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Year Class Strength and Early Life Hisonory of the Pacific Population of Walleye Pollock, *Gadus chalcogrammus*, in Japan

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Abstract

From the 1970s, year round field samplings and observations of Funka Bay have been conducted aboard the *R/V* Ushio-Maru, Faculty of Fisheries, Hokkaido University. The hydrographic, chemical, and biological data have been used to understand the ecosystem of Funka Bay, especially the relationships among the biological production of low trophic levels, nutrient dynamics, and the behavior of the Oyashio Coastal Water (OCW) from winter through early spring. Tagging experiments conducted by the Hokkaido National Fisheries Research Institute have shown that the Pacific population of walleye pollock occurs from the eastern side of Hokkaido Island to northern coastal area of Honshu Island. The distribution of early stage eggs indicates that the spawning grounds are formed from the mouth of Funka Bay to the eastern shelf area outside of the bay. The relationship between the mean days required for 50% hatching (D) and temperature (T) is expressed as follows; D=31.70 exp (−0.12T) by the laboratory experiments, and the surface temperature of Funka Bay in winter is thought to be suitable for pollock embryonic development. Pollock eggs are transported into the bay, where hatchings initiate feeding on copepod nauplii. The feeding success of pollock larvae is higher in Tsugaru Warm Water, which stagnates in winter in the bay, than in OCW, which enters the bay in late January-early February. Early invasion of OCW into the bay is thought to increase the larval pollock mortality due to low temperature and transportation of carnivorous plankton. Strong year classes occurred only in years when late invasions of OCW were observed. With growth, the main food of pollock larvae and juveniles changed to copepodids such as *Pseudocalanus newmanii*, *Neocalanus* spp. and *Eucalanus bungii*. Their biological production might be controlled by the primary production from late winter through early spring, which might be affected by the behavior of OCW. Therefore, the annual fluctuation of the behavior of OCW is a factor affecting complicatedly the year class strength of the walleye pollock Pacific population.

Key words: Walleye Pollock, Early life history, Funka Bay, Food availability, Year class, Conservation

Introduction

In the southwestern region of Hokkaido, Japan, walleye pollock, *Gadus chalcogrammus*, is fished commercially by bottom gill nets from autumn through early winter, and annual harvests have fluctuated from 40,000 to 80,000 metric tons. The annual harvest is considered to be controlled by the size of year class and strong year classes support the fishery (Maeda et al., 1993; Yabuki and Honda, 2004). Tagging experiments conducted by the Hokkaido National Fisheries Research Institute (unpublished data) indicate that the Pacific population is distributed from the shelf region in eastern Hokkaido Island to northern Honshu Island (Tohoku area) (Fig. 1).

Year round field samplings and observations have been conducted in Funka Bay aboard the *R/V* Ushio-Maru, Faculty of Fisheries, Hokkaido University since 1971. From February 1974 to February 1975, monthly hydrographic observations were conducted (The group of Funka Bay studies, 1974, 1975), and Ohtani and Kido (1977, 1980) examined the oceanographic structure in Funka Bay. In this area, the hydrographic conditions are controlled mainly by two water masses. One is the Tsushima Warm Current, which flows along the western coast of Honshu Island in the Sea of Japan and passes through the Tsugaru Strait to the Pacific Ocean (Fig. 1A). This water (the Tsugaru Warm Water: TWW), which is characterized by a high salinity (≧33.8; Ohtani, 1971; Ohtani and Kido, 1980), entering the bay in late summer and/or autumn. TWW stagnates in the whole bay during winter (Fig. 1B). The other water mass is the Oyashio Coastal Water (OCW, 33.0-33.3; Ohtani, 1971; Ohtani and Kido, 1980) enters the bay from late January through February (Fig. 1C). Monthly samplings and hydrographic observations have also been conducted in the adjacent waters of the bay aboard the *R/V* Ushio Maru to examine the life history, feeding habits, and the migration of the walleye pollock Pacific population (Ueno et al., 1975; Maeda et al., 1976, 1981, 1983). According to these studies, walleye pollock is distributed in the east area (200-350 m depth) outside of Funka Bay from May to October during the feeding season. With gonadal maturation, spawners migrate to the shallow area near the bay mouth (100 m depth). Based on this information, the author initiated studies on the early life history of

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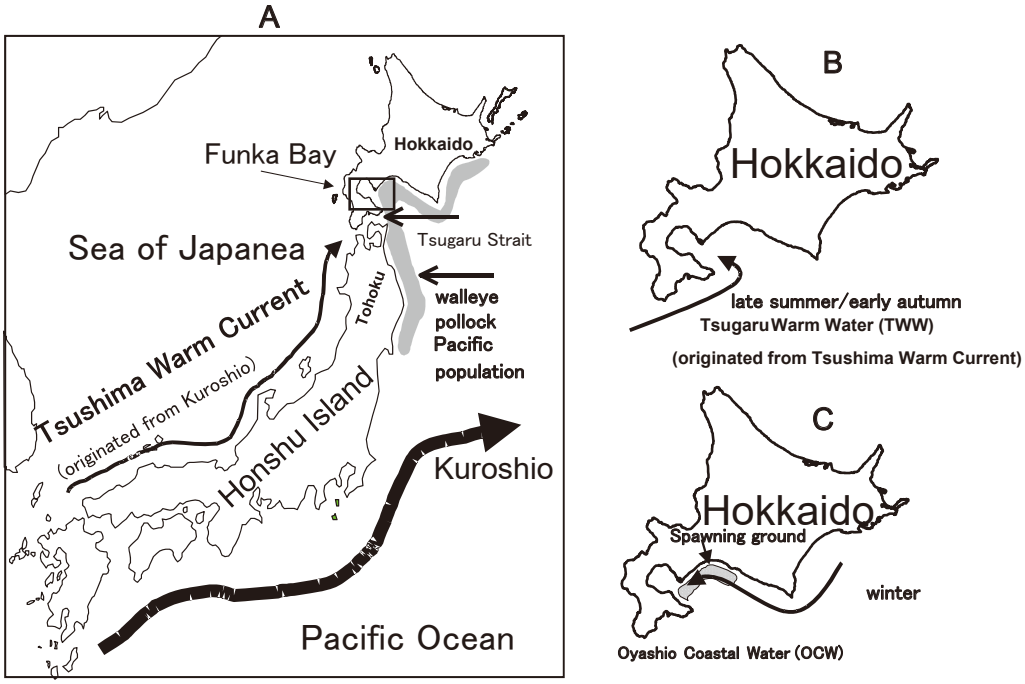

Fig. 1. Distribution of the walleye pollock Pacific population in the coastal area in Hokkaido, Japan.

pollock to understand the mechanism of the annual fluctuation of the year class strength. This review summarizes the reproductive ecology, the early life history, and the conservation biology of the walleye pollock Pacific population.

Spawning grounds

The walleye pollock Pacific population spawns from December to March (Maeda et al., 1979, 1980; Yoon, 1981). To clarify the geographic distribution of its spawning grounds, eggs were collected by vertical hauls from the sea bottom to the surface with a plankton net (0.45 m in diameter, 0.33 mm in mesh size) in February 1988 (Nakatani and Maeda, 1989). The earliest developmental stages (from fertilization to morula stage) of pollock eggs and larvae were counted (Fig. 2). Eggs in early developmental stages were collected from the mouth area of Funka Bay to the eastern shelf area out of the bay. In contrast, larvae were collected in a restricted area inside the bay. The distributions of early developmental eggs and larvae were almost identical in 1988 and in March 1977 (Nakatani and Maeda, 1981). These results indicate that the spawning grounds were formed near the bay mouth, but not in the bay. Pollock eggs are transported into the bay by eddies generated by the combination of the predominant northwesterly winds in winter and the parabolic bottom topography of the bay (Shimizu and Isoda, 1997, 1998). From 1991 to 2003, first-feeding pollock larvae have been abundant in late January in Funka Bay and the bay mouth, and the annual change in the density of pollock larvae was observed (Fig. 3). Monitoring of the annual fluctuation of

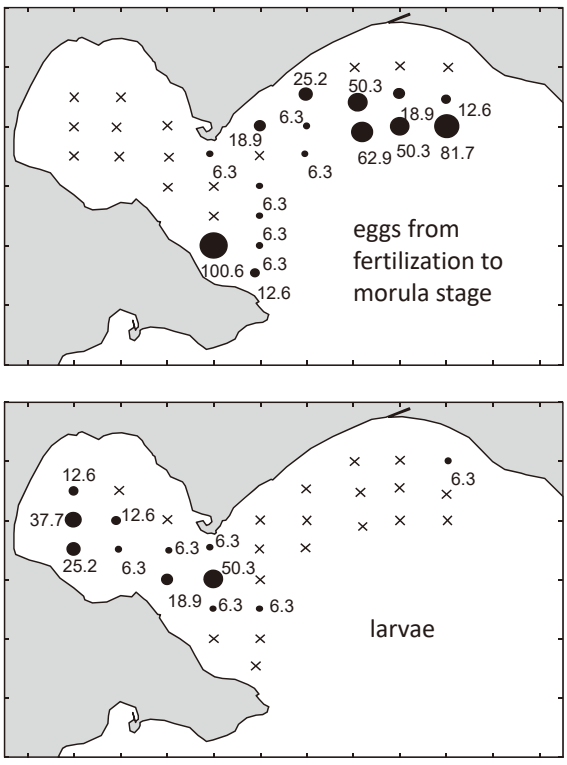

Fig. 2. Distributions of walleye pollock eggs from fertilization to morula stage (upper panel) and larvae (under panel) collected by vertical hauls from the sea bottom to the surface with a plankton net in February 21–25, 1988 in Funka Bay and mouth region, Hokkaido, Japan. (from Nakatani and Maeda, 1989)

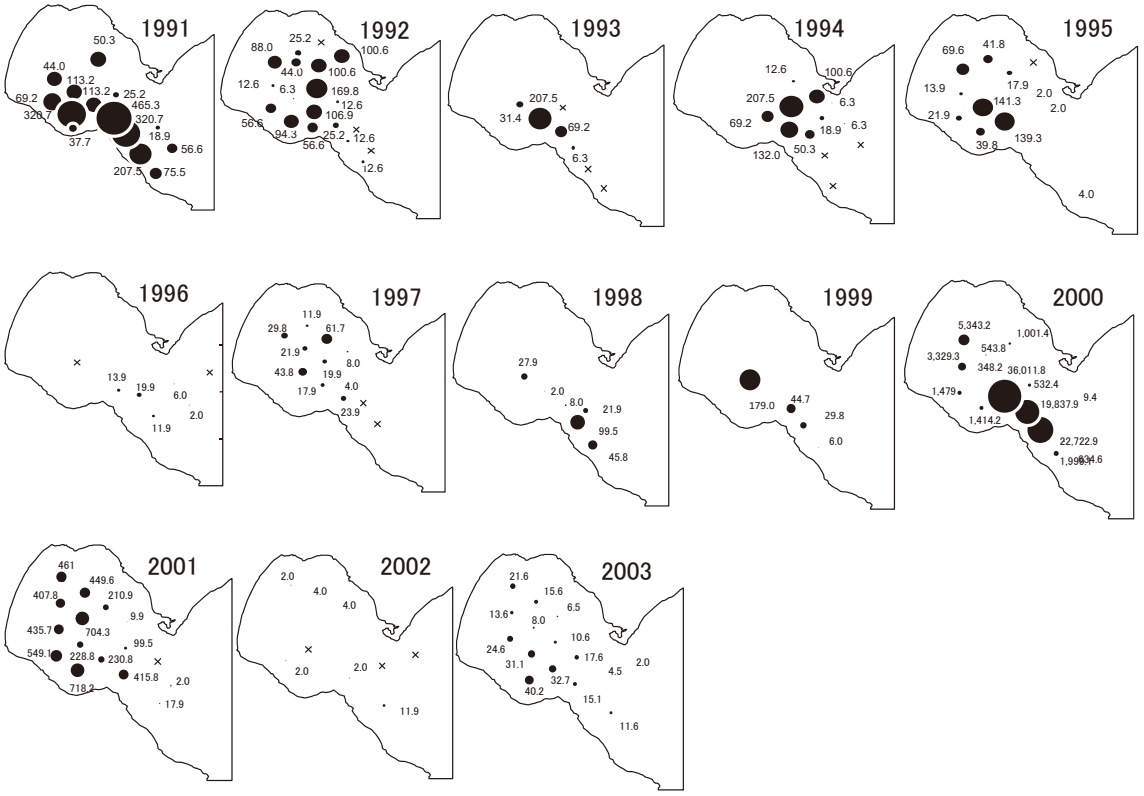

Fig. 3. Annual change in density of walleye pollock larvae (larvae · m^{-2}) in late January from 1991 to 2003 in Funka Bay.

the horizontal distribution of pollock eggs in early developmental stages and the hydrographic conditions are needed to clarify the relationship between the geographic position of the spawning grounds and the hydrographic conditions in winter. Based on the reproductive ecology of this species, commercial fisheries should be prohibited at the spawning grounds in winter to maintain the population size. Furthermore, the commercial fishing should be closed when mature fish just before spawning are collected. It is easy to confirm the maturation by the discharge of transparent mature eggs and/or sperm. Commercial fishing should not disturb the reproduction of the target species.

Table 1. Median days for hatching after fertilization of walleye pollock (from Nakatani and Maeda, 1984)

Temperature	Days	Hatching rate (%)	normal hatching rate (%)
−1°C	46.0–57.0	0–36.7	0–31.0
0°C	31.8–42.0	96.7–98.4	*
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

*All hatched larvae seemed to be normal development.

Enbryonic development of artificially fertilized eggs

Nakatani and Maeda (1984) examined the development of pollock eggs obtained by artificial fertilization at seven temperature levels (Table 1). From the results, the relationship between the mean days required for 50% hatching (D) and temperature (T) is expressed by the following equation;

$$D=31.70 \exp(-0.12T) \quad (1)$$

It takes about 19 days for hatching at the prevailing temperature in the spawning grounds (ca. 4°C). To clarify the low temperature tolerance of eggs to cold OCW, which enters the bay and decreases the surface temperature below 3°C, the hatching rates at four developmental stages of the eggs exposed to low temperatures (from 4°C to −1 and/or 0°C) were examined for three cases of descending speed of temperature (Table 2). The hatching rates of the eggs at the 2-cell stage subjected to a thermal shock from 4°C to −1°C were low (0–37%). In contrast, the hatching rates of more advanced developmental stages were higher (73.9–100%). On the other hand, the hatching rates of the eggs subjected to a thermal shock from 4°C to 0°C were high at four developmental stages (73–97%). From the results obtained by laboratory experiments and the decadal information of surface temperature in winter in the spawning grounds, it is considered that the temperatures in the spawning grounds during the spawning period of the walleye pollock Pacific population are

Table 2. Hatching rates in percentage of walleye pollock eggs subjected to thermal shock at 4 developmental stages (from Nakatani and Maeda, 1984)

Developmental stage	Thermal shock from 4°C to −1°C			Thermal shock from 4°C to 0°C		
	direct**	rapid***	slow****	direct**	rapid***	slow****
2 cells	6.7 (0)	35.6 (31.0)	14.8 (0)	73.4	80.0	96.7
Morula	86.7 (45.2)	73.9 (56.5)	86.7 (100)	86.7	82.8	90.0
Gastrula	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

*Figures in parentheses show the percentages of normal hatching.
**Eggs were transferred from 4°C water to −1 and/or 0°C water directly.
***Thermal change was 0.7°C～1.3°C · 10 min^{-1}.
****Thermal change was 0.1°C · 10 min^{-1}.

suitable for embryonic development.

Food availability of walleye pollock larvae at the first feeding stage in Funka Bay

Kamba (1977) investigated the food of pollock larvae collected at the mouth of Funka Bay and indicated that the main food organisms were copepod nauplii. Copepod nauplii are also the main food for pollock larvae in the southeastern Bering Sea (Dagg et al., 1984), and Shelikof Strait, Gulf of Alaska (Kendall et al., 1987). To assess the food availability of pollock larvae at the first feeding stage (smaller than 7 mm in total length), species composition of copepod nauplii in the intestines of pollock larvae and the density of copepod nauplii at 15 m depth in Funka Bay were observed in winter (Nakatani and Maeda, 1983; Nakatani, 1995a, b). In winter 1991, copepod nauplii were collected at three stations at 15 m depth (Fig. 4). The density of copepod nauplii ranged from 7.80 to 12.69 individuals · L^{-1} in late winter (Table 3). In January, the dominant copepod nauplii were *Oithona* (Fig. 5) and *Paracalanus*. After February, *Pseudocalanus* and *Metridia* increased. In January and February, 2003, *Oithona* nauplii also dominated the copepod naupliar community in Funka Bay, but decreased in March (Table 4; Nakatani et al., 2007). The high *Oithona* % was also observed in 2001 and 2002

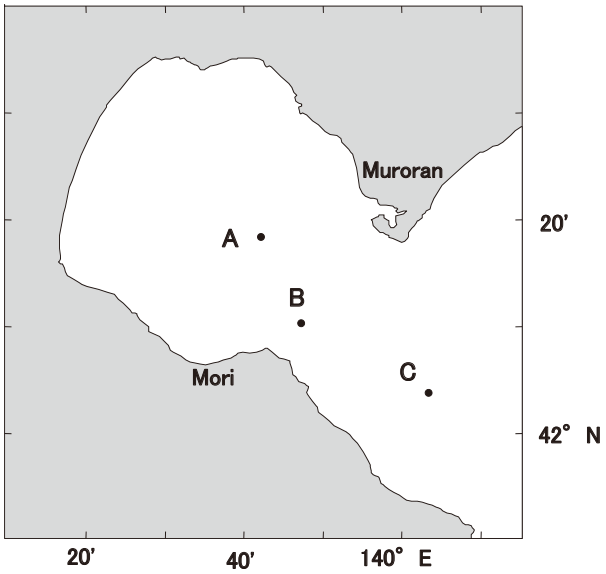

Fig. 4. Location of sampling stations in winter 1991 in Funka Bay. Copepod nauplii were collected at 15 m depth.

(Nakatani et al., 2007).

Pollock larvae at the first feeding stage fed on *Oithona, Paracalanus,* and *Pseudocalanus* nauplii larger than 84 μm in body width of (Nakatani, 1995b). In Funka Bay, copepodids of *Oithona* are present throughout the year and *O. similis*

Table 3. Monthly change in density of copepod nauplii (nauplii · L^{-1}) in 1991 (from Nakatani, 1995a)

	29–30, JAN.			21, FEB.			14, MAR.		
	Station A	Station B	Station C	Station A	Station B	Station C	Station A	Station B	Station C
Calanus	0.30	0.38	0.26	0.27	1.49	0	1.31	0.41	0.11
Paracalanus	2.17	1.68	1.97	0.69	0.96	0	0.19	0.28	0.11
Pseudocalanus and *Metridia*	0.88	0.66	0.97	3.83	1.87	0.86	2.86	0.45	2.13
Acartia	0	0.14	0.10	0.39	0.32	0	0.31	0.69	0.05
Oithona	4.18	8.61	8.59	12.80	13.52	11.28	7.77	2.14	5.78
Oncaea	0.11	0.21	0.35	0.07	0.48	0.26	0	0.06	0
others	0.16	0.05	0.45	0	0	0	0	0.10	0.06
total	7.80	11.73	12.69	18.05	18.64	12.40	12.44	4.13	8.24

Table 4. Densities of copepod nauplii, *Oithona* nauplii (individuals · L^{-1}), and percentage of *Oithona* for total copepod nauplii (*Oithona* %) in Funka Bay and its vicinity in 2003. Samples were collected at a 15 m depth. (from Nakatani et al., 2007)

	January	February	March
copepod nauplii	3.05–7.65	2.25–7.20	11.7–18.6
Oithona nauplii	2.71–5.92	1.80–5.36	4.27–8.60
Oithona %	64.5–85.8	46.2–80.0	33.3–70.5

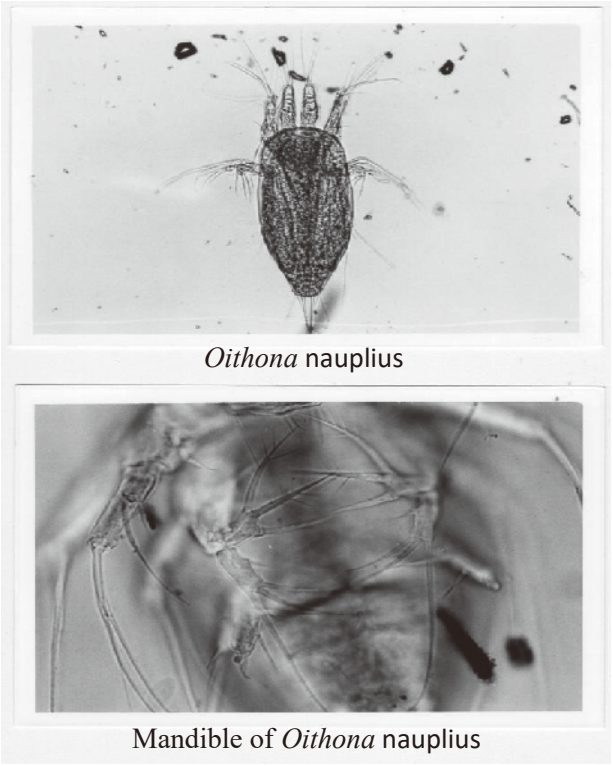

Fig. 5. *Oithona* nauplius collected in Funka Bay.

composes more than 80% of total number of *Oithona* spp. from late spring to autumn (Itoh, 1993; Umezaki, 2000; Ide, 2001). The density of *O. similis* decreases from August to October in the bay (Nakatani et al., 2003b). In January 2003, OCW (<33.0) distributed at the bay mouth (Figs. 6 and 7). In contrast, TWW (33.6) prevailed inside the bay. In the same period, the densities of *Oithona* C6F were higher at Stn. 7 in OCW than at Stn. 30 in TWW (Nakatani et al., 2007; Table 5). But, the densites of *Oithona* N1 at Stn. 7 and Stn. 30 were almost identical (Table 6). These results indicate the reproductive activity of *O. similis* in TWW in the bay is higher than that in OCW at the bay mouth because of warm temperature inside the bay. Therefore, the availability of prey for pollock larvae at the first feeding stage in winter is stable geographically because of high reproductive activity in the warm temperature in TWW in the bay in spite of the low density of *O. similis* C6F. From these observations, it can be considered that food availability for pollock larvae at the first feeding stage is controlled by the reproductive activity of

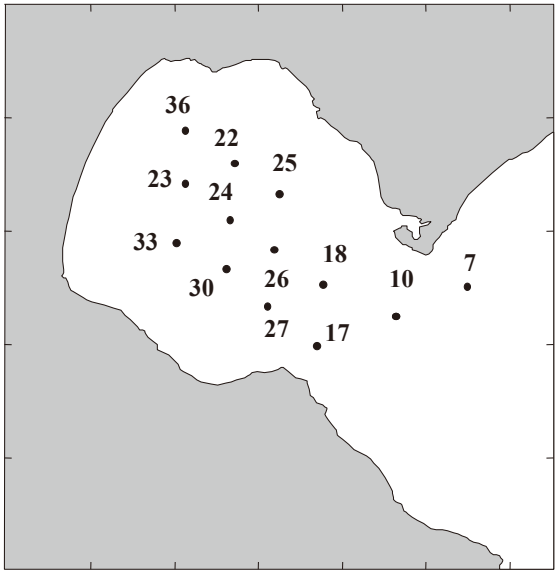

Fig. 6. Location of sampling stations in winter 2003 in Funka Bay.

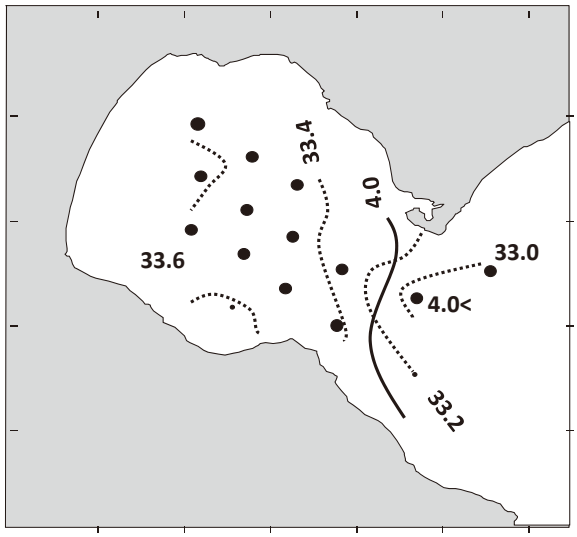

Fig. 7. Distribution of temperature (——— °C) and salinity (- - - - -) at 15 m depth in January, 2003. (from Nakatani et al., 2007)

Oithona similis and existence of TWW before the intrusion of OCW. Haldorson et al. (1989) reported that saturation feeding occurred for pollock larvae in Auke Bay, Alaska at prey

Table 5. Density (individuals · m^{-3}) of *Oithona similis* C6F in winter 2003 (from Nakatani et al., 2007)

	Station 30	Station 7	Station 10
January	273.6	616.0	
February	273.3		144.5
March	310.6		587.9

Table 6. Densities of *Oithona* N1 (individuals · L^{-1}) in Funka Bay and its vicinity in 2003. Samples were collected at 15 m depth. (from Nakatani et al., 2007)

	Station 30	Station 33	Station 24	Station 7	Station 10
January	0.8			0.57	
February		0.14			0.96
March			1.58		0.54

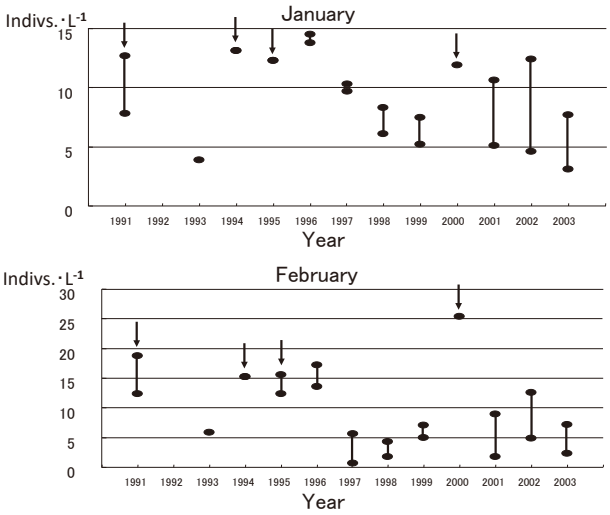

Fig. 8. Annual change in density (nauplii · L^{-1}) of copepod nauplii in Funka Bay and mouth region in late January and February from 1991 to 2003. Samples were collected at 15 m depth. Vertical lines show the range of the density of copepod nauplii. Arrows indicate the years occurring the strong year classes.

densities over 20 copepod nauplii · L^{-1}. From January to February in Funka Bay, such a high density was not observed (Tables 3 and 4; Fig. 8). High densities over 20 copepod nauplii · L^{-1} were observed only in March. Sugimoto (1997) found that the juvenile walleye pollock collected at St. 30 by a bottom trawl net in 1995 had hatched from mid January to mid February. In winter1995, a high density over 20 copepod nauplii · L^{-1} was not observed from late January to mid February (13 to 15 nauplii · L^{-1}; Fig. 8). Therefore, it is inferred that low density prey during the hatching period is not critical for larval pollock at the first feeding stage in Funka Bay. It needs further laboratory studies concerning the relationship among the feeding success of pollock larvae, the density of copepod nauplii, and temperature.

It has been suggested that the food condition is important for the survival of pollock larvae at the first feeding stage (Nakatani, 1988, 1991; Isoda et al., 1998; Nakatani and Sugimoto, 1998). However, the annual change in densities of the copepod nauplii as the main food organisms for pollock larvae at the first feeding stage was not large (Fig. 8). While, Funamoto (2007) demonstrated a positive relationship between the density of copepod nauplii and the year class strength of the walleye pollock Pacific population in all years except in 1996. Field studies of the relationships among hydrographic condition, the reproductive activity of *Oithona similis*, and the magnitude of the spring phytoplankton bloom in Funka Bay are needed.

Recruitment

After transportation into Funka Bay, newly hatched pollock larvae widely occur in the surface layer in the bay (Kamba, 1977; Maeda et al., 1979; Nakatani, 1988). To examine the recruit migration, larvae and juvenile pollock were collected with a larva net (1.3 m in diameter), a frame mid-water trawl net (2.0×2.5 m), and a bottom trawl net (Nakatani and Maeda, 1987). From spring through early summer, the surface and sub surface temperature increased, and juvenile pollock avoiding the warm water migrated vertically to the sea bottom where the temperature was as cold as 3–5°C (Nakatani et al., 2002). During this period, *Pseudocalanus* copepodids decreased in abundance, while large calanoid copepods were abundant near the sea bottom in the bay (Nakatani, 1988). It should be important for juvenile survival to grow enough to be able to feed on the large sized calanoid copepods such as *N. plumchrus*, *N. cristatus*, and *Eucalanus bungii*. Because of the ontogenetic vertical migration of juvenile pollock, the suitable temperature conditions and the food availability should be maintained. After late summer, juvenile pollock migrated to the bottom area in the shelf region outside of the bay where adults were abundant (bottom depth about 300 m depth). Maeda et al. (1983) observed that cannibalism occurred in this area. Koyama (2007) indicated that juvenile pollock that hatched in the late hatching period in March grow faster than that hatched in January and February. Namely, it can be considered that the small juveniles that hatched in late March were consumed selectively by adult pollock in summer in the shelf region outside of the bay. Furthermore, the low growth rate from larvae to juveniles might accelerate the adult cannibalism which may produce the poor year class strength. The author recognizes this as a "second critical period" for the walleye pollock Pacific population. After settlement, it is assumed that they distribute widely from the mouth region of the bay to the eastern area of Hokkaido Island.

Year class strength, feeding success of larval pollock, and hydrographic conditions

Fig. 9 shows the annual fluctuation from 1982 to 2003 of the year class strength of the walleye pollock Pacific population derived from a virtual population analysis (tuning VPA; Yabuki and Honda, 2004). In recent years, strong year classes occurred in 1991, 1994, 1995, and 2000. The other years were relatively stable.

It is considered that warm surface water in Funka Bay increases the survival rates during the early life stages of the walleye pollock Pacific population and subsequent year classes (Isoda et al., 1998; Funamoto, 2007). Nakatani et al. (2003a) suggested that a high density of copepod nauplii does not always determine the year class strength in this area. To examine the annual change of the hydrographic conditions in winter from 1991 to 2003, the surface temperatures and salinity (15 m depth) in late January, when newly hatching pollock larvae were abundant, have been observed (Fig. 10; Nakatani, 2008). Judging from the low salinity of 33.0–33.3, OCW was observed in late January in Funka Bay in 1993, 1998, and 2002. In 1996, hydrographic observations were restricted in the bay mouth, and OCW was observed at all stations. In other years, TWW remained in the bay, and the intrusion of OCW was not observed. Therefore, the strong year classes occurred in years of OCW late intrusions. Recently, the strong year class was confirmed in 2005, and OCW was not found in mid February. Thus, late invasion of OCW is important for the production of the strong year class. In Funka Bay in winter, the OCW intrusion decreases the surface temperature. To compare the feeding activity of pollock larvae in OCW and TWW, the feeding successes of larval pollock at the first feeding stage in OCW, TWW, and mixing region were examined in winter, 2015 (Nakatani and Tamura, submitted). As shown in Fig. 11, TWW occupied the bay and temperature ranged from 5.0 to 6.0°C in late January 2015. In this period, the feeding success of pollock larvae was as high as 81%. The density of copepod nauplii,

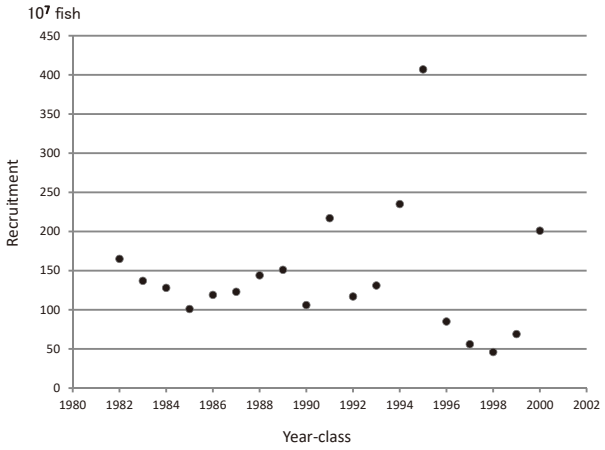

Fig. 9. The year class strengths of the walleye pollock Pacific population derived from virtual population analysis (tuning VPA) from 1981 to 2003. (from Yabuki and Honda, 2004)

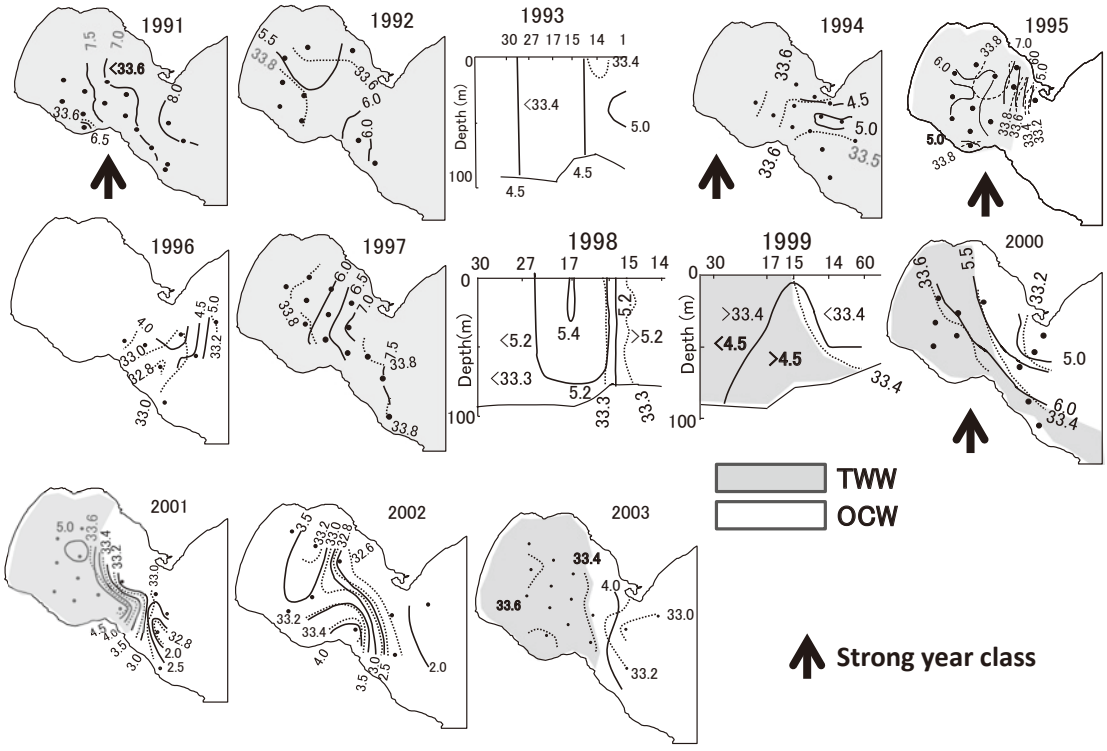

Fig. 10. Horizontal distributions of temperature (——°C) and salinity (- - - - -) at 15 m depth in late January from 1991 to 2003. (from Nakatani et al., 2007)

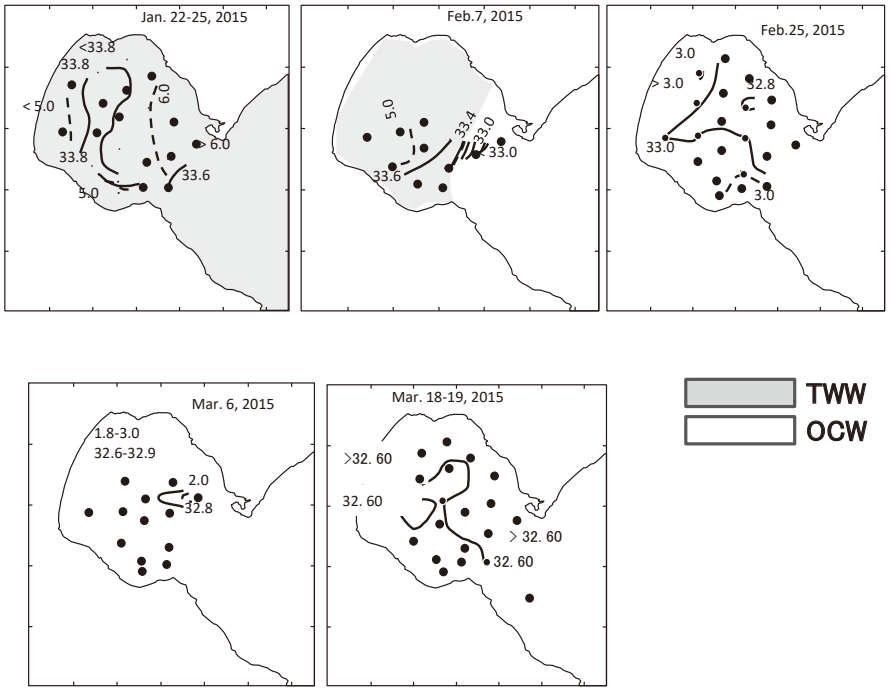

Fig. 11. Horizontal distributions of temperature (——°C) and salinity (- - - -) at 15 m depth in winter 2015. (from Nakatani and Tamura, submitted)

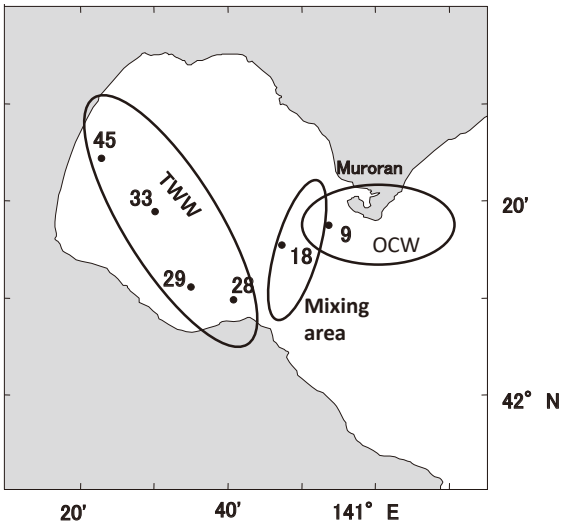

Fig. 12. Sampling stations of pollock larvae collected by vertical hauls from the sea bottom to the surface with a plankton net in Tsugaru Warm Water (TWW), Oyashio Coastal Water (OCW) and the mixing area in Funka Bay on 7 February, 2015. (from Nakatani and Tamura, submitted)

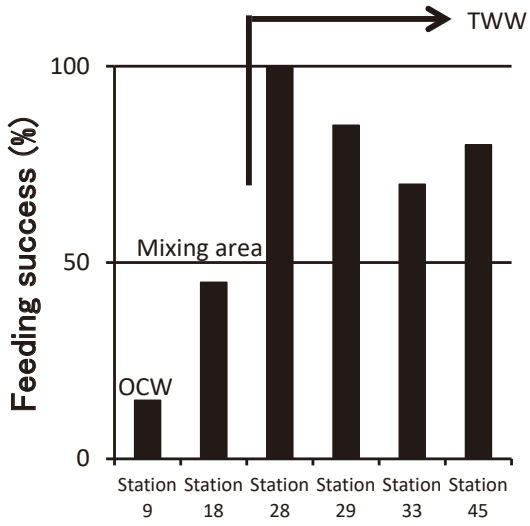

Fig. 13. Feeding success of walleye pollock larvae at the first feeding stage collected in Tsugaru Warm Water, Oyashio Coastal Water, and the mixing area at the bay mouth on 7 February, 2015. (from Nakatani and Tamura, submitted) Feeding success (%) = (individual number of larvae with food) ∗ 100/(number of larvae exmined)

temperature and salinity at 15 m depth were 6.8 –13.9 · L^{-1}, 4.9 – 5.8°C, and 33.75–33.82 , respectively. On 7 February 2015, OCW was found at the bay mouth off Muroran, while TWW remained in the bay. A front between two water masses formed at the bay mouth. In this period, the feeding success of pollock larvae collected in OCW (Stn. 9, see in Fig. 12), TWW (Stns. 28, 29, 33, and 45), and the mixing area (Stn. 18) were examined (Fig. 13). A minimum feeding success for larvae collected in OCW was 15%. At this station, a density of copepod nauplii, temperature, and salinity were 17.3 · L^{-1}, 2.3°C, and 32.81, respectively. In contrast, the feeding success in TWW ranged from 70 to 100%. In TWW, a density of copepod nauplii, temperature, and salinity at 15 m depth were 7.0 – 13.2 · L^{-1}, 4.2 – 5.1°C, and 33.50 –

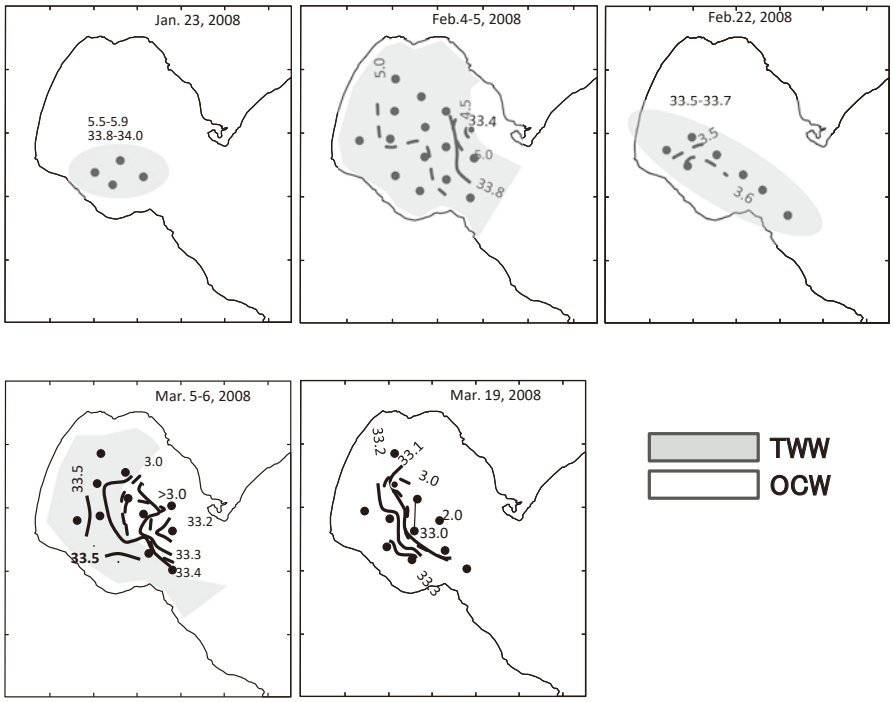

Fig. 14. Horizontal distributions of temperature (——— °C) and salinity (- - - - -) at 15 m depth in winter 2008. (from Nakatani and Tamura, submitted)

33.70, respectively. In the mixing area, intermediate values were observed (feeding success: 45%; naupliar density: 12.5 · L^{-1}; temperature: 3.3°C; and salinity: 33.04). The feeding success differed significantly (ANOVA, p<0.001). In spite of low density of copepod nauplii, high feeding successes were observed in the bay, where warm TWW occurred. After late February, OCW occupied the whole bay, and temperatures were below 3°C. Judging from the feeding success and the hydrographic conditions, the feeding success of pollock larvae should be high in TWW in the bay. Therefore, annual change in the stagnation period by TWW might control the survival of larval pollock. After invasion of OCW, it is considered that the feeding success decreases. In 1991, 1994, 1995, and 2000, it is considered that the strong year classes were produced by the high feeding success of larval pollock at the first feeding stage in the bay occupied by TWW.

In the surface layer of Funka Bay in winter, larvae of walleye pollock and flathead flounder, *Hippoglossoides dubius* are distributed at the same time and their niches likely overlap because of the occurrence period, horizontal and vertical distributions, and food organisms at the first feeding stage. Recently, strong year classes of flathead flounder were observed in 1991, 1995, 2003, and 2008. In late January, 2003, OCW restricted at the mouth region showing a late invasion. However, TWW temperature was as low as 4.0°C. In this year, the year class of the walleye pollock Pacific population was not strong. The relationship between the feeding successes and temperature of the two species may be different. Therefore, laboratory experiments on the feeding successes of larval pollock and flathead flounder are needed. In winter, 2008, the strong class of the flathead Funka Bay popularion was produced. The temperature was 5.0°C and a delayed intrusion of OCW was observed (Fig. 14). From the comparison of the year when the strong year classes of two species were produced, the late invasion of OCW and the area of TWW in Funka Bay should affect the feeding success of fish larvae. Strong year classes occurred for both species in 1991 and 1995, and pollock in 2000, and flathead flounder in 2003 and 2008. Such an asynchrony may indicate a difference of survival strategy after juveniles between pollock and flathead flounder in Funka Bay. With growth, the main food of pollock larvae and juveniles change to calanoid copepods such as *Pseudocalanus newmanii*, *Neocalanus* spp. and *Eucalanus bungii* (Kamba, 1977; Nakatani and Maeda, 1987). The biological production of these calanoid copepods might be controled by the primary production from late winter through early spring after OCW enters in the bay. The activity of the spring bloom and the hydrographic conditions of OCW were considered closely related. Furthermore, an increase of carnivorous plankton such as euphausiids (Bailey et al., 1993), hyperiids, and sagittoids in OCW was observed in the bay (Fujikawa, unpublished data). Therefore, annual fluctuation of the behavior of OCW is a complex factor affecting the year class strength of the walleye pollock Pacific population and the flathead Funka Bay population.

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