the laboratory. Counting of the eggs was made after separating by the stage of development.

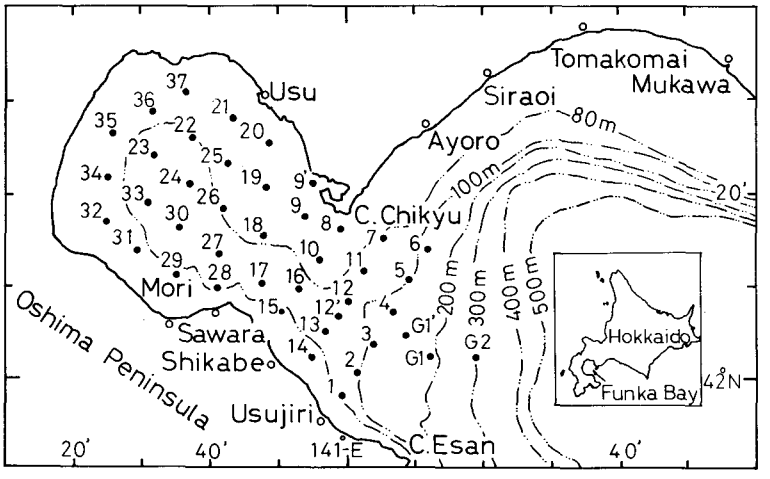

Fig. 1. Location of sampling stations and bottom contours in Funka Bay and vicinity.

Table 1. Positions of sampling stations.

Station	Location		Depth (m)
	Latitude (N)	Longitude (E)	
1	41°58.3′	140°58.9′	86
2	42°00.8′	141°01.0′	96
3	42°03.8′	14.°03.4′	98
4	42°07.2′	141°06.2′	110
5	42°10.7′	141°08.9′	111
6	42°14.1′	141°11.7′	125
7	42°15.1′	141°05.1′	80
8	42°16.2′	140°58.6′	63
9	42°16.1′	140°54.0′	58
9′	42°21.3′	140°47.5′	43
10	42°12.9′	140°56.0′	67
11	42°11.7′	141°02.0′	78
12	42°08.3′	140°59.4′	84
12′	42°06.6′	140°58.0′	83
13	42°04.9′	140°56.6′	85
14	42°02.5′	140°54.6′	76
15	42°07.0′	140°50.5′	78
16	42°09.4′	140°52.7′	80
17	42°10.4′	140°42.7′	92
18	42°15.5′	140°47.7′	73
19	42′20.5′	140°48.3′	56
26	42°18.4′	140°42.1′	75
27	42°13.3′	140°41.5′	91
28	42°09.9′	140°41.1′	87
29	42°11.2′	140°35.4′	84
30	42°16.2′	140°36.0′	91
31	42°14.0′	140°29.9′	81
32	42°16.9′	140°24.4′	56
33	42°19.0′	140°30.5′	94
34	42°21.5′	140°24.8′	70
35	42°26.7′	140°25.0′	66
36	42°29.1′	140°31.2′	78
37	42°31.4′	140°37.6′	68
G1	42°02.3′	141°12.4′	200
G1′	42°05.2′	141°09.2′	122
G2	42°02.6′	141°19.0′	300

The 5 stages used in this study were defined as follows:

Stage 1 — fertilization~morula stage;
Stage 2 — blastula~first gastrula stage;
Stage 3 — apparently germ ring near an equatorial position~blastopore just before closing;
Stage 4 — completely closed blastopore~embryo reaching three-fourths of the yolk circumference;
Stage 5 — embryo reaching over three-fourths of the yolk circumference.

The number of walleye pollock larvae was counted and total length was measured to 0.1 mm. Viscera were dissected out with a fine needle under a binocular microscope and the food organisms ingested were sorted to lowest possible taxa. The number of the food organisms was counted and the maximum width of the organisms was measured to 0.01 mm.

Identification of copepod nauplii is certainly a difficult task, but there are several papers dealing with this (Oberg, 1906; Lebour, 1916; Gibbons and Ogilbie, 1933; Gibbons, 1938; Johnson, 1937) and has been reviewed by Ogilvie (1953) and Lovegrove (1956). In addition, Hanaoka (1952) and Faber (1966) published the keys to the common free-swimming copepod nauplii, based on features of antennule and mandible. In this study, identification was made using these keys and also the relationship between the developmental stage and the body length. However, *Pseudocalanus minutus* in stages I~III are similar in size and diagnostic characters to *Metridia lucens* and it is difficult to distinguish. For this reason, these in stage I~III were classified as *P. minutus* or *M. lucens*.

In addition to the field work, effects of low temperature on embryonic development were examined in the laboratory. The eggs and milt of walleye pollock in mature condition were selected from several spawners collected by a hand line on 3 March, 1982 and 17 February, 1983 off Ainuma in the Sea of Japan and by bottom trawling on 13 January, 1983 in Funka Bay. Fertilization was accomplished by the ordinary dry method and the eggs were reared under 7 temperature conditions (−1°, 0°, 2°, 4°, 7°, 10° and 13°C). To examine development at low temperatures, the eggs at 4 developmental stages (2-cell stage, morula stage, first gastrula stage, and the stage of blastopore closing), which were reared at 4°C, were transfered to beakers held at −1°C and 0°C, respectively. Upward floating velocity (m/h) and specific gravity (g/cm^3) of the eggs reared at 4°C were measured after 2-cell stage until hatching. The design of methods specific to this experiment has been described in detail by Nakatani and Maeda (1984).

From the morphological change, Haryu (1980) reported that walleye pollock larvae can be divided into 7 developmental stages. Owing to his identification the larvae collected during March and April in this study were classified into postlarval stage, while those collected after May were into juvenile stage.

III. Results

1. Distribution of walleye pollock eggs

The horizontal distributions of walleye pollock eggs of 5 developmental stages

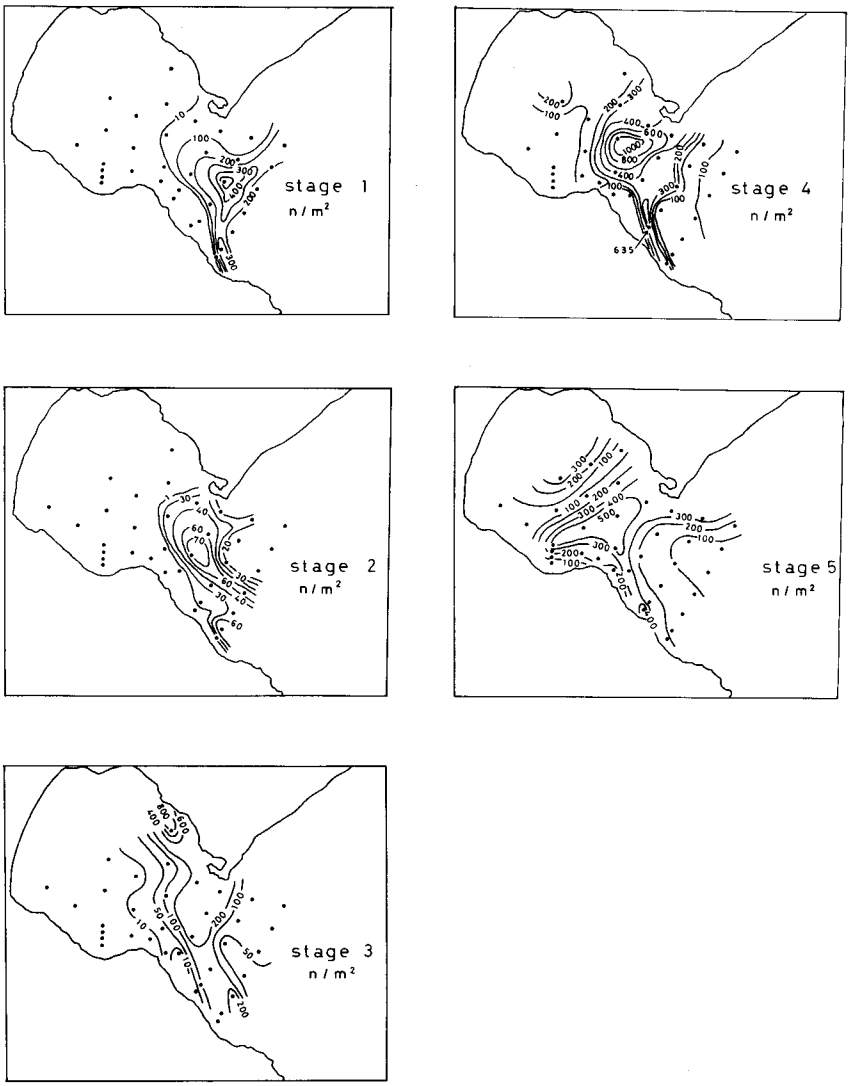

Fig. 2. Distribution of walleye pollock eggs on March 7～15, 1977. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net. (Nakatani and Maeda, 1981)

Stage 1 : fertilization～morula stage
Stage 2 : blastula～first gastrula stage
Stage 3 : apparently germ ring near an equatorial position～blastopore just before closing
Stage 4 : completely closed blastopore～embryo reaching three-fourths of the yolk circumference
Stage 5 : embryo reaching over three-fourths of the yolk circumference

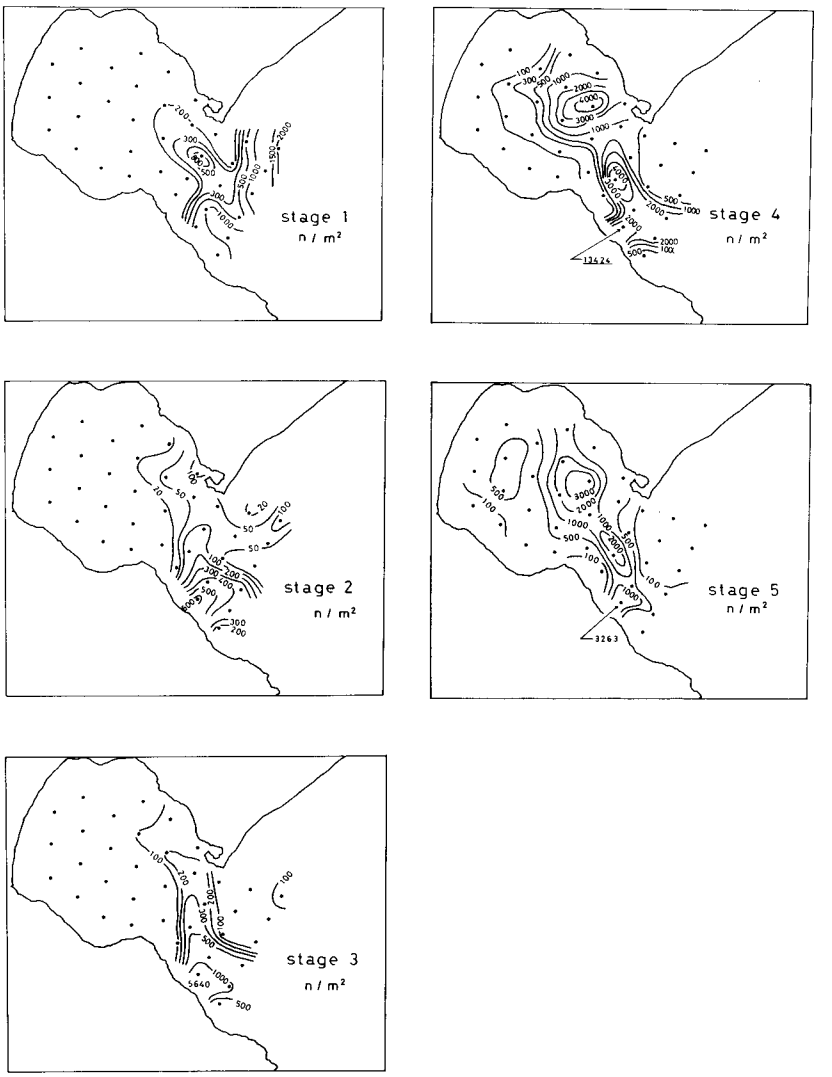

Fig. 3. Distribution of walleye pollock eggs from 24 January to 11 February, 1978. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net. The 5 developmental stages were defined as in Fig. 2.

on March 7～15, 1977 are shown in Fig. 2. Unfertilized eggs were not taken at any station. The earliest developmental stage was in the morula stage (stage 1). Stage 1 eggs were mostly taken in the eastern area of the entrance (from Cape Chikyu to Shikabe) of the bay and collected in a large number at Sta. 12 (541 n/m²). Although many stage 2～3 eggs were also taken outside the bay, the area of most abundant distribution shifted slightly to the west. Stage 4～5 eggs were mostly collected in the entrance and in the inner area of the bay (Fig. 2). A similar pattern

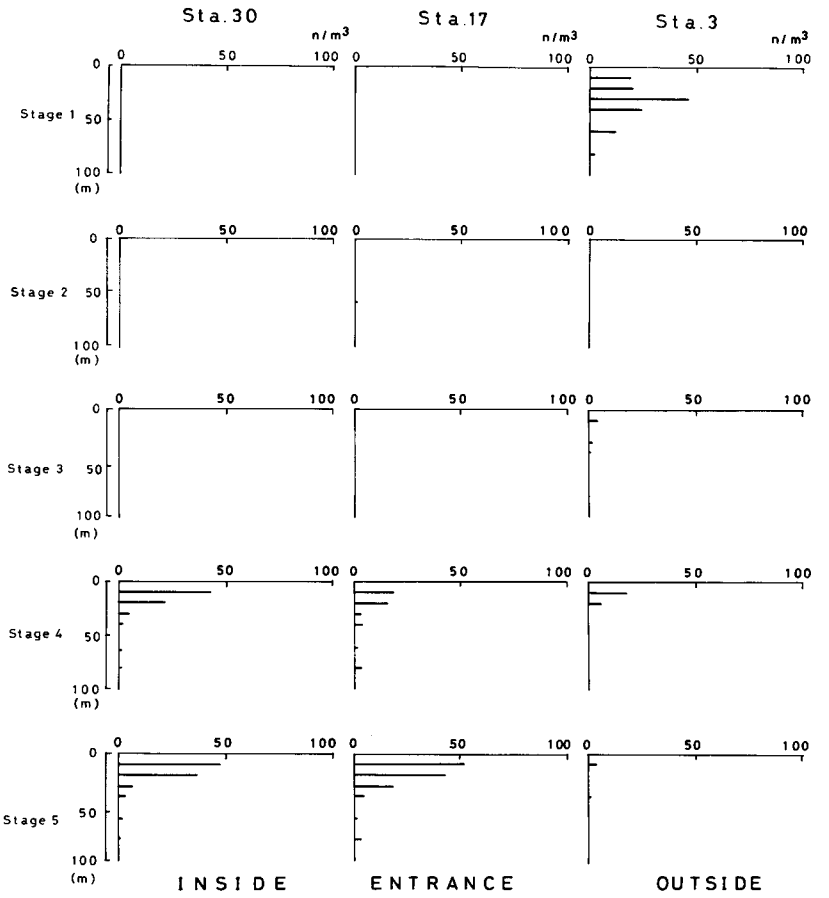

Fig. 4. Vertical distribution of walleye pollock eggs on March 15 and 16, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers (10, 20, 30, 40, 60, and 80 m depth).

was found during the spawning season of 1978 (Fig. 3).

Fig. 4 shows the vertical distribution of the eggs of 5 developmental stages on March 15～16, 1982. Outside the bay (Sta. 3), stage 1 eggs were found from 10 m to 80 m depth with concentration in the surface and subsurface layer (10～40 m depth). Stage 1 eggs, however, were rarely collected at any depth at the entrance (Sta. 17) and in the inner area of the bay (Sta. 30). In addition, may stage 4～5 eggs were obtained in the surface layer (10～20 m depth) at the entrance and in the inner area of the bay.

2. Seasonal change in distribution of walleye pollock larvae and food organisms

2-1. Horizontal distribution of walleye pollock larvae

Fig. 5 shows the distribution of the larvae from 24 January to 11 February,

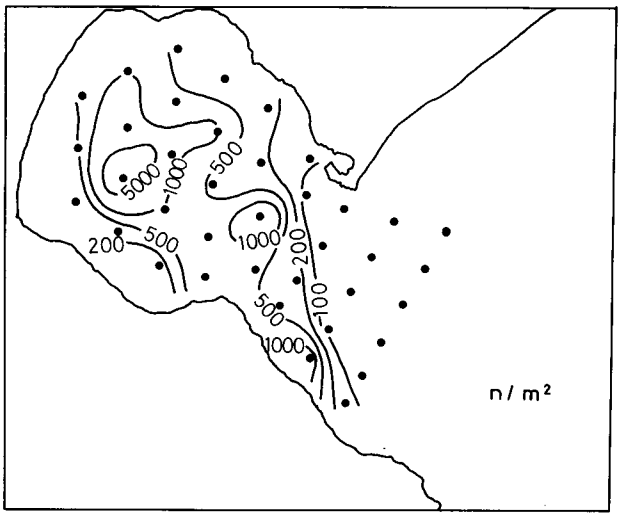

Fig. 5. Distribution of walleye pollock larvae from 24 January to 11 February, 1978. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net.

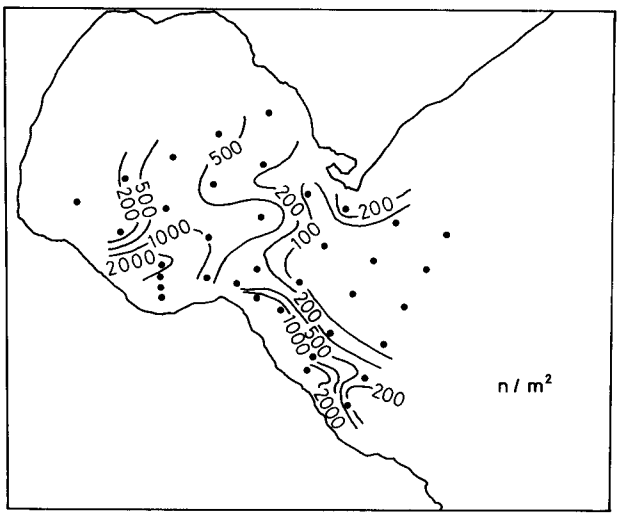

Fig. 6. Distribution of walleye pollock larvae on March 7~15, 1977. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net. (Nakatani and Maeda, 1981)

1978. The many of the larvae were distributed in Funka Bay and coastal area from Sawara to Shikabe and the maximum density of the larvae was observed at Sta. 33 (5132 n/m²). Compared with the distribution of stage 5 eggs, larvae were concentrated to the central area of the bay (off Mori). A similar pattern was observed on March 7~15, 1977 (Fig. 6).

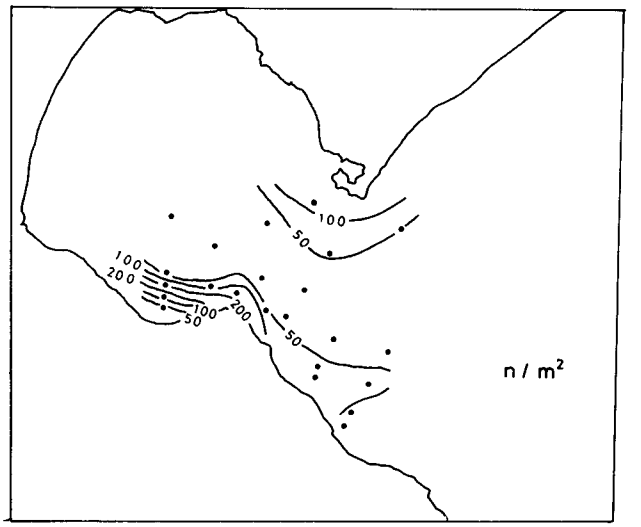

Fig. 7. Distribution of walleye pollock larvae on April 13～15, 1977. Samples were collected by vertical hauls from the sea bottom to the surface with a larval net. (Maeda *et al.*, 1979)

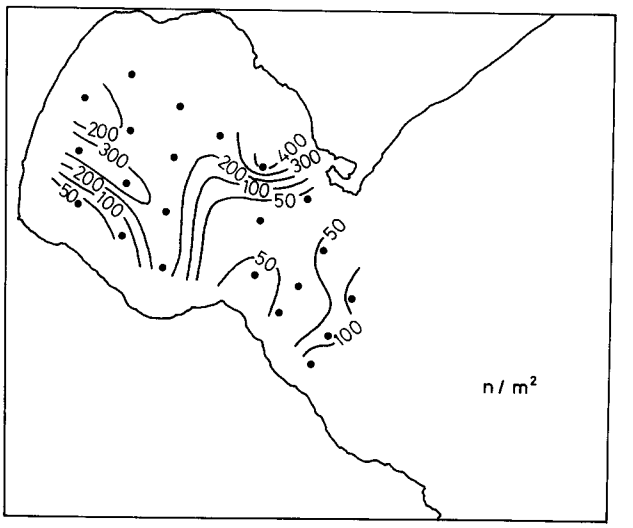

Fig. 8. Distribution of walleye pollock larvae on April 5～10, 1978. Samples were collected by vertical hauls from the sea bottom to the surface with a larval net. (Nakatani and Maeda, 1987)

In April of 1977 and 1978 the distributional pattern of the larvae (Figs. 7 and 8) was similar to that of January (Fig. 5) and March (Fig. 6).

The maximum density of the larvae in May, 1977 (Fig. 9) was measured at Sta. 29 (off Mori in the inner area of the bay). The concentration of the larvae was found not only in the entrance and the inner area of the bay including the Stas. 9,

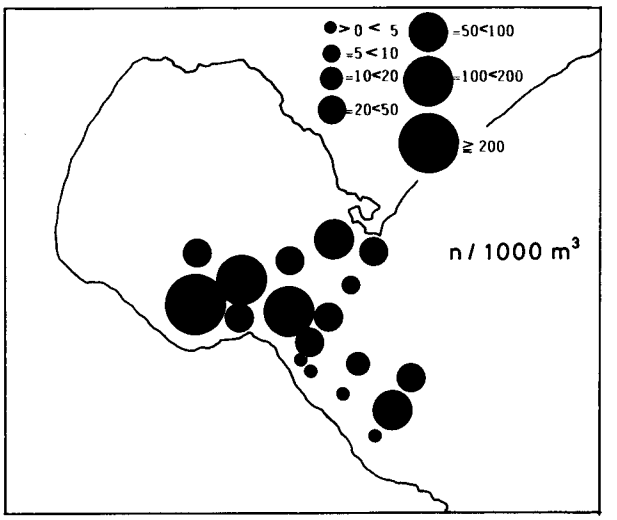

Fig. 9. Distribution of walleye pollock larvae on May 9~11, 1977. Samples were collected by beam trawling. (Maeda *et al.*, 1979)

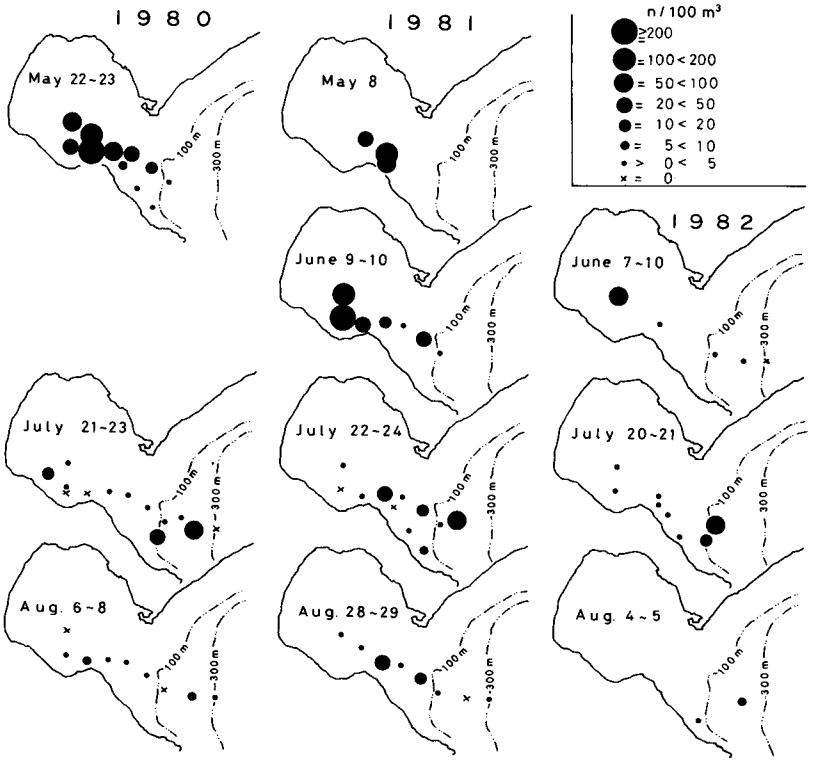

Fig. 10. Monthly change in distribution of walleye pollock larvae from May to August. The collection was made by beam trawling in May and otter trawling from June to August. (Nakatani and Maeda, 1987)

Table 2. Density (n/1000 m³) and mean total length (mm) of walleye pollock larvae on July 4 and 5, 1982 in Funka Bay and vicinity. Samples were collected by otter trawl net on July 4-5, 1982.

Station	Depth (m)	Density (n/1000 m³)	Mean total length (mm)
3	60-70	1.36	66.33
	bottom	3.02	70.85
12′	50～55	0.80	62.52
16	56	4.32	64.04
17	45～50	3.85	65.32
28	60	2.47	67.85
G1′	55～60	1.19	68.58
	160～190	0	
G2	30～35	35.50	67.82
Total			66.81±0.29*

*95% confidence interval

17, and 27 but were also found outside the bay (Sta. 2 ; 77 n/1000 m³) except in the coastal area from Sawara to Usujiri. The distributional pattern in May (Fig. 9) was also observed in 1980 (Fig. 10).

In June of 1981, larvae were collected in large numbers at Stas. 29 and 30. (Fig. 10). A similar pattern was observed in 1982.

Table 2 shows the density of the larvae in early July, 1982. Larvae were widely distributed from Sta. 29 (off Mori in the inner area of the bay) to Sta. G2 (in the eastern area outside the bay) and were collected in large numbers at Sta. G2 (36 n/1000 m³). In late July of 1980, many larvae were also found in the eastern area outside the bay, though some of them still remained in the inner area of the bay (Fig. 10). The distributional pattern of the larvae was also observed in 1981 and 1982.

In August of 1980 and 1981, some of the larvae were collected at Sta. G2 (in the eastern area outside the bay).

2-2. Vertical distribution of walleye pollock larvae

In March 1982, larvae collected by MTD nets were distributed near the surface layer to 80 m depth with the highest concentration found at 20 m depth (Fig. 11). This is slightly deeper when compared with the distribution of stage 5 eggs just prior to hatching (Fig. 4). It has been suggested that the eggs sink from the surface to subsurface layers and hatch out there (Serobaba, 1974 ; Kamba, 1977).

In April 1982, larvae ranged from 6 to 24 mm in total length were collected by horizontal tows with MTD nets and a larval net at Sta. 29 (off Mori in the inner area of the bay) and were concentrated in the surface layer (Fig. 12). This distribution was similar to found in March (Fig. 11). The sampling efficiency of the larval net (mouth diameter = 1.3 m) was approximately identical with that of the MTD net (mouth diameter = 0.56 m).

From May (Fig. 13) to early July (Table 2), the density of the larvae in the

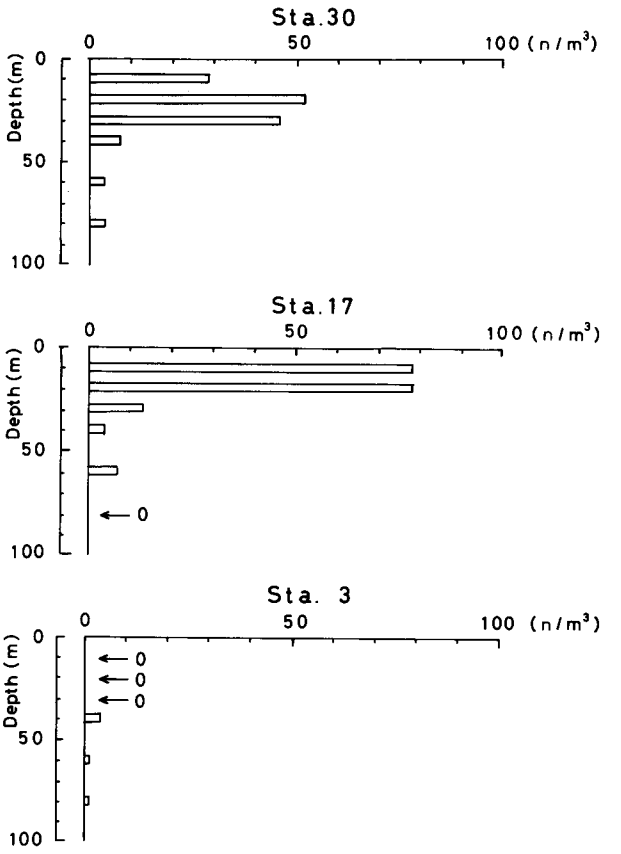

Fig. 11. Vertical distribution of walleye polock larvae on March 15 and 16, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers (10, 20, 30, 40, 60, and 80 m depth). (Nakatani and Maeda, 1987)

surface layer (10～20 m depth) at Stas. 17 and 27 was much higher than those in mid-water (30～50 m depth) and in late July (Fig. 13), a greater part of the larvae were collected on the sea bottom.

Kamba (1977) demonstrated that the small sized larvae collected in April performed a circadian vertical migration. In this study, the distribution of large sized larvae (24～73 mm in total length) during day light hours (14 : 04～16 : 30) was compared with that at night (19 : 20～21 : 42) at Sta. 30 on 8 June, 1982. During the day, many of the larvae were found at 25～30 m depth, while at night, they were chiefly found at 10～15 m depth (Fig. 14). This confirms the works of Kamba (1977) that the larvae at juvenile and young stages migrate to the surface after sunset.

Difference between the mean total length of the larvae collected on the sea bottom and that in the midwater (20～102 m depth) is clearly shown in Table 3 ($p < 0.001$). The mean total lengths and 95% confidence intervals of the larvae collected

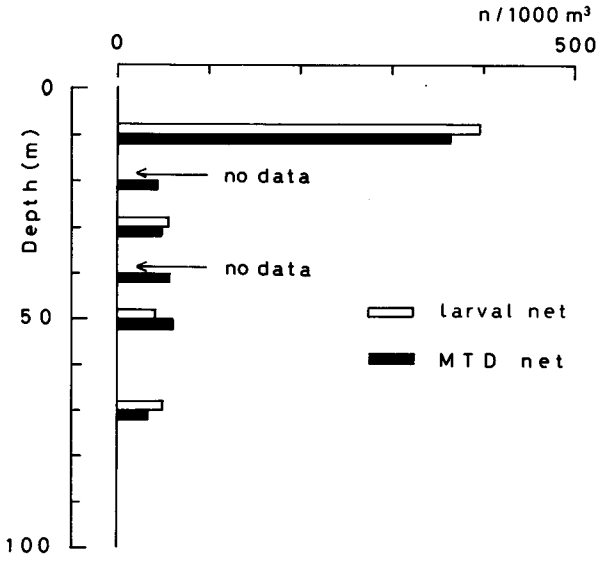

Fig. 12. Vertical distribution of walleye pollock larvae at Sta. 29 on 27 April, 1982. (Nakatani and Maeda, 1987)

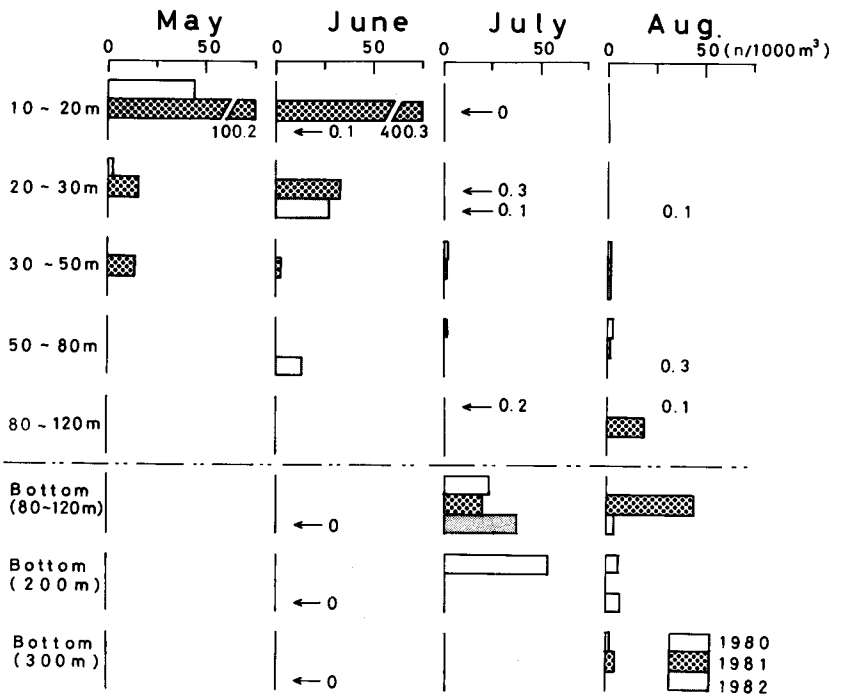

Fig. 13. Monthly change in vertical distribution of walleye pollock larvae from May to August. The collection was made at the stations shown in Fig. 10 by beam trawling in May and otter trawling from June to August. (Nakatani and Maeda, 1987)

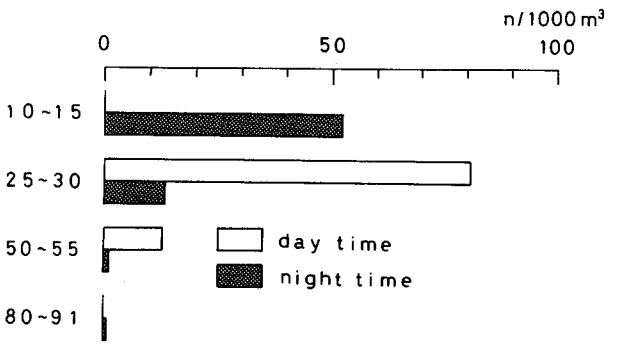

Fig. 14. Vertical distribution of walleye pollock larvae collected by otter trawling at Sta. 30 during daytime (14:03~16:30) and night (19:20~21:42) on 8 June, 1982. (Nakatani and Maeda, 1987)

Table 3. Mean total length (mm) of walleye pollock larvae ($\bar{x}$) and 95% confidence interval (CI) in the midwater and on the bottom in late July from 1980 to 1982 in Funka Bay and vicinity. Samples were collected by otter trawl net. n=sample size (Nakatani and Maeda, 1987)

Date	Midwater			bottom		
	$\bar{x}$	CI	n	$\bar{x}$	CI	n
21~22 July 1980	77.51	±0.69	297	84.74	±0.70	597
22~24 July 1981	63.39	±2.25	87	80.68	±0.74	833
20~21 July 1982	54.99	±2.21	81	88.21	±1.37	182

on the sea bottom in 1980, 1981, and 1982 were 84.74±0.70 mm, 80.68±0.74 mm, and 88.21±1.37 mm, respectively ($p<0.001$).

In August, larvae were concentrated on the sea bottom with a few remaining in mid water as well as in late July (Fig. 13).

2-3. CHANGE IN FOOD OF WALLEYE POLLOCK LARVAE WITH GROWTH

Fig. 15 shows the stomach content composition (percentage by wet weight) of the larvae collected at 4 different stations on March 5~7, 1980. Most of the larvae smaller than 5 mm in total length had not absorbed the yolk completely and few had initiated feeding. The food organisms of the larvae (5 mm and more in total length) at the stage of initial feeding were crustacean eggs (98~519 μm in diamter) and copepod nauplii (148~568 μm in cepharothorax length). With the exception of the larvae in the 7~8 mm size class collected at Sta. 29, copepodids (mainly *Pseudocalanus minutus* and *Oithona similis*) made up over half of the food organisms eaten by the larvae larger than 7 mm in total length.

The copepodid of *P. minutus* is obviously principal food organism of the larvae less than 30 mm in total length (Fig. 16). On the other hand, some of the larvae more than 30 mm in total length collected in midwater fed on *Calanus plumchrus*

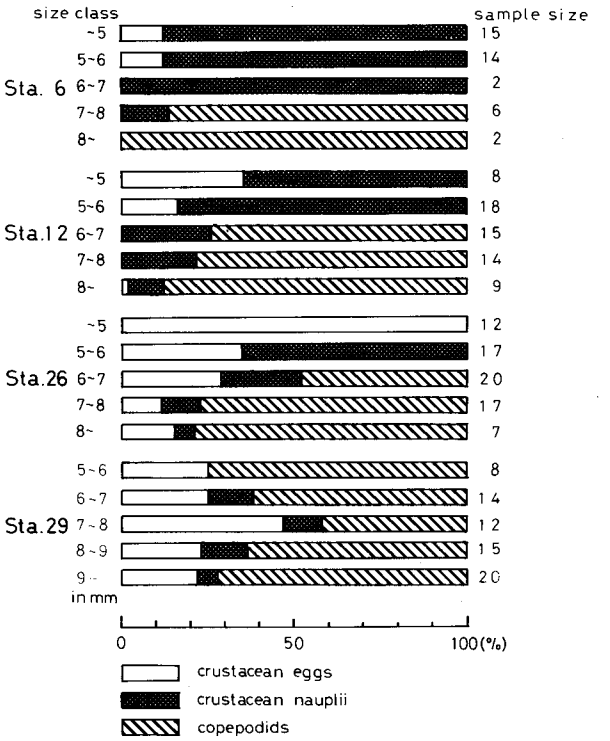

Fig. 15. Wet weight composition of stomach contents of walleye pollock larvae. Samples were collected by horizontal tows with MTD nets at 3 layers (10, 20, and 30 m depth) on March 5~7, 1980. (Nakatani and Maeda, 1983)

and the proportion of this species in the stomach contents increased with growth. Large sized copepodids, *Calanus cristatus*, *Eucalanus bungii bungii*, a euphausiid, *Euphausia pacifica*, and an amphipod, *Parathemisto japonica* were more prevalent in stomachs of the larvae collected on the sea bottom (70 mm and more in total length).

From the results it appears that the main food organisms of the larvae changed from small copepodids and copepod nauplii to large sized copepodids, euphausiids, and amphipods.

2-4. Species composition and vertical distribution of copepod nauplii

As mentioned before, copepod nauplii were the most important food organisms of walleye pollock larvae at the stage of initial feeding. Table 4 shows the species composition and stage structure of copepod nauplii collected by vertical hauls with a NORPAC net (mesh size=0.10 mm) from February to March of 1982. In February, the density (n/m^2) of copepod nauplii near the entrance of the bay was 32~449 and the dominant species was *P. minutus* in the nauplius stages IV~V, followed by *Oithona* spp. and *M. lucence*. In contrast, the number of *Eucalanus bungii bungii* was small, and *Calanus* sp. was not found at all.

In March, the number of copepod nauplii increased dramatically. *P. minutus*

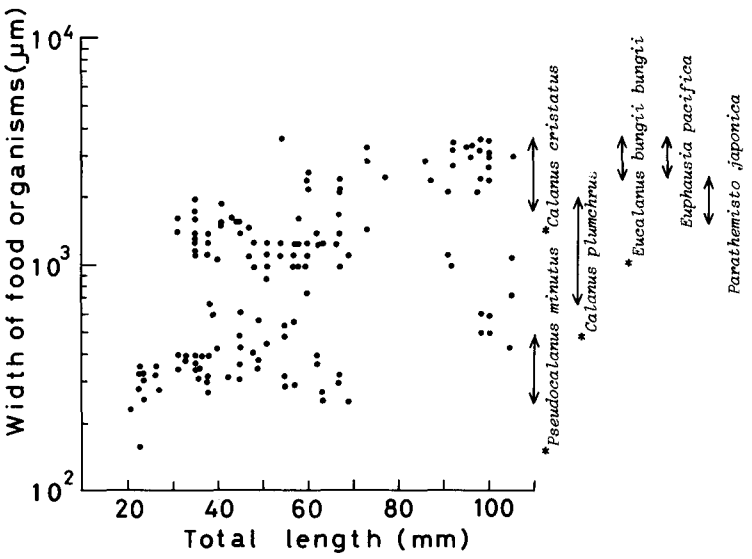

Fig. 16. Relationship between total length of walleye pollock larvae and width of food organisms ingested. The samples were collected from May 1980 to August 1982.
*: copepodids (Nakatani and Maeda, 1987)

Table 4. Density (n/m²) of copepod nauplii on February 1 and 2, and March 15 and 16, 1982 in Funka Bay and vicinity. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net (mesh size=0.10 mm). (Nakatani, 1984)

Species	Stage	February			March				
		Sta. 1	Sta. 2	Sta. 6	Sta. 3	Sta. 12	Sta. 16	Sta. 17	Sta. 30
Pseudocalanus minutus or *Metridia lucens*	Stage I	0	0	0	0	155.5	195.1	0	191.4
	Stage II	0	0	1.0	120.2	517.3	1072.8	0.9	574.3
	Stage III	53.2	25.6	9.6	1201.9	2121.1	1950.5	0.9	1866.6
Pseudocalanus minutus	Stage IV	124.0	15.3	3.1	465.6	465.6	439.9	0.9	574.4
	Stage V	48.7	14.1	1.6	200.3	620.8	341.3	3.5	526.5
	Stage VI	4.4	0	0	0	0	0	1.8	0
Metridia lucens	Stage IV	35.4	11.6	4.9	560.9	258.7	97.5	0	239.3
	Stage V	44.3	5.1	1.6	200.3	51.7	0	0	47.9
Calanus spp.		0	0	0	0	103.5	48.8	28.2	143.6
Eucalanus bungii bungii		0	1.3	0	0	0	0	0	0
Oithona spp.		199.6	37.1	10.2	1282.1	672.5	341.3	11.4	430.7
Other nauplii		13.3	2.6	0	0	200.9	390.1	0.9	47.9
Total		449.2	116.3	31.9	4006.4	5173.3	4876.2	48.4	4642.4

Table 5. Density (n/m³) of copepod nauplii collected with a Van at Sta. 3 on 19 March 1983.

Species	Stage	10 m	20 m
Pseudocalanus minutus or *Metridia lucence*	Stage I	3457.7	3713.4
	Stage II	4226.0	3427.7
	Stage III	11525.5	6569.8
Pseudocalanus minutus	Stage IV	4994.4	3142.1
	Stage V	2689.3	1142.6
	Stage VI	0	0
Metridia lucens	Stage IV	1152.6	285.6
	Stage V	384.2	285.6
Calanus spp.		384.2	856.9
Eucalanus bungii bungii		0	0
Oithona spp.		8836.2	9426.2
Total		37650	28850

Table 6. Species composition of copepodids at Stas. 1, 2, and 6 on February 1 and 2, 1982. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net.

Species	n/m²		
	Sta. 1	Sta. 2	Sta. 6
Calanus plumchrus	125.8	578.5	251.5
C. pacificus	226.4	119.5	37.5
C. tenuicornis	163.5	150.9	301.8
**Calanus* spp.	1056.3	1200.9	1773.1
Paracalanus parvus	1779.4	314.4	150.9
Sseudocalanus minutus	6803.2	1446.1	4891.8
Scolecithricella spp.	213.8	62.9	628.8
Centropages abdominalis	276.7	37.7	100.6
Metridia spp.	3776.0	1339.3	2565.3
Candacia spp.	12.6	0	0
Acartia clausi	176.1	144.6	415.0
Oithona spp.	2024.6	4269.3	3973.8
Oncaea spp.	25.2	31.4	12.6
Corycaes spp.	75.5	50.3	62.9
Total	16435.8	9745.8	15165.7

* copeopodite stage I～IV

Dorn water sampler at 10 m intervals from 10 m to 80 m depth

Depth					
30 m	40 m	50 m	60 m	70 m	80 m
3084.0	2842.9	3664.4	1645.2	1097.4	822.8
2864.8	3127.1	3664.3	1451.6	404.3	1116.7
5456.4	2558.6	2850.0	1064.5	288.8	176.3
2609.6	568.6	407.1	96.8	57.8	0
948.9	568.6	0	193.6	0	58.8
0	0	0	96.8	0	0
237.2	568.6	407.1	871.0	173.3	58.8
237.2	284.3	814.3	193.6	57.8	58.8
711.7	199.0	407.1	193.6	173.3	58.8
0	284.3	0	0	0	0
7828.7	17057.1	7735.7	3193.6	1097.4	999.1
22300	29850	19950	9000	3350	3350

Table 7. Species composition of copepodids on March 15 and 16, 1982 in Funka Bay and vicinity. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net.

Species	n/m^2				
	Sta. 3	Sta. 12	Sta. 16	Sta. 17	Sta. 30
Calanus cristatus	0	0	150.9	50.3	194.9
C. plumchrus	2125.2	855.1	830.0	1509.0	1649.3
C. pacificus	0	182.3	603.6	1861.1	2515.0
C. tenuicornis	50.3	18.9	125.8	100.6	150.9
Calanus spp.	1471.3	3062.0	1207.2	3018.0	3420.5
Eucalanus bungii bungii	339.5	50.3	0	0	0
Paracalanus parvus	25.2	37.7	25.2	100.6	0
Pseudocalanus minutus	10990.7	47961.8	29400.8	51155.9	58286.1
Scolecithricella spp.	100.6	31.5	75.5	100.6	301.8
Centropages abdominalis	0	3131.2	1483.9	2640.8	1307.8
Metridia spp.	691.6	1187.8	4250.4	8802.6	8844.3
Acartia clausi	100.5	1785.7	1156.9	2716.2	1307.8
Tortanus discaudatus	0	25.2	50.3	100.6	50.3
Oithona spp.	6124.1	7073.6	2791.7	4929.5	10016.2
Oncaea spp.	0	0	0	25.2	0
Corycaes spp.	0	25.2	50.3	25.2	100.6
Total	22019.0	65428.3	42202.0	77136.0	87787.5

Table 8. Species composition of copepodids collected at 3 stations on March 15 and 16, 1982.

Species	Sta. 3 (n/100 m³)							
	10 m	20 m	30 m	40 m	60 m	80 m	10 m	20 m
Calanus cristatus	0	0	0	0	0	0	0	0
C. plumchrus	28.1	17.5	2294.0	5079.0	673.5	305.2	112.2	112.2
C. pacificus	0	14.0	14.0	0	21.0	0	84.2	196.4
C. tenuicornis	0	0	42.1	0	105.2	42.1	196.4	203.4
Calanus larvae	1375.0	371.8	2714.9	603.3	175.4	701.5	427.9	659.4
Eucalanus bungii bungii	0	0	399.9	645.4	42.1	7.0	0	0
Paracalanus parvus	28.1	10.5	21.0	0	21.0	7.0	0	7.0
Pseudocalanus minutus	16219.3	4630.1	5563.1	1234.7	1115.4	2437.8	46132.3	14388.3
Eucaeta spp.	0	0	0	0	0	0	0	0
Scolecithricella spp.	0	3.5	21.0	84.2	161.4	119.3	0	0
Centropages abdominalis	0	7.0	7.0	0	7.0	3.5	2918.3	2651.8
Meridia spp.	0	17.5	7.0	14.0	1606.5	1708.2	3.5	0
Acartia clausi	280.6	24.6	35.1	0	0	0	333.2	1241.7
Tortanus discaudatus	0	3.5	0	0	0	0	56.1	105.2
Oithona spp.	1599.5	217.5	1276.8	491.9	1985.3	1504.8	392.9	912.0
Oncaea spp.	0	0	0	0	7.0	7.0	0	0
Corycaeus spp.	0	0	14.0	14.0	0	3.5	28.1	21.0
Total	19530.5	5327.6	12410.0	8249.9	6348.8	6320.7	53315.9	20267.1

and *M. lucence* were dominant in the entrance and the inner area of the bay and *Oithona* spp. were mostly collected in the coastal area outside the bay.

Copepod nauplii on 19 March 1983 were mainly distributed in shallower layers from 10 m to 50 m depth (Table 5). Among them, *P. minutus* in the nauplius stages IV～V was abundant from 10 m to 30 m depth. *Oithona* spp. were widely distributed from 10 to 50 m depth and the maximum density was found on 40 m depth. While, the number of *M. lucens* was small.

2-5. Seasonal change in abundance and species composition of copepodids

Tables 6 and 7 show the species composition of copepodids during February 1～2 and March 15～16, 1982, respectively. In February, copepodids of *P. minutus*, *Metridia* spp., and *Oithona* spp. dominated and comprised 72.4～76.6% of copepodids. In March, large numbers of copepodids were collected in the entrance (Sta. 17) and the inner area (Sta. 30) of the bay.

Table 8 presents the species composition of copepodids by depths on March 15～16, 1982. *P. minutus* was dominated at all depths and at 10 m depth comprised about 96% of total copepodids at Sta. 30 (Fig. 17). In contrast, *Metridia* spp. and *Oithona* spp. were mainly distributed in deeper layers. Especially *Metridia* spp. were concentrated at 60～80 m depth. Such a distributional pattern of *Metridia* spp. was also observed on 19 March, 1983 (Table 9).

Samples were collected by horizontal tows with MTD nets at 6 layers. (Nakatani, 1984)

Sta. 17 (n/100 m³)				Sta. 30 (n/100 m³)					
30 m	40 m	60 m	80 m	10 m	20 m	30 m	40 m	60 m	80 m
0	0	0	0	0	0	28.1	14.0	280.6	196.4
238.5	1711.7	505.1	842.0	0	392.9	4602.0	2918.3	449.0	28.1
392.9	542.7	687.5	2216.8	224.5	224.5	1431.1	1066.3	1038.3	1038.3
238.5	98.2	126.3	449.0	0	56.1	84.2	42.1	392.9	589.3
569.4	2808.9	2038.3	701.5	392.9	645.4	3535.7	1711.7	898.0	617.3
0	70.2	0	0	0	0	0	0	0	0
28.1	0	42.1	196.4	0	0	140.3	0	0	84.2
16598.1	14956.5	24076.3	23487.1	114601.1	37489.5	27808.4	11827.7	21101.9	18828.9
0	0	0	0	0	0	0	0	0	28.1
0	56.1	140.3	364.8	0	0	28.1	0	140.3	533.2
701.5	168.4	519.1	449.0	2132.6	3199.0	1178.6	112.2	140.3	140.3
14.0	0	3142.8	18464.1	280.6	56.1	140.3	168.4	8755.0	21438.6
266.6	98.2	308.7	420.9	1403.0	1571.4	1375.0	322.7	0	0
28.1	14.0	42.1	140.3	56.1	168.4	56.1	0	28.1	28.1
1613.5	2357.1	1304.8	982.1	392.9	336.7	2411.3	1192.6	3928.5	13637.6
0	0	28.1	28.1	0	0	0	0	0	28.1
14.0	14.0	42.1	56.1	0	0	28.1	0	56.1	28.1
20793.2	21901.6	32003.6	48040.4	119483.7	44139.9	42877.2	19376.1	37180.8	57861.8

P. minutus, which predominated in the surface layer of the bay in March, sharply decreased in number during May and later months (Tables 8～12, Fig. 18). *Calanus plumchrus*, which was the primary food item of walleye pollock larvae larger than 30 mm in total length, was concentrated at 30～40 m depth from March to April (Tables 8～12, Fig. 18). In June, they were concentrated in deep layers (60～80 m depth). *Eucalanus bungii bungii*, which was fed upon by walleye pollock larvae larger than 70 mm in total length, was few in number from March to June and then increased in deep layers in July (Tables 8～12, Fig. 18).

3. THERMAL EFFECT ON EMBRYONIC DEVELOPMENT

In Funka Bay and vicinity, mature walleye pollock spawn near the sea bottom at a depth of 100～120 m (Maeda *et al.*, 1976) and the pelagic eggs rise to the sea surface. At this period, the Oyashio Water is characterized by temperatures below 2°C (Ohtani, 1971; Ohtani *et al.*, 1971) and enters the inner area of Funka Bay. Hamai *et al.* (1971) and Maeda *et al.* (1979) reported that the temperature at which maximum hatching of walleye pollock eggs occured was 2.0°～4.0°C. However, it is unknown whether the eggs would be able to hatch at temperatures below 2°C.

3-1. RATES OF EMBRYONIC DEVELOPMENT AT 7 TEMPERATURE CONDITIONS

Artificially fertilized eggs were reared at 7 test temperatures (−1°, 0°, 2°, 4°, 7°, 10°, and 13°C). Incubation time in days required for 50% hatching ranged from 8 days at 13°C to 57 days at −1° (Table 13). At 0°～10°C, high hatching rates of 86

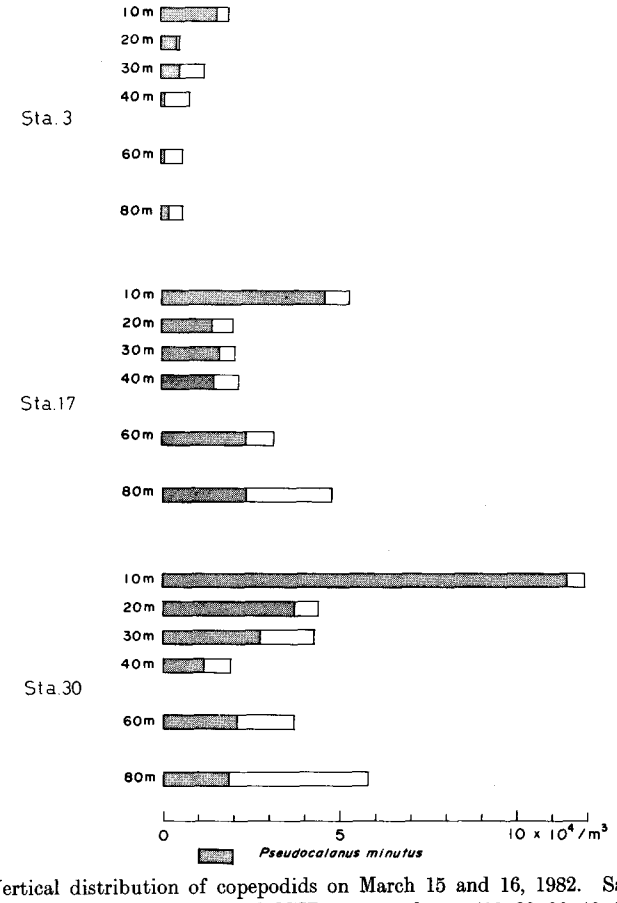

Fig. 17. Vertical distribution of copepodids on March 15 and 16, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers (10, 20, 30, 40, 60, and 80 m depth).

~100% were obtained. Conversely, the hatching rate was low at −1°C (0~36.7%) and at 13°C (66.7%).

The relationship between water temperature and time required for hatching was calculated by using the formula of Higurashi and Tauchi (1925). The relationship (Fig. 19) was found to be:

$$T = 31.70 \cdot \exp(-0.12 \cdot \theta)$$

T : time in days required for 50% hatching

θ : water temperature, °C

$r^2 = 0.98$

The data obtained at −1° and 13°C were omitted from the calculation because the normal hatching rates were low.

Time in days required for 50% hatching calculated with this formula were 23.5 days at 3°C, 18.1 days at 5°C, and 15.9 days at 6°C. These results were 2~3 days

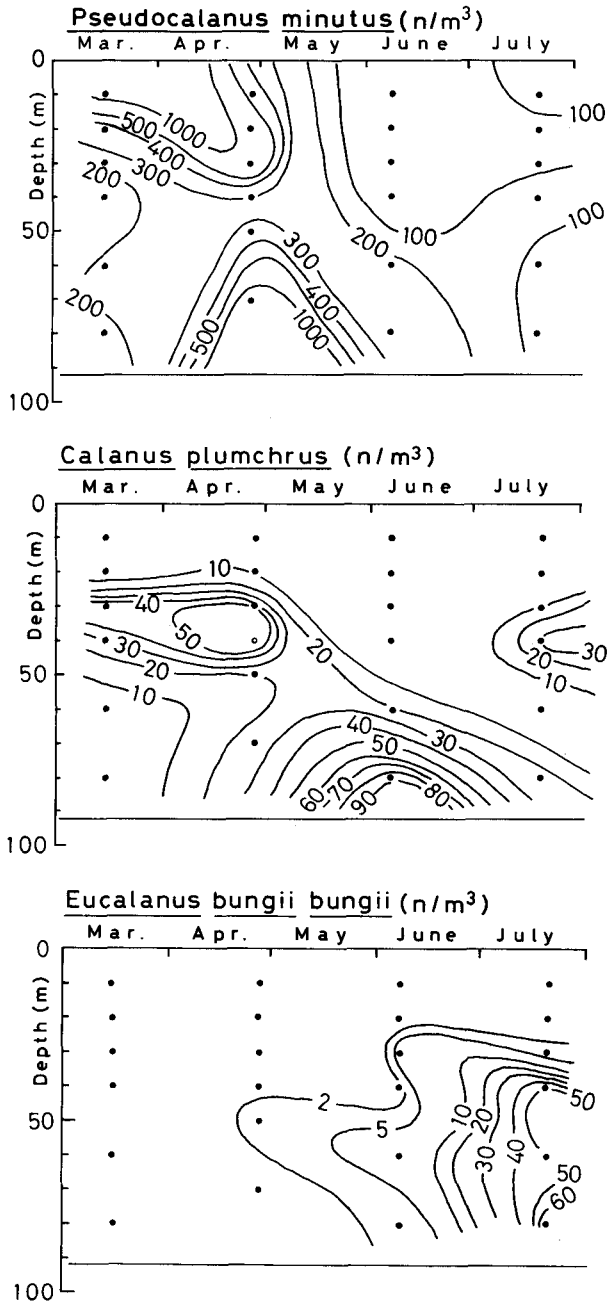

Fig. 18. Seasonal change in vertical distribution of *Pseudocalanus munutus*, *Calanus plumchrus*, and *Eucalanus bungii bungii* at Sta. 30 (Sta. 29 on 27 April) from March to July, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers (10, 20, 30, 40, 60, and 80 m depth). (Nakatani and Maeda, 1987)

Table 9. Species composition of copepodids at Sta. 3 on 19 March, 1983. Samples were collected by horizontal tows with MTD nets at 6 layers.

Species	n/100 m³					
	10 m	20 m	30 m	40 m	60 m	80 m
Calanus cristatus	0	0	0	0	0	56.1
C. plumchrus	392.9	785.7	280.5	505.1	8362.2	785.7
C. pacificus	0	112.2	0	0	561.2	280.6
C. tensuicornis	0	224.5	112.2	56.1	0	729.6
Calanus spp.	2020.4	2020.4	1795.9	2301.0	2525.5	617.3
Eucalanus bungii bungii	56.1	336.7	224.5	673.5	4882.2	1122.4
Paracalanus parvus	0	0	0	56.1	0	280.6
Pseudocalanus minutus	78683.0	190927.0	111121.5	108203.2	17397.8	79581.0
Scolecithricella spp.	0	0	0	56.1	0	56.1
Centropages abdominalis	56.1	112.2	56.1	0	0	0
Metridia spp.	0	0	0	56.1*	1739.9	13581.5
Acartia clausi	112.2	112.2	280.6	0	0	168.4
A. longicornis	1066.3	1234.7	1346.9	449.0	112.2	505.1
Tortanus discaudatus	0	112.2	168.4	112.2	0	0
Oithona spp.	673.5	2244.9	280.6	617.3	505.1	2750.0
Oncaea spp.	0	0	0	0	0	56.1
others	336.7	224.5	112.2	280.5	56.1	56.1
Total	83397.3	198447.4	115779.7	113366.4	36142.5	100626.7

* larvae

Table 13. Median days for 50% hatching after fertilization of walleye pollock eggs from Ainuma, the Sea of Japan. (Nakatani and Maeda, 1984)

Temperature	Days	Percentage of hatching rate	Normal hatching rate**
−1°C*	57.0	0-11.7	0-11.7
−1°C	46.0	6.7-36.7	0-31.0
0°C*	42.0	98.4	
0°C	31.8	96.7	
2°C	26.0	85.7	
4°C	19.1	96.7	
7°C	12.4	90.0	
10°C	10.0	100	100
13°C	8.0	66.7	50.0

* Funka Bay sample

** All hatched larvae seemed normal where no figures were given.

Table 10. Species composition of copeopdids at Sta. 29 on 27 April, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers.

Species	n/100 m³					
	10 m	20 m	30 m	40 m	50 m	70 m
Calanus cristatus	0	0	0	112.2	56.1	0
C. plumchrus	463.0	398.0	5163.2	5724.4	1852.0	2750.0
C. pacificus	1375.0	1178.6	785.7	4209.2	3311.2	3086.7
C. tenuicornis	0	224.5	0	0	0	0
Calanus spp.	1487.2	1739.8	2244.3	2581.6	4994.9	2637.7
Eucalanus bungii bungii	0	0	0	112.2	224.5	0
Paracalanus parvus	42.1	0	0	0	0	0
Pseudocalanus minutus	43213.9	66616.8	80703.4	24693.7	35244.6	110335.3
Scolecithricella spp.	0	0	0	0	0	280.6
Centropages abdominalis	1445.1	1571.4	392.9	1908.2	168.4	1122.4
Metridia spp.	70.2	449.0	2806.1	5219.3	3928.5	2076.5
Acartia clausi	519.1	729.6	392.9	1739.8	1010.2	2525.5
A. tumida	617.3	336.7	224.5	1459.2	4040.3	1234.7
A. longiocornis	126.3	336.7	224.5	56.1	56.1	112.2
Tortanus discaudatus	406.9	336.7	158.4	392.9	112.2	1010.2
Oithona spp.	42.1	0	505.1	280.6	224.5	1964.3
Total	49808.2	74955.3	93611.6	48489.4	55224.0	129136.6

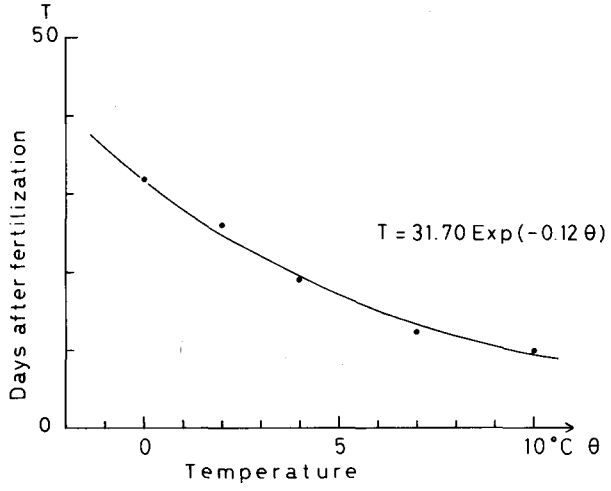

Fig. 19. Relationship between temperature and time in days required for 50% hatching. (Nakatani and Maeda, 1984)

Table 11. Species composition of copepodids at Sta. 30 on 7 June, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers.

Species	n/100 m³					
	10 m	20 m	30 m	40 m	60 m	80 m
Calanus cristatus	0	0	0	0	0	336.7
C. plumchrus	0	0.9	49.1	115.6	2006.4	9091.0
C. pacificus	0	1.8	0	0	14.0	3030.6
Calanus spp.	0	0.9	3.5	0	0	392.9
Eucalanus bungii bungii	5.3	101.7	648.9	136.8	799.7	392.9
Pseudocalanus minutus	81.6	46.5	1476.7	214.0	23908.0	24918.2
Scolecithricella spp.	1.8	0	56.1	0	112.2	0
Centropages abdominalis	31.6	16.7	73.7	7.0	14.0	0
Metridia spp.	3.5	3.5	94.7	3.5	1375.0	25647.3
Candacia spp.	0	0	0	0	0	0
Acartia clausi	0.9	4.4	7.0	0	28.1	0
A. tumida	0	0	0	0	0	56.1
A. longicornis	54.4	8.3	256.1	7.0	84.2	56.1
Tortanus discaudatus	0.9	0.9	7.0	0	28.1	56.1
Oithona spp.	0	13.2	445.5	17.5	280.6	0
Oncaea spp.	0	0	0	0	0	0
Corycaes spp.	0	0	0	0	14.0	0
Total	180.0	199.3	3118.3	501.6	28664.3	63979.2

longer than those of Hamai *et al.* (1971) and Fukuchi (1976). The Arrhenius' temperature characteristics were 17752 at the closure of the blatopore and 20865 at 50% hatching (Fig. 20), which were a little higher than those found by Hamai *et al.* (1971). As stated before, most of stage 1 eggs collected in the eastern area of the entrance of Funka Bay were in the morula stage. From these results of the rearing experiment and the temperature of the spawning season in this study area (0°~4°C), it is suggested that the stage 1 eggs were collected within 20.7~30.0 hours after fertilization (Table 14).

3-2. Tolerance for low temperatures

Walleye pollock eggs at 4 developmental stages (2-cell stage, morula stage, first gastrula stage, and the stage of blastopore closing) maintained at 4°C were reared at −1°C and 0°C until hatching and the hatching rate and development were observed. Acclimation was following 3 ways.

rapid : from 4°C to −1°C and 0°C directly.
medium : Thermal change from 4°C to −1°C and 0°C was −0.7°C~−1.3°C/10 min.
slow : Thermal change from 4°C to −1°C and 0°C was −0.1°C/10 min.

Table 12. Species composition of copeopdids at Sta. 30 on 20 July, 1982. Samples were collected by horizontal tows with MTD nets at 6 layers.

Species	n/100 m³					
	10 m	20 m	30 m	40 m	60 m	80 m
Calanus cristatus	0	0	28.1	196.4	0	280.6
C. plumchrus	0	7.0	1080.1	2946.4	589.3	2581.6
C. pacificus	14.0	161.4	154.3	1487.2	2609.7	5724.4
C. tenuicornis	854.1	435.0	168.4	280.6	112.2	56.1
Calanus spp.	70.2	14.0	28.1	84.2	28.1	56.1
Eucalanus bungii bungii	42.1	21.1	392.9	5163.2	4770.2	6959.1
Paracalanus parvus	126.3	14.0	0	252.6	0	0
Pseudocalanus minutus	15335.3	6187.5	771.7	14002.4	6313.7	3929.5
Scolecithricella spp.	140	7.0	0	34.2	0	0
Centropages abdominalis	42.1	49.1	14.0	28.1	0	0
Metridia spp.	238.5	35.1	28.1	477.0	3676.0	2525.5
Candacia spp.	0	0	0	0	28.1	0
Acartia clausi	98.2	378.8	14.0	252.6	84.2	0
A. longiocornis	28.1	84.2	42.1	757.7	0	0
Tortanus discaudatus	0	7.0	0	56.1	0	0
Oithona spp.	84.2	175.4	14.0	392.9	308.7	280.6
Oncaea spp.	14.0	0	0	0	0	0
Corycaea spp.	84.2	28.1	0	0	0	0
Total	17145.3	7604.7	2736.1	26461.5	18520.4	22392.5

As shown in Table 15, the hatching rate of the eggs reared at −1°C after the 2-cell stage was not high at any cases (6.7～36.7%). In contrast, the hatching rate of the eggs reared at −1°C from the morula stage was high (45.2～68.6%) and then it increased with development.

After acclimation at 0°C, a hatching rate of eggs reared from the 2-cell stages was much higher (73.4～96.7%) than that at −1°C. Among 3 types of acclimation, the maximum hatching rate was obtained at slow acclimation (96.7%). At the morula and more developed stages, high hatching rates were obtained (82.8～93.3%).

4. SPECIFIC GRAVITY AND UPWARD FLOATING VELOCITY OF WALLEYE POLLOCK EGGS

Specific gravity (g/cm³) of walleye pollock eggs after the 2-cell stage before hatching was measured (Fig. 21). The mean specific gravity of artificially fertilized eggs collected in Funka Bay and the coastal area off Ainuma was 1.0226 g/cm³ and 1.0201 g/cm³, respectively, which is significantly different ($p<0.01$). Field studies and results from laboratory experiments show that the pelagic eggs of fish sink down during the progress of development (Sundness *et al.*, 1964; Tanaka, 1976). However, an increase of specific gravity of walleye pollock eggs with advancement of development was not observed.

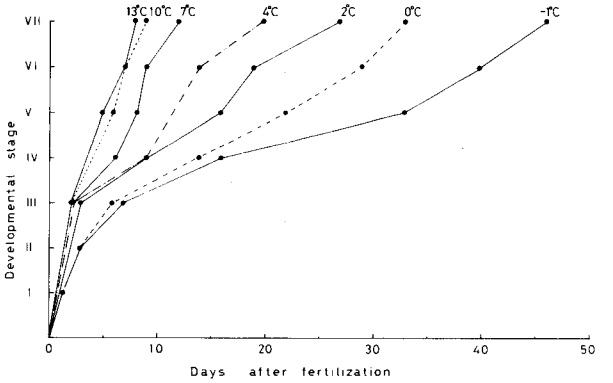

Fig. 20. Relationship between embryonic developmental stage and days after fertilization at 7 temperature conditions. (Nakatani and Maeda, 1984)
Stage I: morula stage
Stage II: blastula stage
Stage III: first gastrula stage
Stage IV: closure of blastopore
Stage V: embryo as three-fourths of the yolk circumference
Stage VI: embryo as full circle of the yolk circumference
Stage VII: 50% hatching

Table 14. Hours after fertilization required for walleye pollock eggs to develop to the morula stage.

Water temperature (°C)	Hours
−1	32.0
0	30.0
4	20.7

Table 15. Hatching rates in percentage of walleye pollock eggs subjected to a thermal change at 4 developmental stages. Figures in parentheses show the percentages of normal hatching. (Nakatani and Maeda, 1984)

Initial stage of experiment	Thermal change from 4°C to −1°C			Thermal change from 4°C to 0°C		
	rapid*	medium**	slow***	rapid*	medium**	slow***
2-cell stage	6.7(0)	36.7(31.0)	14.8(0)	73.4	80.0	96.7
morula stage	86.7(45.2)	73.9(56.5)	86.7(68.6)	86.7	82.8	90.0
first gastrula stage	96.3(96.3)	96.7(52.7)	100 (96.6)	—	—	—
closure of blastopore	—	100 (77.8)	100 (80.0)	93.3	93.3	93.3

* to −1°C and 0°C directly
** Thermal change was −0.7 ~ −1.3°C/10 min.
*** Thermal change was −0.1°C/10 min.

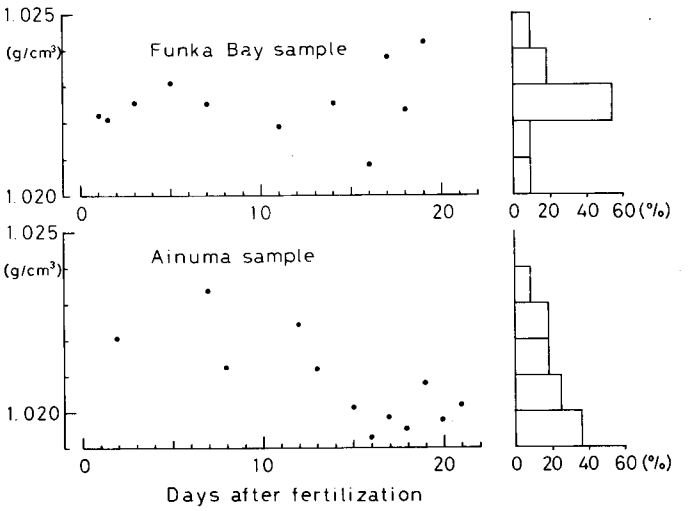

Fig. 21. Frequency distribution of specific gravity of walleye pollock eggs. (Nalatani and Maeda, 1984)

From the results of the experiment on thermal tolerance, it was observed that the hatching rate of eggs after the morula stage was high even at a low temperature of −1°C (Table 15). It is probable that the mortality of eggs, which were spawned near the sea bottom, depends on the stage of development. If eggs do not develop to morula stage by the time when they should have risen to the surface layer, they will miss successful survival at a low temperature occupying in the surface layer in the spawning season. Upward floating velocity of eggs was measured after the 2-cell stage before hatching (Fig. 22) to calculate the time required for eggs to rise from the sea bottom to the surface. Mean floating velocity of eggs collected in Funka Bay and Ainuma was 4.90 m/h and 8.56 m/h, respectively. Time in hours required to rise from the sea bottom (100～120 m depth) to the surface was calculated to be 20.4 ～24.5 hours for Funka Bay data and 11.7～14.0 hours for Ainuma data, respectively.

IV. Discussion

1. Relationship between hydrographic conditions and larval food availability

Hydrographic conditions in Funka Bay and vicinity are largely affected both Oyashio Water and Tsugaru Warm Water, which are seasonally replaced (Ohtani and Akiba, 1970). The Oyashio Water, which is characterized by salinity below 33.0‰ (Ohtani, 1971), flows into the bay from February to June and replaces the more saline and denser Tsugaru Warm Water (Ohtani and Kido, 1980). In this period, many walleye pollock eggs and larvae occur in the inner area of the bay (Maeda *et al.*, 1976, 1979; Nakatani and Maeda, 1981, 1983). In March 1977, the Oyashio Water entered from the northeastern area to the inner area of the bay (Fig.

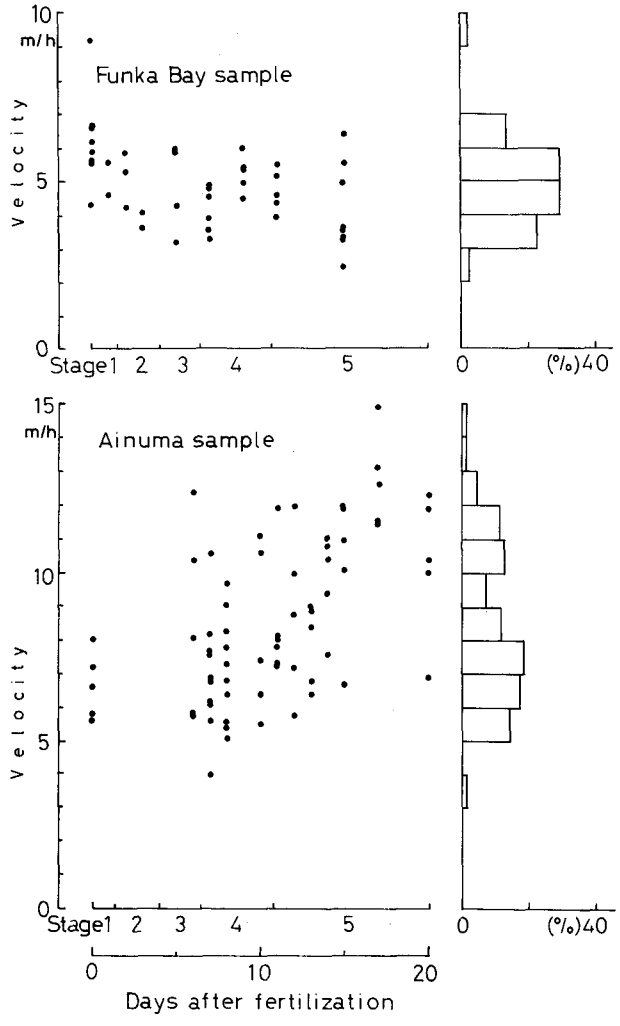

Fig. 22. Upward floating velocity of walleye pollock eggs. The 5 developmental stages were defined as in Fig. 2. (Nakatani and Maeda, 1984)

23). The temperature and salinity in the northeastern area out of the bay were below 0.5°C and below 32.8‰, respectively, while those in the inner area of the bay were 2.0°~2.5°C, 33.0‰, respectively. From the distributional pattern of walleye pollock eggs of 5 developmental stages in this period (Figs. 2 and 3), it is apparent that the eggs are transported into Funka Bay by the Oyashio Water.

After being transported into the bay, larvae hatch out and initiate feeding. According to Takeuchi (1961) and Kamba (1977), small sized copepods and copepod nauplii are indispensable food organisms for walleye pollock larvae. In this study, it is confirmed that copepod nauplii are the most important food organisms of larvae at the stage of initial feeding and small sized copepodid, *Pseudocalanus minutus* is

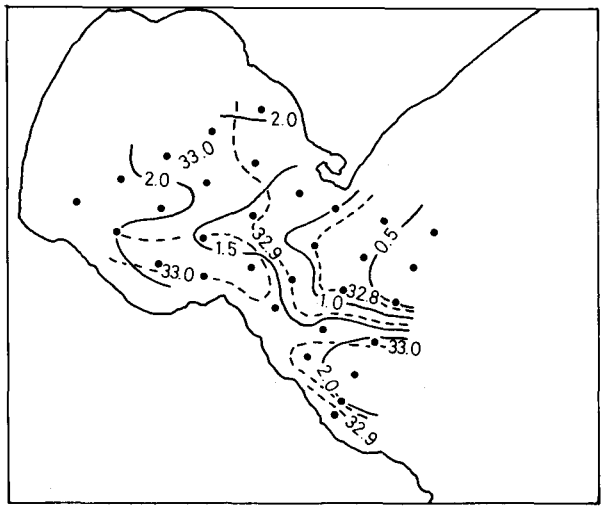

Fig. 23. Surface distribution of temperature (——°C) and salinity (- - -‰) on March 7 ~15, 1977. (Nakatani and Maeda, 1981)

the primary food item of larvae larger than 7 mm in total length (Fig. 15). Species composition and its seasonal change of zooplankton in Funka Bay have been studied by Tamura (1951) and Hirakawa and Kawamura (1977). From these results, it is apparent that copepods dominate in the zooplankton community throughout the year and the species composition of copepods changes with seasonal changes in

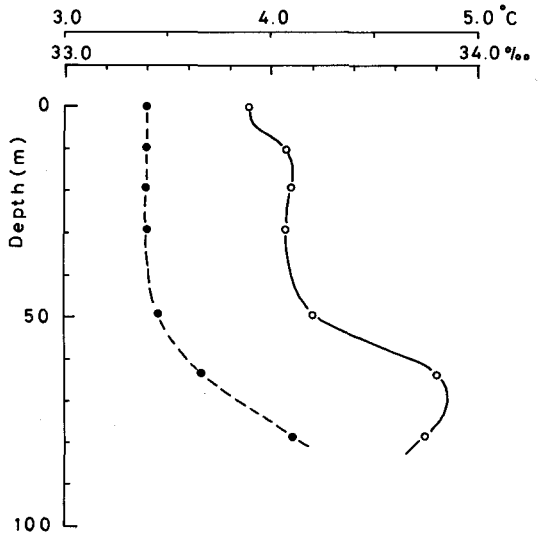

Fig. 24. Vertical profile of temperature (——°C) and salinity (- - -‰) at Sta. 2 on 1 February, 1982.

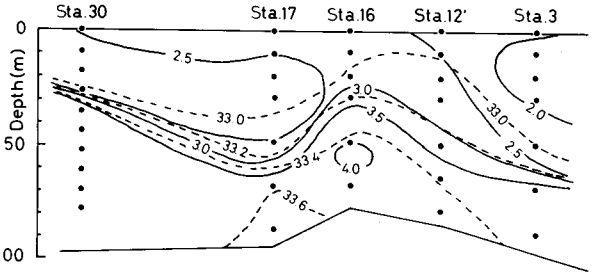

Fig. 25. Vertical profile of temperature (——°C) and salinity (- - -‰) on March 15 and 16, 1982. (Nakatani, 1984)

hydrographic conditions. In March, 1982, copepodids are abundant, especially in the surface layer of the bay. (Table 8 and Fig. 17). In this period, number of copepod nauplii increases in the entrance and the inner area of tha bay and *P. minutus*, *Metridia lucence*, and *Oithona* spp. predominated (Tables 4 and 5).

In the entrance of the bay on 1 February 1982, the water from the surface to 50 m depth is of about 4.0°C and 33.2‰, respectively (Fig. 24). This homogeneous water originated from Tsugaru Warm Water by cooling and convectional mixing in winter (Winter Funka Bay Water) (Ohtani, 1971). Then the surface water in the inner area of the bay is replaced by the Oyashio Water in March (Fig. 25). At this period, *P. minutus*, which is dominant in the Oyashio water in spring (Tamura, 1951; Hirakawa and Kawamura, 1977), appears to be in large number at the entrance (Sta. 17) and in the inner area (Sta 30) of the bay (Table 8 and Fig. 17). It is probable that *P. minutus* spawns in the Oyashio water in the surface layer as evidenced by the presence of nauplii at younger nauplius stage (Table 5).

The Tsugaru Warm Water, which enters the bay in late summer, transforms in winter and its thermosteric anomaly decreases to less than 150 cl/ton (26.55 kg/m^3 in sigma-t). This water (Winter Funka Bay Water) is heavier than the waters outside the bay at the same depth (Kido and Ohtani, 1981). In spring the Oyashio Water, which is characterized by large thermosteric anomaly (more than 160 cl/ton), enters the bay and the water becomes strongly stratified. This typical hydrographic structure was also observed during March 15 and 16 in 1982 (Figs. 25 and 26).

In general, stratification of the water forms a suitable food conditions for fish

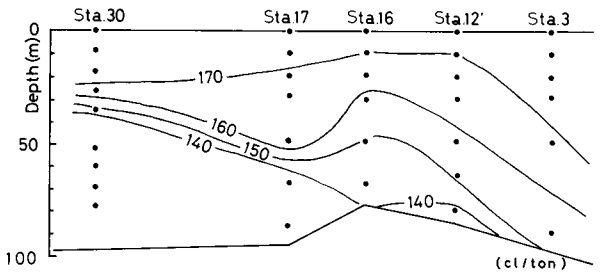

Fig. 26. Vertical profile of thermosteric anomaly on March 15 and 16, 1982. (Nakatani, 1984)

larvae at the stage of initial feeding. The water which is shallower than thermocline is favourable for the growth of phytoplankton (Taniguchi, 1969) and the stratified surface layer maintains phytoplankton in the euphotic zone (Taniguchi, 1981). Lasker (1975, 1978) found that the main food for northern anchovy larvae, *Engraulis mordax*, was the naked dinoflagellate, *Gymnodinium splendens*, in the water of the chlorophyll maximum layers and the upper mixed layer of the ocean must be in a stable state for survival of larval anchovy. In Funka Bay, the vernal phytoplankton bloom occurs from February to March and the chlorophyll maximum layer develops at the surface (Kido and Ohtani, 1981; Dohi, 1982; Nakata, 1982). Zooplankton such as copepods (Kamba, 1977), tintinids (Dohi, 1982) and polychate larvae (Yokouchi, 1984), are abundant in the surface layer of the bay. Copepod nauplii also occur in large numbers in the surface layer (Table 5). In this period, the surface layer of the bay occupied by the Oyashio Water is strongly stratified (Fig. 26). The occurrence of walleye pollock larvae at the stage of initial feeding coincides with the presence of an abundance of food organisms.

2. RELATIONSHIP BETWEEN THE MOVEMENT OF WALLEYE POLLOCK LARVAE AND HYDROGRAPHIC CONDITIONS

From the distributional pattern of walleye pollock eggs (Figs. 2 and 3) and

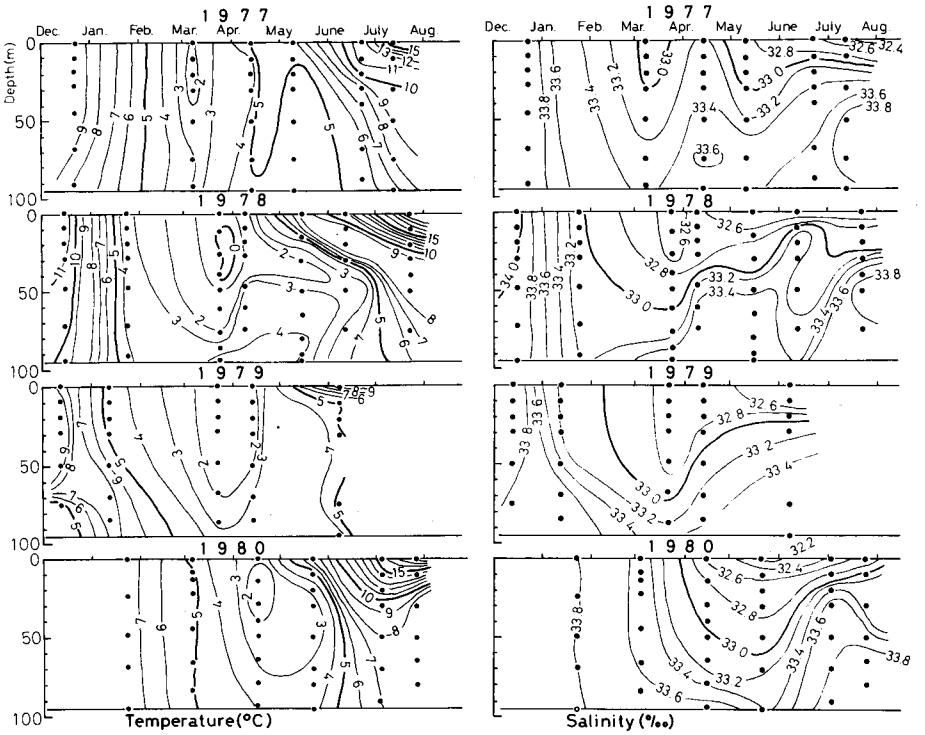

Fig. 27. Vertical profile of temperature (——°C) and salinity (- - -‰) at Sta. 3 (at Sta. 1 on 12 July and 22 July, 1978) from December to July.

larvae (Figs. 5 and 6) and the hydrographic conditions (Fig. 23) in Funka Bay and vicinity, it is postulated that many of the larvae hatch out in the coastal area of the bay. After being transported by the Oyashio Water to the surface layer of Funka Bay, walleye pollock larvae remain in the surface layer until early July (Fig. 13, Table 2). In late July, larvae are concentrated on the bottom (Fig. 13), when larvae have grown to about 83 mm in total length, though considerable fluctuations in its size are noted among several years (Table 3). During this period, the Oyashio Water stagnates untill late summer and the hydrographic structure is strongly stratified from May (Fig. 27). The surface temperature in the bay rises from 4°C in April to 19°C in August, but the bottom temperature changes very little (3°~6°, Fig. 27). In general, the larvae of demersal fish move from the sea surface to the deeper layers with growth. Such an ontogenetic vertical migration is related to the depth of the thermocline and cold middle waters (Kelley and Barker, 1961). Walleye pollock larvae change their vertical habitat with progress of season from the surface layer in spring to the deeper layers in Funka Bay and the eastern area out of the bay after summer (Figs. 10 and 13). It seems likely that the vertical movement of walleye pollock larvae in Funka Bay is affected by the seasonal changes of the hydrographic conditions, especially high temperature in the surface layer in early summer.

Larvae initiate to feed on copepod nauplii, but main food organisms change with growth from copepodids of *P. minutus* to large sized copepodids, i.e., *C. plumchrus*, *E. bungii bungii*, with a euphausiid and an amphipod (Figs. 15 and 16). A change in the food organisms of the small larvae with growth is similar to that reported by Kamba (1977). Copepod nauplii and copepodids of *P. minutus* are abundant in the surface layer in March and March~April, respectively (Table 5, Fig. 18). After the phytoplankton bloom, *P. minutus* decreased dramatically (Fig. 18). *C. plumchrus* is concentrated in deep layers in June and *E. bungii bungii* is also abundant in the deep layers after June. Density (n/100 m^3) of *E. bungii bungii* and *C. plumchrus* is smaller than in *P. minutus* (Fig. 18). But the dry body weight of *C. plumchrus* (850 μg) and *E. bungii bungii* (930 μg) is about 70~186 times as much as *P. minutus* (5~12 μg) (Conover, 1959; Ikeda, 1970). Dry weight of *P. minutus* in March was calculated to be 0.28~0.67 mg/100 m^3 in the surface layer (10~30 m depth), and *C. plumchrus* and *E. bungii bungii* at 80 m depth are 21.94 mg/100 m^3 in June and 66.11 mg/100 m^3 in July, respectively. From late summer to autumn, many walleye pollock larvae were collected on the sea bottom in the eastern area out of the bay (200~300 m depth) (Fig. 13). Some of them were eaten by adult walleye pollock in the Oyashio Water (Maeda *et al.*, 1979, 1981, 1983). Maeda *et al.* (1980) mentioned that a euphausiid, which is main food organisms for large sized larvae (Fig. 16) and adults of walleye pollock (Maeda *et al.*, 1981, 1983), increases in number from July to January in the eastern area out of the bay. These results indicate that the larvae pursue the location of habitat where food is available.

3. Reproductive strategy

3-1 Geographic position of the spawning ground

In Funka Bay and vicinity, the walleye pollock fishery is conducted by bottom

gill nets from October to March. A major part of the catch is comprised of spawning fish. At the fishing season of December 1976, the main fishing ground occurred at the shallow waters from Muroran to Shiraoi (Hakodate Fish. Exp. St., Muroran Branch, 1976) and an echo sounder recorded the fish schools near the sea bottom only at the entrance of the bay on March 7~15, 1977. In this period, walleye pollock eggs were distributed widely in Funka Bay and the area adjacent to the bay (Fig. 2). Most of the eggs at the morura stage were taken near the entrance of the bay. From the results obtained by the rearing experiment and temperature of the spawning season in this study area (0°~4°C) it is believed these eggs were collected within 20.7~32.0 hours after fertilization (Table 13). According to the hydrographic observation in this period the Oyashio Water had entered from the northeastern area to the inner area of the bay (Fig. 23) and the dynamic calculation represented that the current speed on the surface was about 10 cm/s. Observed current speeds in the entrance of the bay in March 1982 were 28.5 cm/s at 38 m depth and 15.5 cm/s at 80 m depth, respectively (Miyake, personal communication). Judging from these current speeds and hours from fertilization to the morula stage, it is expected that the spawning ground in 1976/1977 had been in a narrow area near the entrance of the bay. The distributional pattern of walleye pollock eggs observed in 1977 was also found in 1974 (Maeda *et al.*, 1976), 1976 (Maeda *et al.*, 1979) and 1978 (Fig. 3). Ito *et al.* (1955) and Ito and Kurahashi (1955) reported that the spawning grounds were formed in the inner area of the bay and the northeastern coastal area of Oshima Peninsula. But, from the facts mentioned above, there seems no doubt that spawning in recent years has been occurring near the entrance of the bay (100~120 m depth).

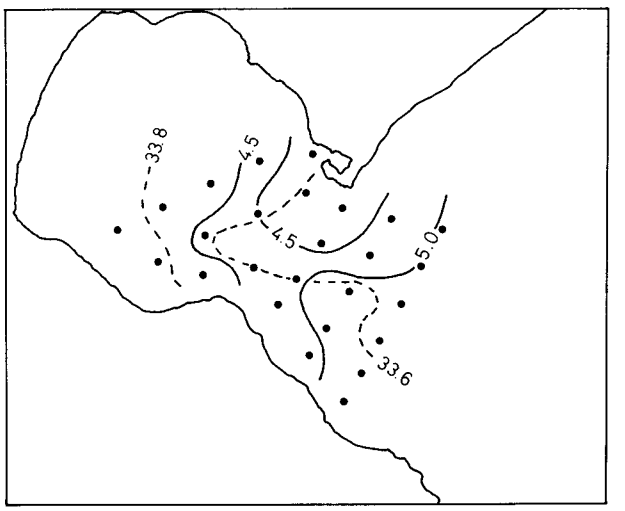

Fig. 28. Surface distribution of temperature (——°C) and salinity (- - -‰) on March 5~7, 1980. (Nakatani and Maeda, 1983)

3-2 Relationship between the geographic position of the spawning ground and survival in early life stages

Walleye pollock eggs, which are spawned near the entrance of Funka Bay, are transported to the inner area of the bay and the northeastern area of Oshima Peninsula by the Oyashio Water (Figs. 2, 3, and 23). It is expected that the distribution of walleye pollock in early life stages will change according to the hydrographic conditions of this water, e.g., change in time of inflow to the bay.

The Oyashio Water flows into the bay at some point of the period from late January to late March as suggested by the distribution of salinity 33.0‰ (Fig. 27). Hakodate Marine Observatory (1980) reported that the invasion of the Oyashio Water from February to March in 1980 was small in comparison with that in an average year. The Tsugaru Warm Water still remained in Funka Bay in early March 1980 and both surface water temperature and salinity were higher than those in an average year (Fig. 28). In this period, walleye pollock larvae were concentrated in the entrance of the bay (Fig. 29) in contrast to the concentration in the inner area of the bay in 1977 (Fig. 5) and 1978 (Fig. 6). In addition, the main fishing grounds in 1979/1980 were formed in the northeastern area from Shiraoi to Mukawa (Hakodate Fish. Exp. St., Muroran Branch, 1980), where the Oyashio Water flowed earlier than in Funka Bay. In a warm year when the inflow of the Oyashio Water is delayed, the spawning grounds may be formed in the northeastern area out of the bay and many larvae hatch out before they are transported to the inner area of the bay.

Pianka (1978) mentioned the large variation of reproduction modes which fits the strategy of greater survival of a population. During the early life stages of walleye pollock, water temperature and food availability may be the main factors

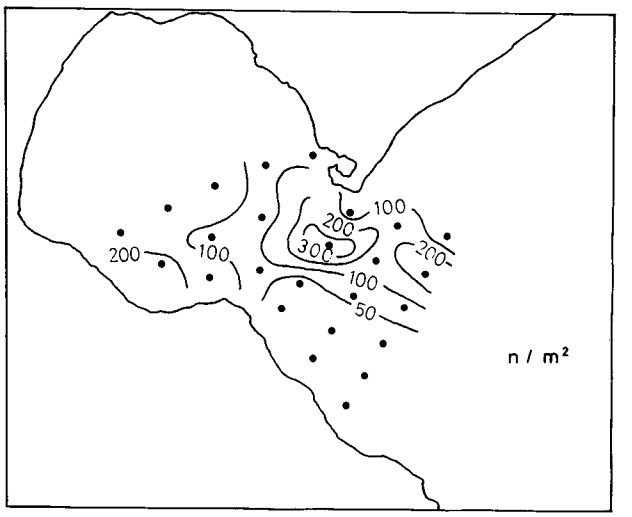

Fig. 29. Distribution of walleye pollock larvae on March 5~7, 1980. Samples were collected by vertical hauls from the sea bottom to the surface with a Norpac net. (Nakatani and Maeda, 1983)

which affect mortality. The results of the rearing experiment show that the hatching rate of walleye pollock eggs is high at 0°～10°C and maximum percentage of hatching is obtained at 10°C (Table 13). However, Hamai *et al.* (1971) observed that the hatching rate was low at 10°C (0.3～35.8%). In the present experiment, eggs were reared in 100 ml beakers at 4°C after fertilization. Then they were transfered into the incubator and the tempesature was elevated to 10°C. Change of the temperature was regurated 0.5 °C/h. By the time the temperature had been raised from 4°C to 10°C, most of the eggs had developed from the 2-cell stage to the morula tage. Hamai *et al.* (1971) mentioned that the hatching rate of eggs incubated in a closed circulation system at 10°C was lower than that incubated in still sea water. This suggests a low tolerance to the physical disturbance for eggs reared at 10°C. Although a temperature of 10°C is experimentally suitable for walleye pollock egg development (Table 13), it is unlikely true under natural conditions. During the early spawning season in December, the water temperature is 9°～11°C (Fig. 27). Such a high temperature is presumably unsuitable for the egg development.

The Oyashio Water flowing into the bay in the spawning season is characterized by temperatuse minimums ranging from −0.09°C in 1984 to 1.37°C in 1980. The minimum temperature is restricted in the surface layer during late spawning season (Fig. 27). Upon the acclimation of −1°C, a high hatching rate was obtained at morula and more developed stages (Table 15). In the field, only few eggs just after fertilization (fertilization～64-cell stage) were collected in the surface layer (Fig. 30). Judging from the upward floating velocity of the eggs (Fig. 21) and the depth of the spawning grounds (100～120 m depth), most of the eggs develop to morula stage by the time they rise to the surface layer. It can be considered that there is no effect of a low temperature on the mortality of walleye pollock eggs in this study area.

During the initial feeding stage, the mortality of the larvae is affected by the amount and kind of food available (Hjort; 1914, 1926) as well as the water tempera-

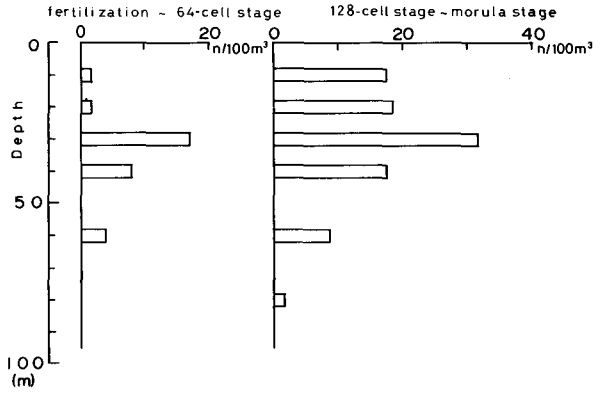

Fig. 30. Vertical distribution of walleye pollock eggs of early developmental stages. Samples were collected by horizontal tows with MTD nets at 6 layers (10, 20, 30, 40, 60, and 80 m depth) at Sta. 3 on 15 March, 1982.

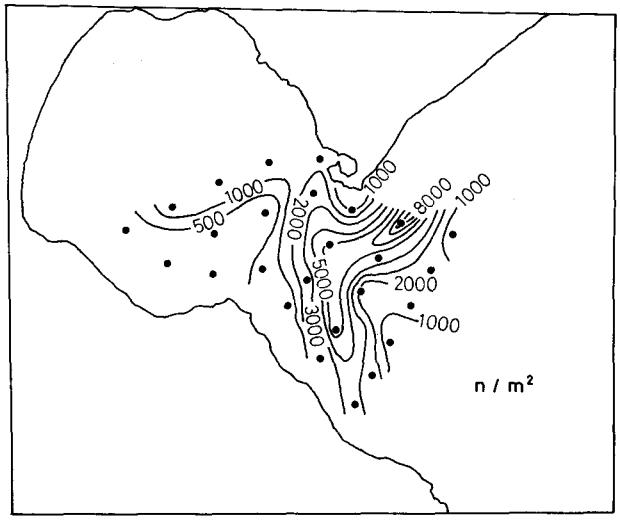

Fig. 31. Distribution of copepodids *Pseudocalanus minutus* on March 5~7, 1980. Samples were collected by vertical hauls from the sea bottom to the surface with a NORPAC net. (Nakatani and Maeda, 1983)

ture. In this study, it was found that both walleye pollock larvae and food organisms were concentrated in the surface layer in the bay (Figs. 11 and 18). In a warm year, however, many of the larvae at the stage of initial feeding were collected near the entrance of the bay (Fig. 29) because the spawning grounds have formed in the northeastern area out of the bay. In this period, *P. minutus* at the copepodite stage were abundantly concentrated in the entrance of the bay and lesser numbers in the inner area of the bay (Fig. 31). *P. minutus* is dominant in the Oyashio Water (Tamura, 1951 ; Hirakawa and Kawamura, 1977) and its nauplius is a primary food item for walleye pollock larvae at the stage of initial feeding. Therefore, the annual change in the geographic position of the spawning grounds correspond to the hydrographic conditions of the Oyashio Water related to a suitable temperature condition for walleye pollock egg development and the larval food availability.

4. RELATIONSHIP BETWEEN THE ANNUAL FLUCTUATION IN WALLEYE POLLOCK CATCH AND THE HYDROGRAPHIC CONDITIONS DURING EARLY LIFE STAGES

As shown in Fig. 32, the annual catch of walleye pollock fluctuated greatly in Funka Bay and vicinity, and large catches occurred in the fishing seasons of 1974 (from October 1973 to March 1974), 1978 and 1982 (Hakodate Fish. Exp. St., Muroran Branch, 1980). These fluctuations are mainly caused by the annual change in a year class strength which sustains the major part of the population. In general, it is known that there is often no correlation between the spawning population size of pelagic fish and the resultant year class. The strength of a year class depends more strongly on high or low mortality during early life stages, which is, in turn, affected by the hydrographic conditions and the food availability.

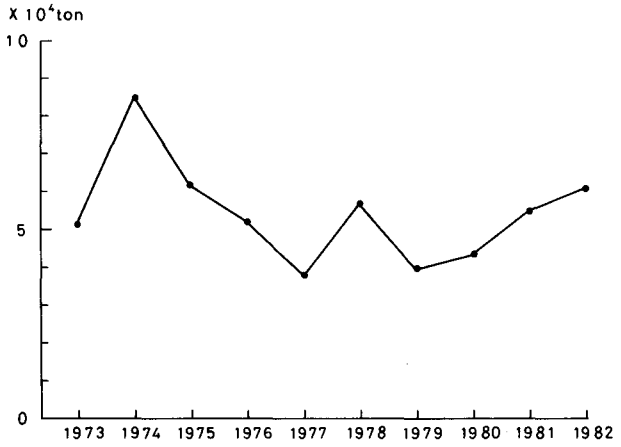

Fig. 32. Annual change in walleye pollock catch in Funka Bay and vicinity (Oshima and Iburi Prefectures) from 1973 to 1982. Data are for fishing seasons; e.g., 1973 data are for the season October 1972 through March 1973. (Hakodate Fish. Exp. St., Muroran Branch, 1982).

Walleye pollock spawning grounds in this study area shift according to the location and the strength of the Oyashio Water. Hydrographic conditions during the spawning season of 1980 was characterized as a warm year, because the invasion of the Oyashio Water was delayed (Figs. 27 and 28) and the spawning ground was

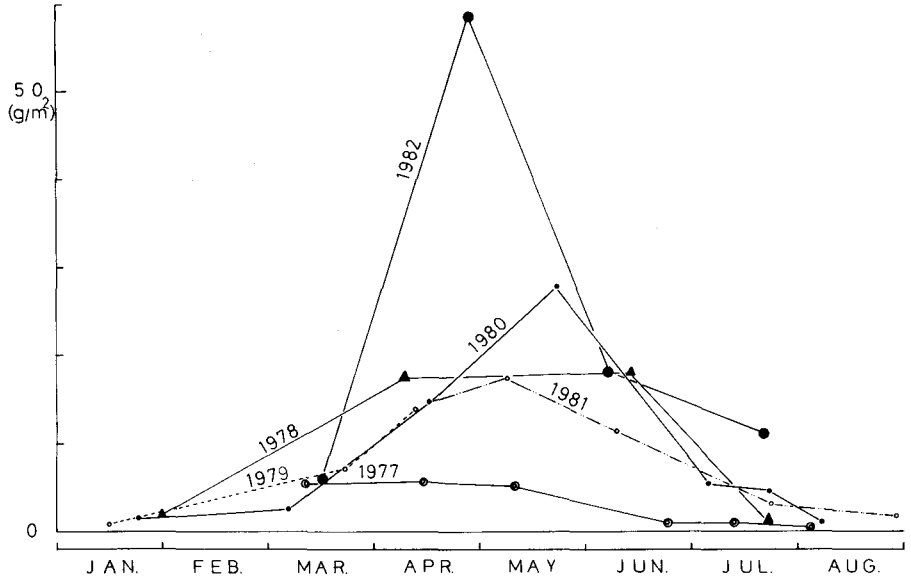

Fig. 33. Seasonal change in biomass of copepodids from January to July. Biomass was indicated as mean wet weight of copepodids collected by vertical hauls from the sea bottom to the surface with a NORPAC net at 6 stations (Stas. 3, 12′, 16, 17, 27, and 30).

formed in the northeastern area out of the bay. This provides an advantage to the larvae by encountering sufficient food (Figs. 29 and 31). As mentioned before, food conditions for the larvae become available in the surface layers of Funka Bay after the invasion of the Oyashio Water. However, the larvae transported into the bay in 1980 may be small in number, because the spawning grounds was formed in the northeastern area far from the bay. In contrast, the spawning ground in 1978 was formed near the entrance of the bay (Fig. 3) and the hydrographic conditions were severe (low temperature) during the spawning season. In this year the Oyashio Water entered the bay earlier as compared with an average year (Fig. 27). Such conditions were also observed in 1974 and 1982 (Hakodate Marine Observatory, 1974, 1982). In addition, a large biomass of copepodids existed in 1978 and 1982, and they increased earlier than in 1980 (Fig. 33). In general the majority of larvae spawned from the strong year class suffer an insufficient food supply. However, as shown in Fig. 33, the larval food conditions in 1978 and 1982 were not unfavorable in Funka Bay, though a great number of larvae were transported into the bay (Fig. 5).

The annual catch of walleye pollock (Fig. 32) shows that a large catch has occurred at an interval of 4 years and coincided with the year in which the Oyashio Water enters the bay earlier than in an average year. It is probable that the larval food conditions are maintained suitably and they recruit as the spawning population after 4 years, because most of walleye pollock mature at an age of 4 years (Zver'kova, 1978).

The early life history of walleye pollock investigated in the present study shows that the spawning behavior is closely related to the mortality during early life stages and the year class strength is affected by the hydrographic conditions of the Oyashio Water. The prediction of walleye pollock population size requires further observation concerning the birth date frequency, predation, and stervation during larval stage.

V. Summary

1) This study has observed the distribution of pelagic eggs and larvae of walleye pollock and the larval food organisms in Funka Bay and vicinity, southeastern Hokkaido. In addition, the hatching rate of eggs under different temperatures ($-1°\sim13°C$) has been investigated.

2) The Oyashio Water invades Funka Bay in spring and remains at the subsurface layer of the bay under the overlaying Tsugaru Warm Water untill summer. During the stratified season, surface temperatures rise from 4°C to 19°C while bottom temperatures remain unchanged ($3°\sim6°C$).

3) Field surveys indicate that walleye pollock eggs at the morula stage are concentrated from 10 m to 40 m depth in the eastern area of the bay mouth in spring, but the eggs gradually appear in the surface layer as the season progresses. These eggs mainly occur in the inner area of the bay in spring. The eggs just befor hatching and larvae at the initial feeding stage are mainly distributed in the surface layer in the inner area of the bay and the northeastern coastal area of Oshima Peninsula. This suggests that walleye pollock eggs are spawned around the mouth

of Funka Bay and transported to the inner area. The eggs hatch out in the surface layers and the larvae occur in the surface layers of the bay until June and they start to sink down to the bottom in late July. Thereafter, the larvae move to the deep layers (200～300 m depth) in the eastern area outside the bay.

4) Walleye pollock larvae, 7 to 30 mm in total length, feed on copepodids of mainly *Pseudocalanus minutus* and *Oithona similis*. When the larvae grow more than 30 mm in total length, they feed on copepodids of *Calanus plumchrus*. Larvae of 70 mm or more in total length, inhabiting the bottom water, feed mainly on large crustacean plankton such as *Calanus cristatus*, *Eucalanus bungii bungii*, *Euphausia pacifica*, and *Parathemisto japonica*.

5) The periods of occurrence of these food organisms in Funka Bay coincide with the time of requirement of walleye pollock larvae. Copepod nauplii abundantly appear in the vicinity of the bay from February to March. Copepodids of *P. minutus* and *Metridia lucence* become dominant in the entrance and the inner area of the bay in March. Copepodids of *P. minutus* are abundant in the surface layer of the bay in March, comprising about 96% of total copepodids at 10 m depth in the inner area of the bay. On the contrary, copepodids of *Oithona* spp. and *Metridia* spp. (mainly *M. lucens*) are mainly distributed in deep layers of the bay at this time. Copepodids of *P. minutus* decrease in number in May and latter months. Copepodids of *C. plumchrus*, which are fed upon by walleye pollock larvae larger than 30 mm in total length, inhabit the deep layers of the bay in June. Copepodids of *E. bungii bungii* increase in number in deep layers in June and latter months.

6) Laboratory experiments show that high hatching rates of artificially fertilized eggs of walleye pollock were obtained at 0°～10°C (86～100%), and low at −1°C (0～31%). Hatching rates of the eggs reared from the morula stage at −1°C were high (45～60%) and the rate increased with progressive developmental stages. The relationship between water temperature and time in days required for 50% hatching was calculated as:

$$T = 31.70 \exp(-0.12\theta)$$

T: time in days required for 50% hatching
θ: water temperature, °C
$r^2 = 0.98$

Mean specific gravity of artificially fertilized eggs collected in Funka Bay was 1.0226 g/cm^3 and that in the coastal area off Ainuma in the Sea of Japan was 1.0201 g/cm^3. The upward floating velocity of eggs was observed as 4.9 m/h (Funka Bay sample) and 8.6 m/h (Ainuma sample), respectively. From this, it is suggested that the eggs develop to the morula stage by the time they rise to the surface layer.

7) The surface water of Funka Bay is highly productive in spring after the invansion of the Oyashio Water. Walleye pollock eggs which had been spawned near the entrance of the bay are transported by this water.

8) Seasonal changes in the distribution of the larvae and the food organisms indicate that the larvae pursue the location of habitat where food is available.

9) In recent years, large catches of walleye pollock in this study area occurred at an interval of 4 years (1974, 1978, and 1982). The invasion of the Oyashio Water

into the bay in these years occurred earlier (late January) than in average years (late February). Early invasion of this water may favorably affect production of food available to walleye pollock larvae resulting in a high survival rate. A large population of larvae may result in a large spawning population 4 years later. This hypothesis requires further investigation.

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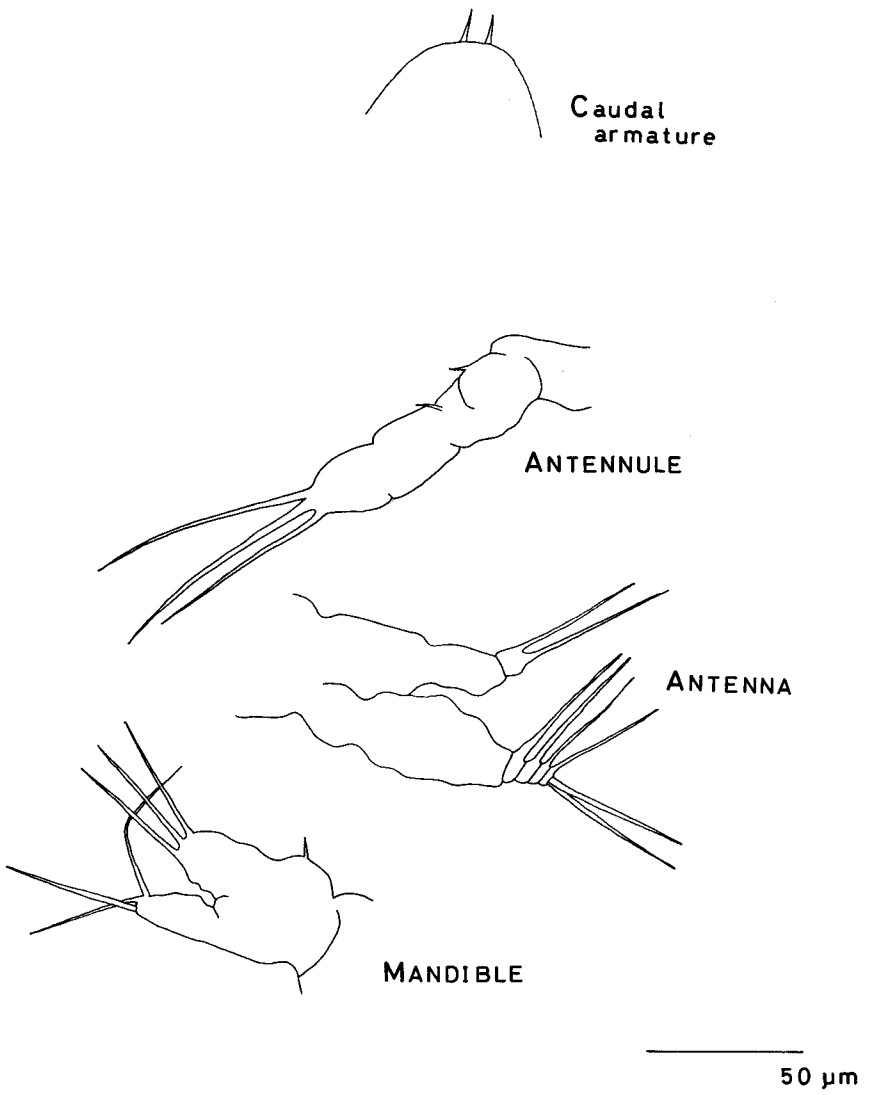
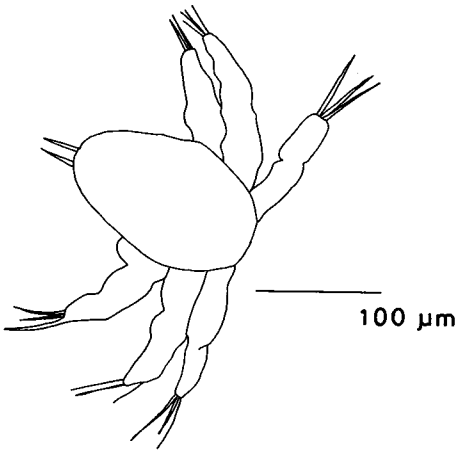
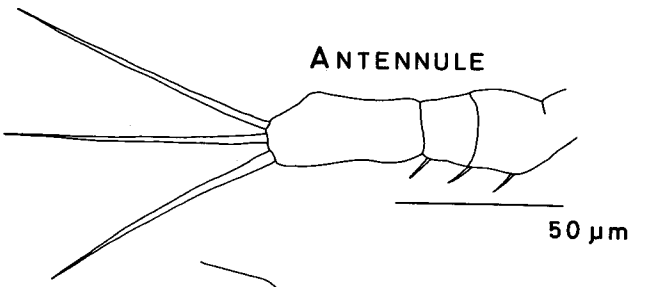
Explanation of Plates

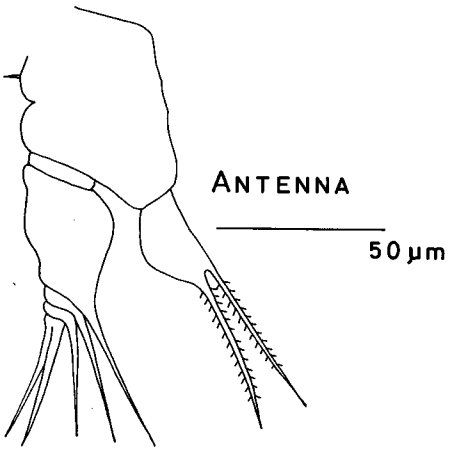
Plate I	Nauplius of *Pseudocalanus minutus* or *Metridia lucens* Stage I
Plate II	Nauplius of *Pseudocalanus minutus* or *Metridia lucens* Stage I
Plate III	Nauplius of *Pseudocalanus minutus* or *Metridia lucens* Stage II
Plate IV	Nauplius of *Pseudocalanus minutus* or *Metridia lucens* Stage III
Plate V	Nauplius of *Pseudocalanus minutus* Stage IV
Plate VI	Nauplius of *Pseudocalanus minutus* Stage V
Plate VII	Nauplius of *Metridia lucens* Stage V
Plate VIII	Nauplius of *Oithona* sp. Stage IV
Plate IX	Nauplius of *Calanus* sp. Stage IV
Plate X	Nauplius of *Calanus* sp. Stage VI
Plate XI	Nauplius of *Eucalanus bungii bungii* Stage II



NAKATANI: Early life history of walleye pollock







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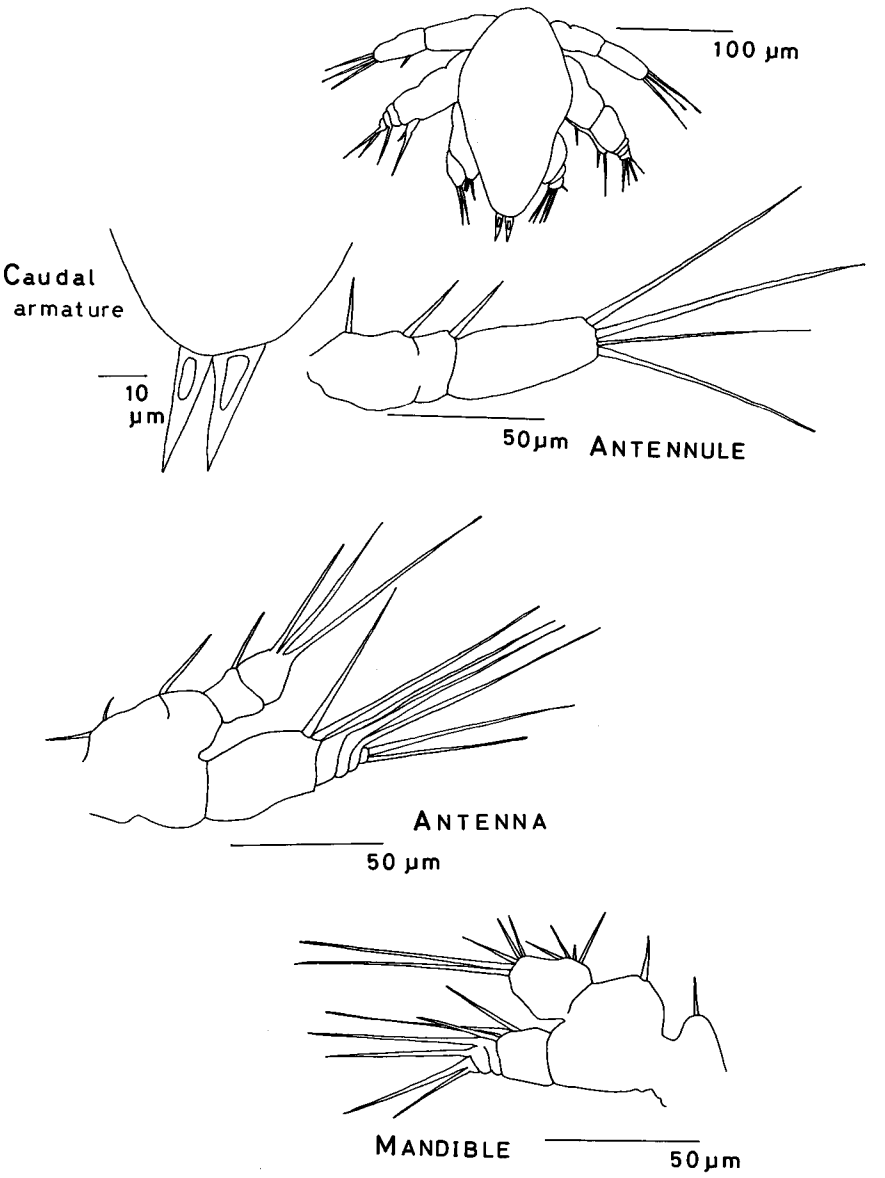

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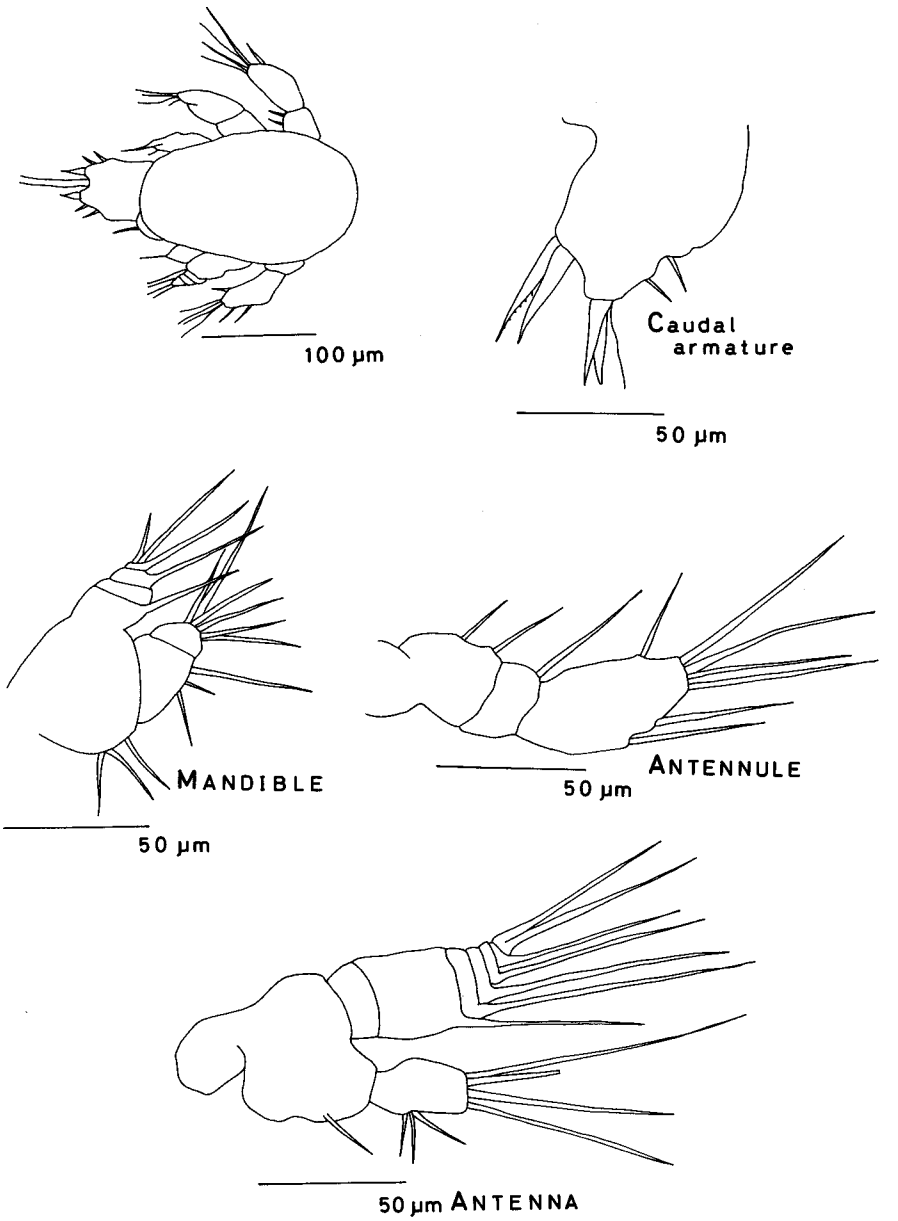

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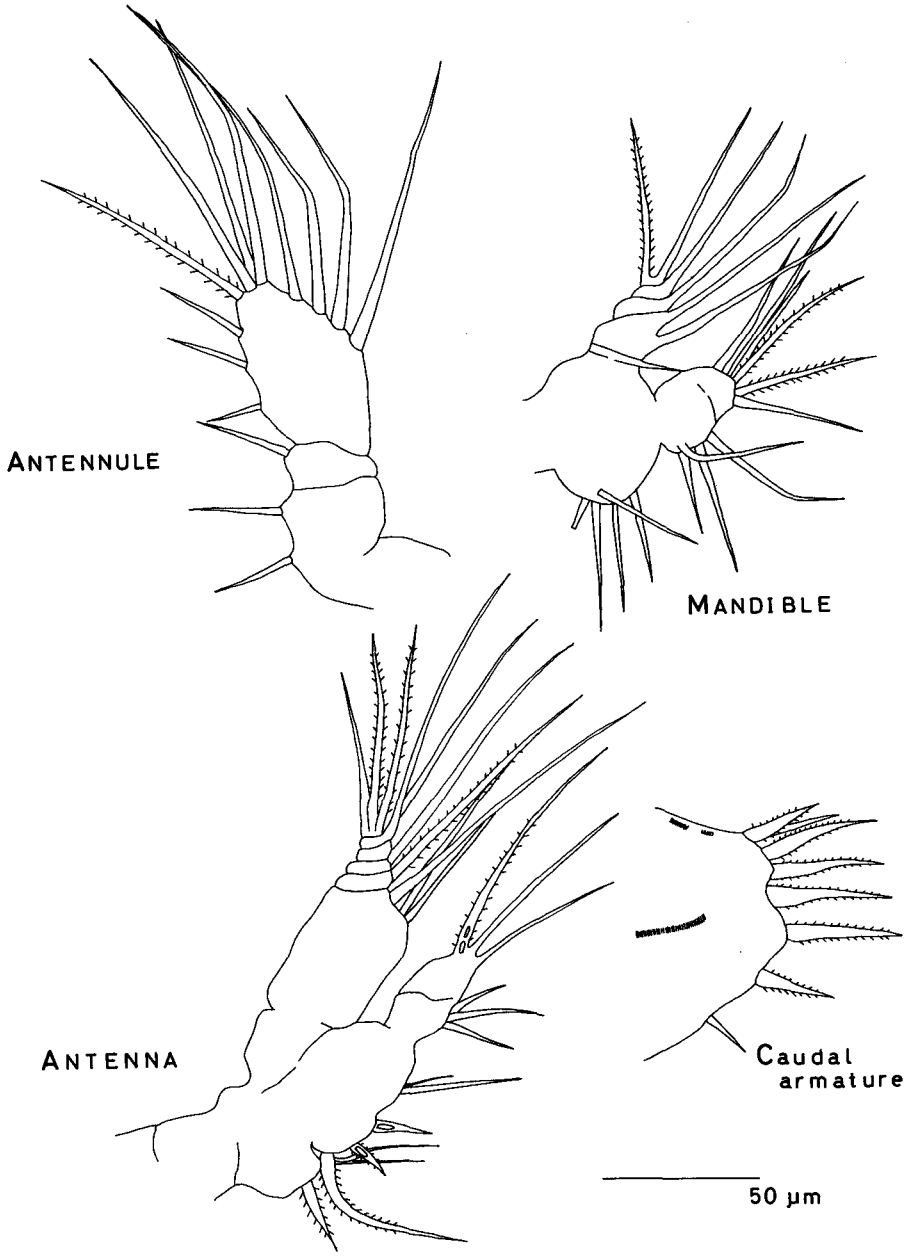
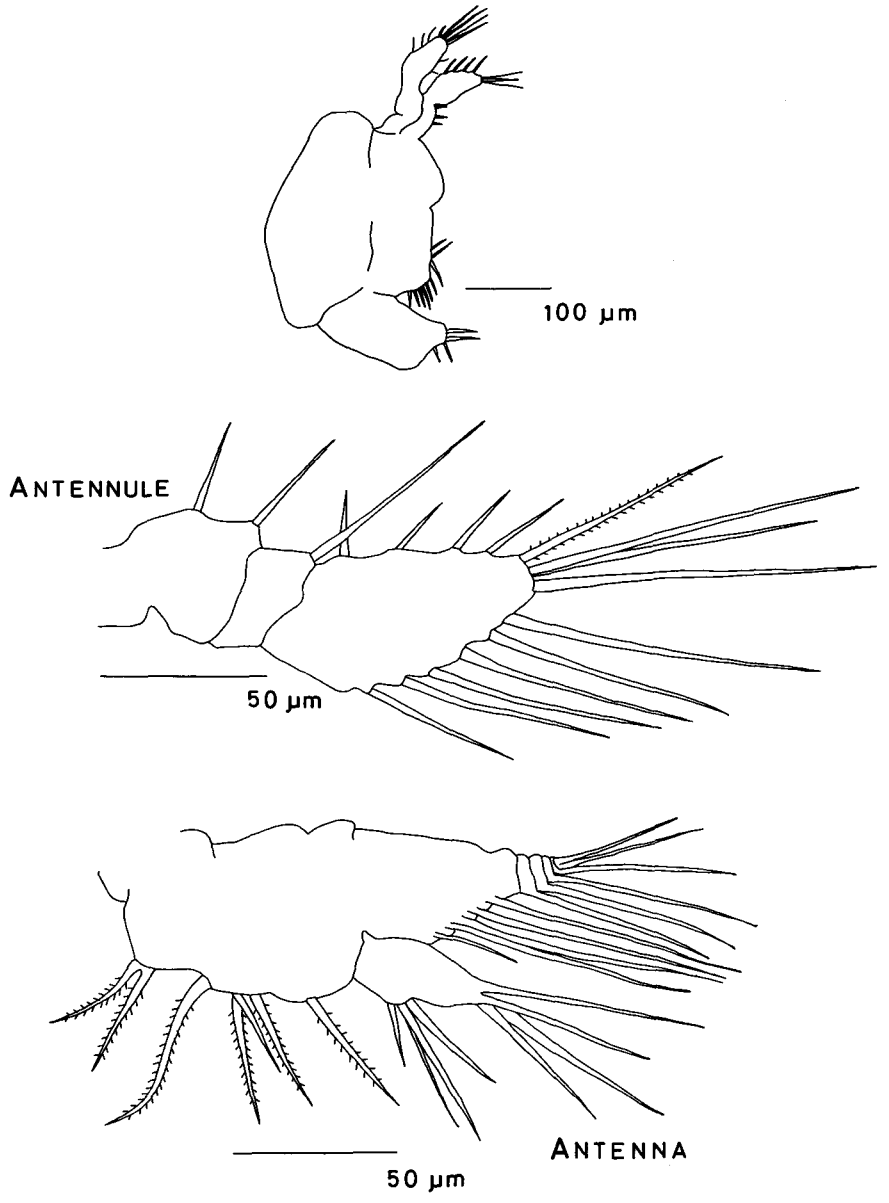


NAKATANI: Early life history of walleye pollock



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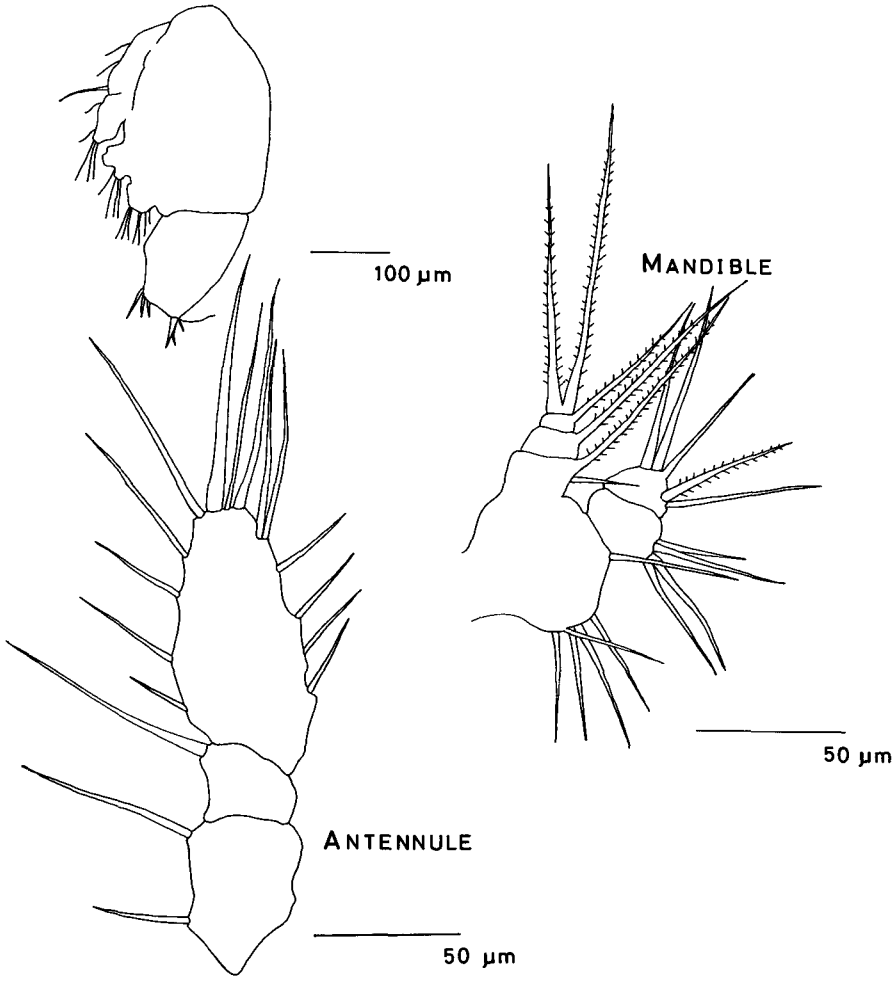

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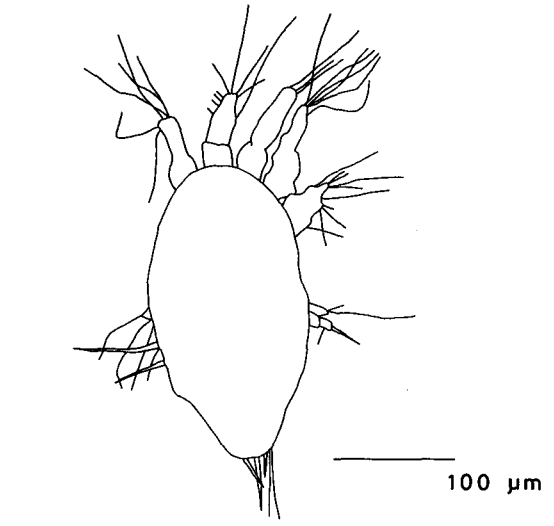

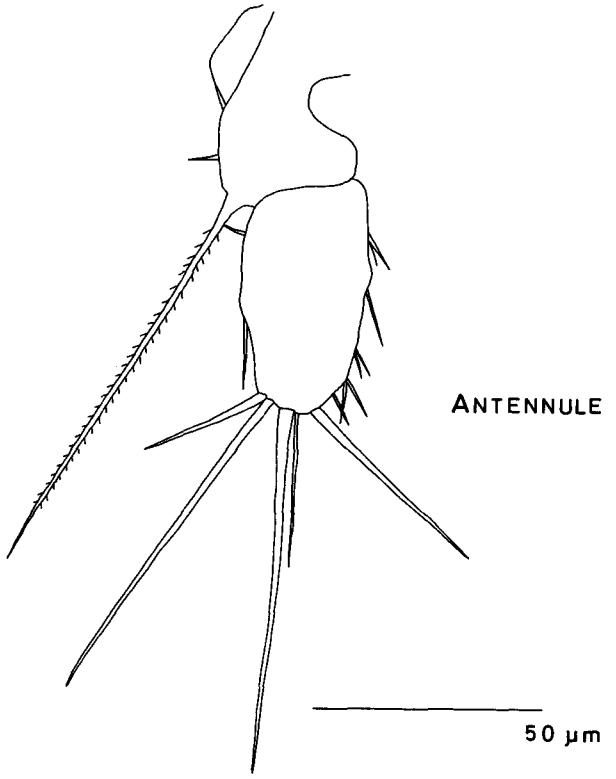

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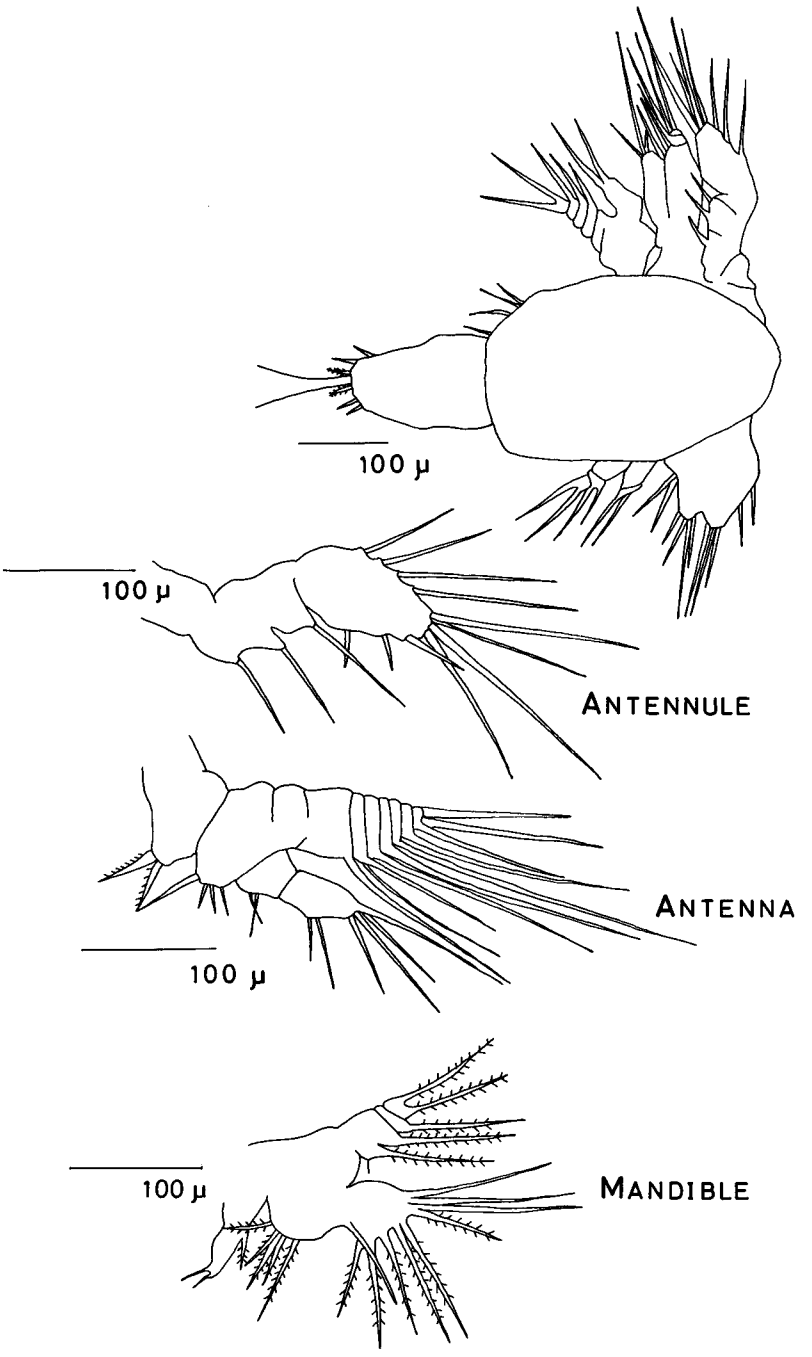

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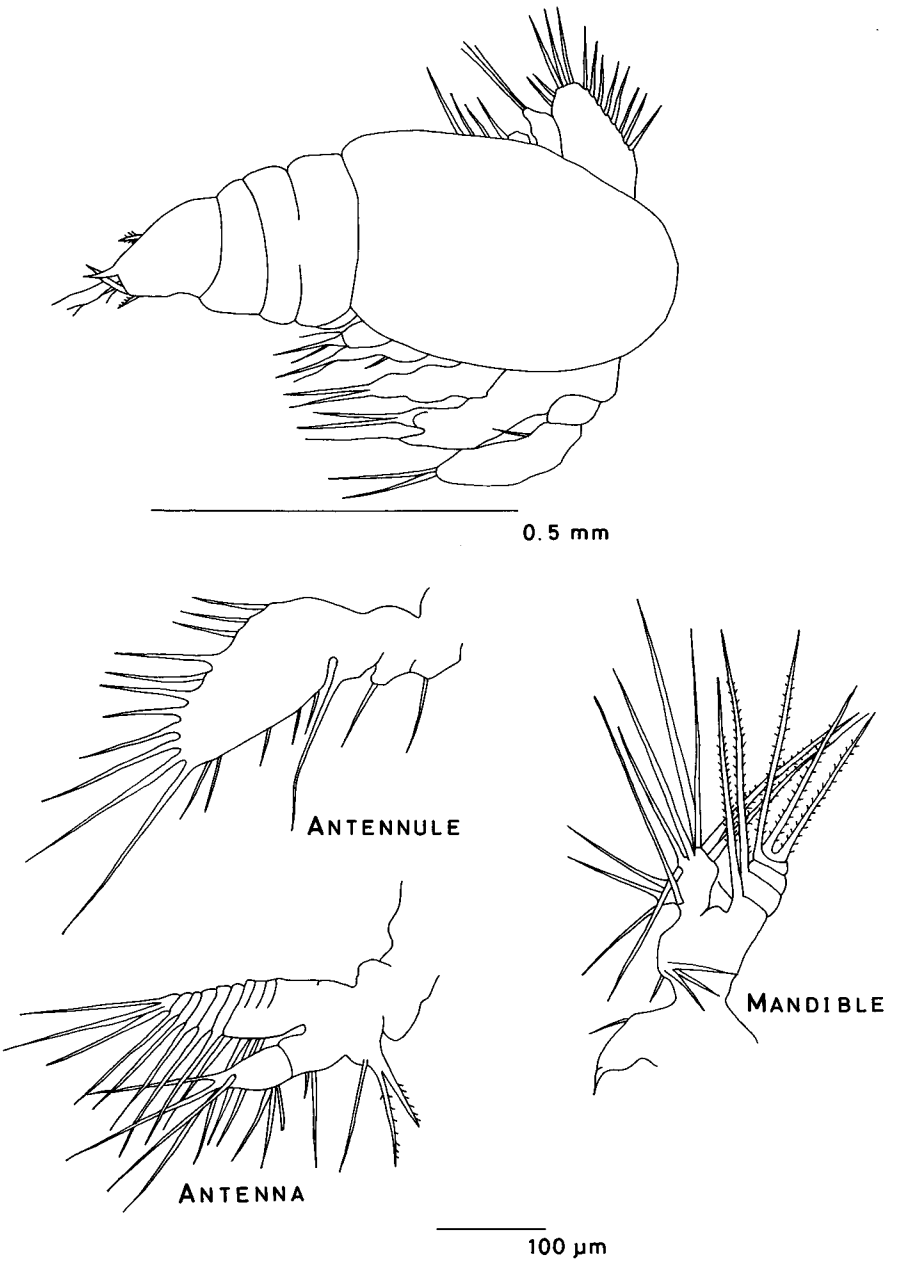

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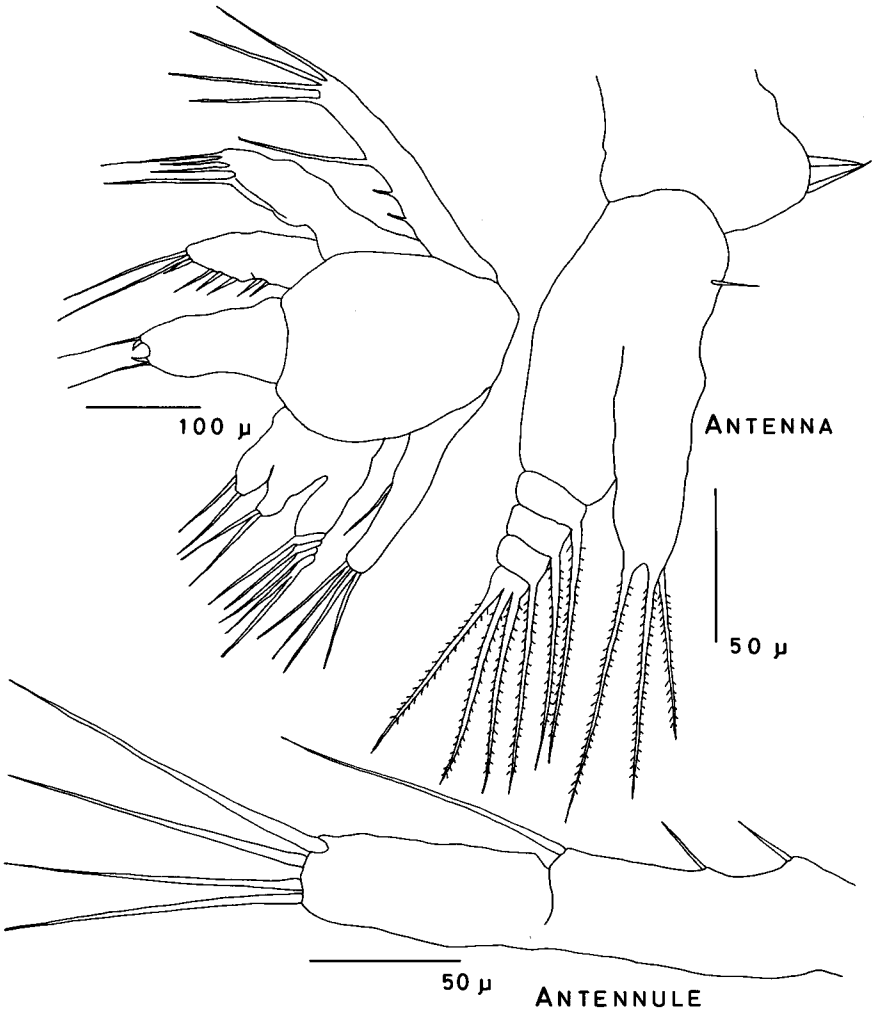

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