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Vertical Distribution and Prey of Walleye Pollock in the Northern Japan Sea

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Vertical distributions of adult walleye pollock *Theragra chalcogramma* and oceanographic conditions were examined in the northern Japan Sea. In the daytime, most walleye pollock were distributed from 150 to 250 m depth in April and from 400 to 500 m depth in October. Between 150 and 500 m depth, temperatures in October (0.4–8.8°C) were similar to those in April (0.5–5.4°C), salinity levels were fairly uniform in both months (34.0–34.2 PSU), and dissolved oxygen concentrations were 4.6–6.1 m*l*/*l* in April and 4.7–6.4 m*l*/*l* in October. The main foods of walleye pollock in April were the amphipod *Themisto japonica*, the euphausiid *Thysanoessa longipes*, and the chaetognath *Sagitta elegans*. Daytime weighted mean depths of *T. longipes* were significantly greater in October than in April. Biomass of *T. longipes* in the habitat of walleye pollock was significantly greater than other layers in both months. The seasonal change in vertical distribution of walleye pollock is presumably related to food availability of *T. longipes*.

Key words: walleye pollock, vertical distribution, *Themisto japonica*, *Thysanoessa longipes*, *Sagitta elegans*, Japan Sea

Adult walleye pollock *Theragra chalcogramma* migrate to off the southwestern coast of Hokkaido in October,[1] and spawn from December to March.[2] Thereafter they diffuse horizontally for feeding in the Japan Sea.[3] The spawning school is epi- and mesopelagic, and caught by long-line commercially in the midwater as an important fisheries resources off the southwestern coast of Hokkaido. Walleye pollock population in the northern Japan Sea show a slower growth pattern than that in the other areas around Hokkaido.[*1] Ishida[4] also described that the population in the northern Japan Sea grew slower than in the southwestern Okhotsk Sea. Fish growth is affected by many factors, including water temperature, food condition, and concentration of dissolved oxygen.[5] Walleye pollock inhabited the 150–250 m depth in April,[3] and 400–500 m depth (relatively cold water) in October off the southwestern coast of Hokkaido.[1] Kooka *et al.*[6] revealed that the main food items of walleye pollock off the southwestern coast of Hokkaido were the amphipod (*Themisto japonica*), the euphausiid (*Thysanoessa longipes*), and the chaetognath (mostly *Sagitta elegans*). However, relationship of vertical distributions between walleye pollock and their prey has never been investigated in this area. In this paper, the vertical distributions of walleye pollock and their prey, and abiotic environment in the northern Japan Sea are examined in April (initial phase of feeding period) and October (final phase of feeding period).

Materials and Methods

Field Samplings

Samples were collected on five cruises of the T/S Oshoro Maru (in April) and T/S Hokusei Maru (in October) of Hokkaido University between 1994 and 1996 in the northern Japan Sea (Fig. 1). The vertical distribution of adult walleye pollock was recorded acoustically with a 24 kHz Kaijo echo sounder (model R-41). To identify species

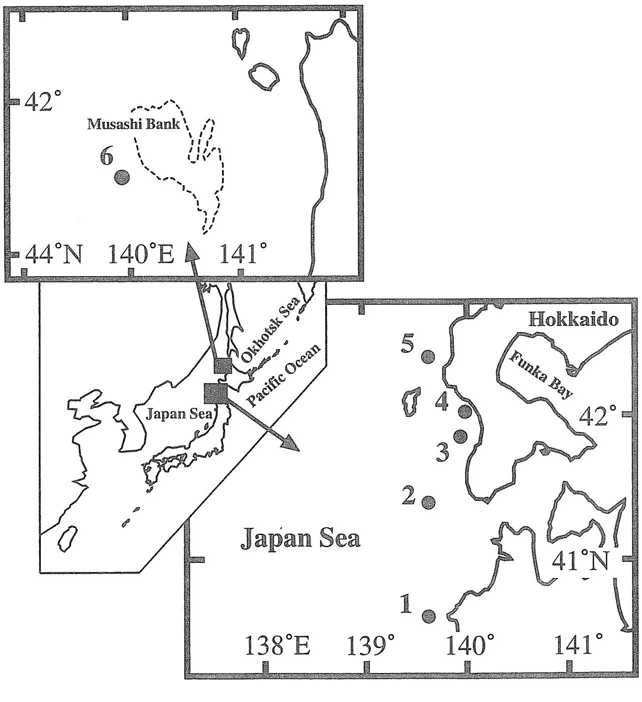

Fig. 1. Study area and sampling stations in the northern Japan Sea.

[*1] Hokkaido Fish. Exp. Stn.: Fisheries resources in the water around Hokkaido, pp. 44–53 (1990) (in Japanese).

Table 1. Data on samplings of zooplankton with MTD nets and stomachs of walleye pollock in the northern Japan Sea

Station number	Depth (m)	Date	Sampling layer (m)	DN[*1]	Trawl[*2]	DVM[*3]	WMD[*4]	Bio[*5]
1	1,650	12 Oct. 1995	Surface, 50, 75, 100, 200, 300, 450, 600, 700, 800	DN	√	√	√	√
2	1,000	11, 13 Oct. 1995	Surface, 50, 75, 100, 200, 300, 450, 600, 700	DN	√	√	√	√
3	1,309	6 Apr. 1994	15, 30, 75, 130, 230, 330	DN	√	√	√	
		6 Apr. 1995	10, 100, 200, 300, 500	D	√		√	√
		24 Oct. 1994	10, 50, 100, 200, 300, 425, 550	DN		√	√	√
4	1,120	5, 6 Apr. 1995	10, 80, 180, 280, 380, 480	DN	√	√	√	√
		21, 24 Oct. 1994	10, 50, 100, 200, 300, 425, 550	DN	√	√	√	√
		14 Oct. 1995	Surface, 10, 50, 75, 100, 200, 300, 450, 600, 700	DN	√	√	√	√
		3, 4 Apr. 1996	Surface, 150, 200, 250, 350, 450	DN	√	√	√	√
5	1,428	1 Oct. 1995	Surface, 10, 50, 75, 100, 200, 300, 450, 600, 700	N	√			
6	809	27 Aug. 1996			√			

[*1] DN, D, and N represented samples were collected daytime and nighttime, only daytime, and only nighttime, respectively.
[*2] Stomach contents analysis of walleye pollock.
[*3] Comparison of *WMD* of three prey zooplankton between daytime and nighttime.
[*4] Comparison of daytime *WMD* of three prey zooplankton between April and October.
[*5] Comparison of biomass of three prey zooplankton between 150–250 m and 400–500 m depth.
Check represented data were used for each analysis.

recorded on the echogram, an otter trawl net was towed in the center of the main scattering zone for 1 or 2 hours at 3–3.5 knots. All fishes were identified and counted on board, and walleye pollock were frozen immediately. Zooplankton collections were made with MTD closing nets[7)] (56 cm mouth diameter, 0.33 mm mesh) during day-night series and a non-closing beam trawl net[8)] (2.0 × 2.5 m mouth, 13 mm mesh, and 0.508 mm cod-end mesh) during the day. MTD nets were towed horizontally for 15–60 minutes at approximately 2 knots in 6–10 different strata. The volume of water filtered was measured with a flowmeter mounted on each MTD net ring, and tow depths were estimated from the wire length and angle. The beam trawl net was towed horizontally for 20 or 30 minutes at approximately 3 knots in the same strata that samplings for walleye pollock were conducted with an otter trawl net. The depth of tow was observed with a Kaijyo Net Monitor. At each sampling station, towing of MTD nets and beam trawl net were not replicated. Samples were fixed in 5% buffered formalin/seawater solution. Zooplankton sampling procedures are summarized in Table 1. Temperature, salinity, and dissolved oxygen were measured with a Neil Brown CTD-system. In addition, adult walleye pollock collected with an otter trawl net in the 410–440 m depth by Hokkaido Fisheries Experimental Station on a cruise in August were used for stomach contents analysis (Sta. 6, Fig. 1).

Laboratory Measurements

For analysis of stomach contents, 214 adult walleye pollock stomachs (20–30 stomachs from each station, Table 1) were examined under a microscope. Stomach contents were sorted to the lowest possible taxonomic level, counted, and weighed to the nearest 1 mg. Frequency of occurrence (F%) and percent by wet weight (W%) were calculated, and F% and W% were weighted by relative abundance (number of individuals/hour) at each sampling station on each cruise. The fork length of analyzed fish was 396.7 ± 38.3 mm (mean ± SD). To evaluate feeding intensity, *SCI* (stomach contents wet weight/fish body wet weight × 100) of each walleye pollock was calculated for station 4 where the highest relative abundance was observed on each cruise. Fish body wet weight contained the stomach contents wet weight. Chesson's feeding selectivity index (α_i)[9)] was calculated as $\alpha_i = (r_i/p_i)/\Sigma(r_i/p_i)$, where r_i is proportion by number of prey type i in the diet and p_i is proportion by number in the environment. Calculation of p_i for zooplankton prey was based on beam trawl net samples. Nine prey categories were used to estimate feeding selectivity. Accordingly, the selectivity index value of neutral selection is $1/9 = 0.11$. The body size (*T. japonica* in BL: from the head to the end of the uropod; *T. longipes* in TL: from the rostrum to the end of the telson; *S. elegans* in BL: from the head to the end of the tail) of broken food items was estimated by regression equations that converted the size of several parts of each species into the body size (Table 2). Body size and several body parts of subsamples of the three species were measured to the nearest 0.1 and 0.05 mm, respectively.

Table 2. Regression equations to estimate the body length of each prey items for walleye pollock

Species name	Equation	
Themisto japonica	$BL = 10.29P3 + 1.196$	$(N = 70,\ R^2 = 0.92)$
Thysanoessa longipes	$TL = 13.42ED - 4.886$	$(N = 60,\ R^2 = 0.96)$
Sagitta elegans	$BL = 17.42Hk + 2.949$	$(N = 64,\ R^2 = 0.96)$

P3: Length of third pereon, *ED*: Eye Diameter, *Hk*: Maximam hook length.

The three zooplankton prey collected with MTD nets (*T. japonica*, *T. longipes*, *S. elegans*) were sorted and counted. Body sizes of three zooplankton prey were measured to the nearest 5 mm. Individual wet weight of three zooplankton prey in April (150–250 m depth) and October (400–500 m depth) was measured to the nearest 1 mg. The biomass of three zooplankton prey were expressed as wet weight (g)·1,000 m^{-3}. The weighted mean depth (WMD)[10,11] of the three zooplankton species was calculated as $WMD = \Sigma n_i d_i / \Sigma n_i$, where n_i is the abundance (individuals·1,000 m^{-3}) at depth d_i (m).

Statistical Analyses of Zooplankton Prey Data

Differences in the vertical distributions of zooplankton prey between daytime and nighttime were tested by paired *t*-tests to determine if diel vertical migration (DVM) occurred. Differences in the daytime WMD between April and October were tested by the Mann-Whitney *U*-test. To compare biomass between 150–250 and 400–500 m depth, data were subjected to paired *t*-tests. Wet body weight per individual of zooplankton prey and *SCI* data of walleye pollock were analyzed by a one-way ANOVA. If mean wet body weight and *SCI* were significantly different, Scheffé's multiple comparison was conducted. *SCI* data of walleye pollock and wet weight data of zooplankton collected with MTD nets were log x-transformed to obtain uniform variances. In all statistical analyses, significant differences were established at $P < 0.05$.

Results

Abiotic Environment

In the 0–200 m layer, temperature, salinity, and dissolved oxygen levels in April were considerably different from those in October (Fig. 2). In contrast, measurements below 200 m were similar in both months. Temperatures between 150 and 250 m depth ranged from 1.6 to 5.4°C in April, and from 1.3 to 8.8°C in October. Temperatures between 400 and 500 m depth ranged from 0.5 to 1.1°C in April, and from 0.4 to 1.0°C in October. Below 150 m, salinity was fairly uniform (34.0 to 34.2 PSU) in both months. Concentrations of dissolved oxygen between 150 and 250 m depth ranged from 5.8 to 6.1 m*l*/*l* in April, and from 6.0 to 6.4 m*l*/*l* in October. Concentrations between 400 and 500 m depth ranged from 4.6 to 5.4 m*l*/*l* in April, and from 4.7 to 5.3 m*l*/*l* in October.

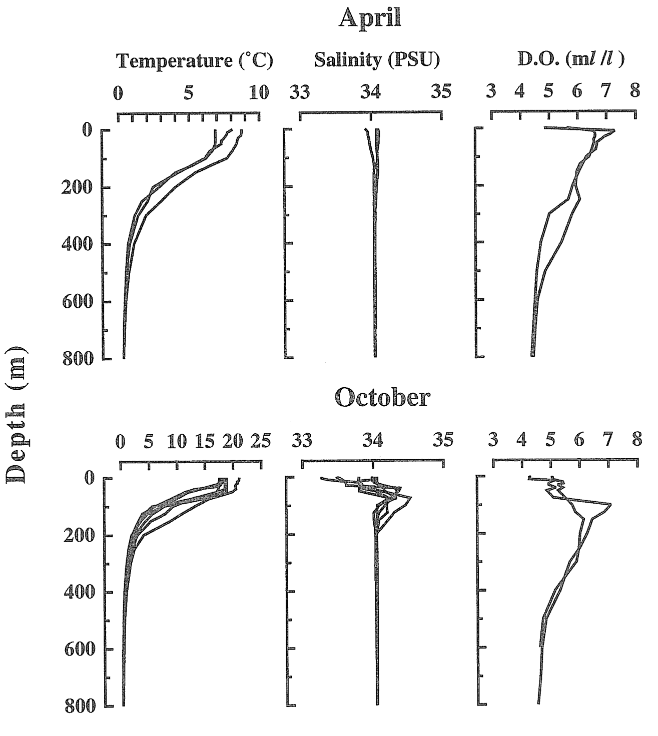

Fig. 2. Vertical profiles of water temperature, salinity, and dissolved oxygen in April and October.

Temperature and salinity: April: Stn. 3 (1994 & 1995) and Stn. 4 (1996) October: Stns. 1–5.

Dissolved oxygen: April: Stn. 3 (1994 & 1995) October: Stn. 3, 4 (1994).

Vertical Distribution of Walleye Pollock

Most acoustical targets were identified as walleye pollock, which comprised more than 99.6% of the fish collected with the midwater trawl at depths where strong acoustical images occurred. Other species collected included arabesque greenling *Pleurogrammus azonus*, smooth lumpsucker *Aptocyclus ventricosus*, and masu salmon *Oncorhynchus masou masou*. In the day, walleye pollock was chiefly distributed between 150 and 250 m depth in April, and between 400 and 500 m depth in October (Fig. 3). Mean towing depths (±SD) of midwater trawl net were 203±14 m in April and 430±14 m in October. Day-night vertical distribution patterns of walleye pollock in April were slightly different from those in October. At night, the acoustic scattering layers diffused both upward and downward in April, while those in October diffused only upward. However, the depth range of the main strong scattering zone was nearly the same both day and night. These results are similar to those of previous studies.[1,3)]

Stomach Contents and Feeding Selectivity of Walleye Pollock

In April 1995, *T. japonica* (29.1% by weight), *Neocalanus cristatus* (24.7%), *T. longipes* (19.8%), and chaetognaths (19.6%) dominated the diet of walleye pollock

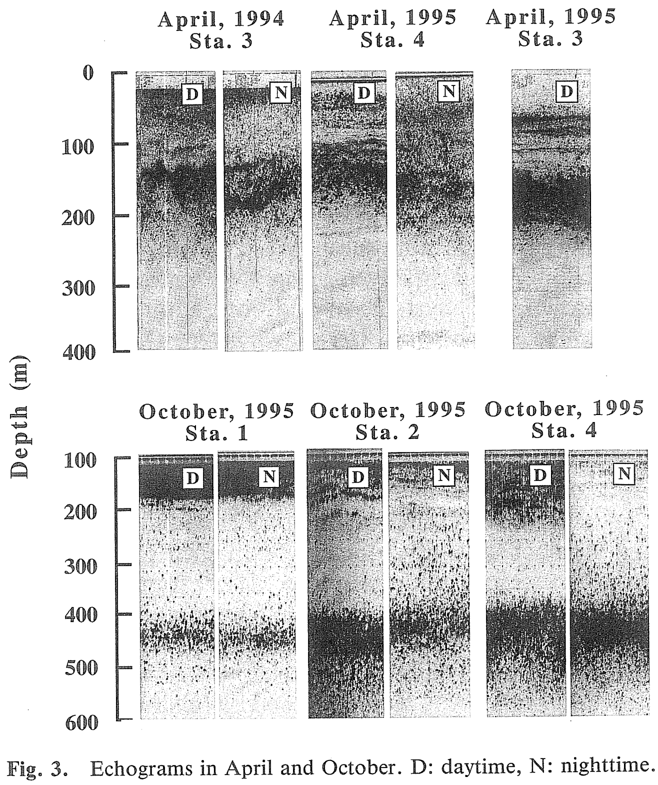

Fig. 3. Echograms in April and October. D: daytime, N: nighttime.

Table 3. Overall diet* of walleye pollock collected with midwater trawl in the northern Japan Sea

Prey	October 1994		April 1995		October 1995		April 1996		August 1996	
	F%	W%	F%	W%	F%	W%	F%	W%	F%	W%
CRUSTACEA										
Amphipoda										
Themisto japonica	23.3	13.1	96.5	29.1	78.3	30.0	55.0	0.9	100.0	18.0
Primno abyssalis	36.7	22.1	29.4	2.6	43.3	11.7	10.0	1.2	100.0	18.5
Euphausiacea										
Euphausia pacifica	10.0	13.1	6.5	0.6	23.0	8.9	30.0	4.4	41.7	16.8
Thysanoessa longipes	6.7	7.3	82.9	19.8	16.6	13.4	10.0	4.8	50.0	21.5
Thysanoessa inermis	3.3	10.4	3.6	0.6	6.5	11.3	70.0	70.9	12.5	5.4
Mysidacea										
Meterythrops microphtalma	6.7	7.7	17.9	0.6	28.0	5.5	20.0	2.1	62.5	0.8
Calanoida										
Neocalanus cristatus	6.7	0.2	87.9	24.7	2.7	0.1	45.0	2.1	33.3	0.3
Pareuchaeta japonica	23.3	14.4	48.7	1.6	55.3	15.4	50.0	3.1	100.0	10.1
Metridia pacifica	10.0	<0.1	5.6	<0.1	19.8	<0.1	35.0	0.1	37.5	0.1
CHAETOGNATHA										
Sagittoidea	0.0	0.0	83.4	19.6	5.2	0.3	50.0	8.7	45.8	1.3
Other prey	16.7	11.6	51.3	0.9	42.5	3.5	15.0	1.7	91.7	7.2
Number of stomachs examined	30		40		100		20		24	

* Data on April 1995 and October 1995 were weighted by the relative abundance of each sampling station. F%: frequency of occurence, W%: percent by weight.

Table 4. Feeding selectivity of walleye pollock collected with midwater trawl in the northern Japan Sea

Prey	Chesson's α			
	April 1994	April 1995	October 1994	October 1995
CRUSTACEA				
Amphipoda				
Themisto japonica	0.31	0.39	0.50	0.18
Primno abyssalis	0.01	0.20	0.047	0.073
Euphausiacea				
Euphausia pacifica	0.008	0.009	0.001	0.099
Thysanoessa longipes	0.62	0.11	0.001	0.059
Mysidacea				
Meterythrops microphtalma	<0.001	<0.001	0.43	0.22
Calanoida				
Neocalanus cristatus	0.030	0.23	0.00	0.00
Pareuchaeta japonica	0.009	0.011	0.012	0.080
Metridia pacifica	<0.001	0.001	<0.001	0.002
CHAETOGNATHA				
Sagittoidea	0.012	0.024	<0.001	0.007
α-value of neutral selection	0.11			

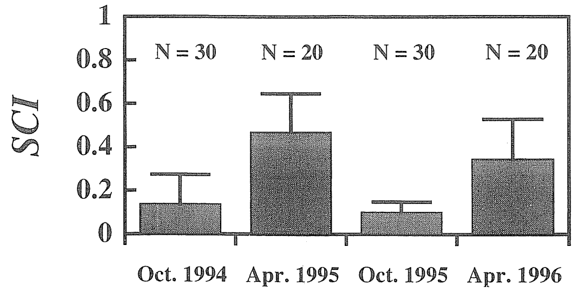

Fig. 4. Mean *SCI* of walleye pollock at station 4 in April 1995-96 and October 1994-95.
Error bars represent standard deveation.

(Table 3). In April 1996, *Thysanoessa inermis* dominated (70.9%) and followed by chaetognaths (8.7%). In October 1994, *Primno abyssalis* (22.1%), *Pareuchaeta japonica* (14.4%), *T. japonica* (13.1%), and *Euphausia pacifica* (13.1%) dominated the diet. In October 1995, *T. japonica* (30.0%), *P. japonica* (15.4%), and *T. longipes* (13.4%) dominated the diet. In August 1996, *T. longipes* (21.5%), *P. abyssalis* (18.5%), *T. japonica* (18.0%), and *E. pacifica* (16.8%) dominated the diet near the Musashi Bank (Sta. 6). Mean values of *SCI* were significantly different among four cruises ($P<0.0001$, Fig. 4). Multiple comparison indicated that mean values of *SCI* in April were significantly higher than those in October ($P<0.0001$). *T. japonica* was positively selected by walleye pollock in both months (Table 4). *T. longipes* was actively selected or neutrally selected in April, but did not selected in October. *P. abyssalis* and *N. cristatus* were selected in April 1995, while not selected in April 1994.

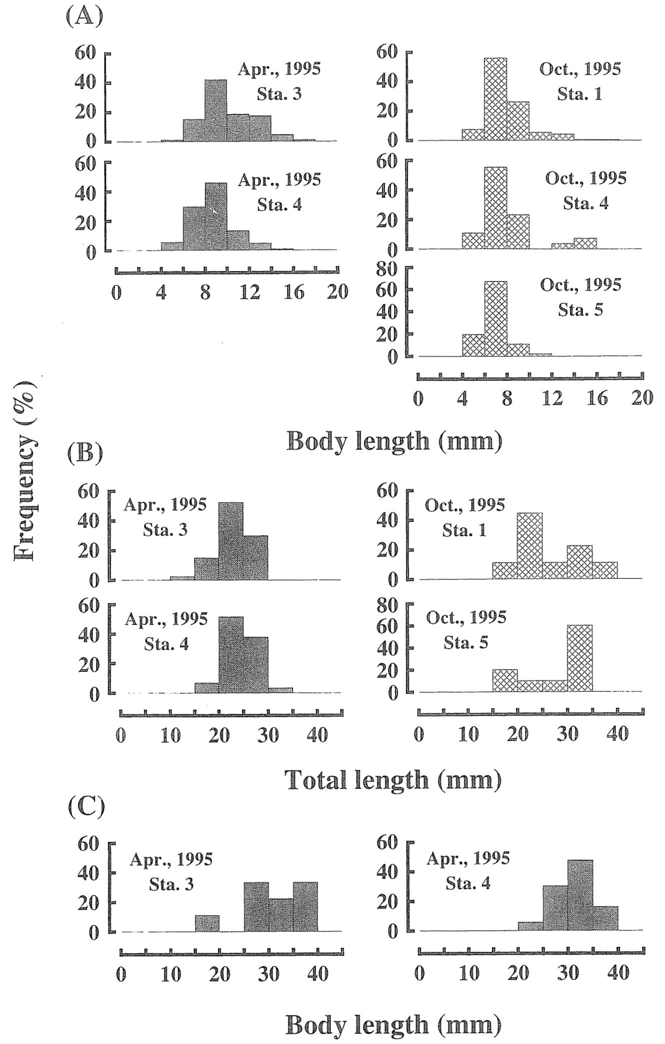

Fig. 5. Prey size distributions for stomach contents of walleye pollock estimated.

A: *Themisto japonica*; B: *Thysanoessa longipes*; C: *Sagitta elegans*.

Table 5. Comparison of mean biomass (g·1000 m^{-3}) between 150–250 and 400–500 m layer for each zooplankton prey collected with MTD nets during the day in October and April

Depth range (m)	Biomass (Mean±SD)		
	T. japonica	*T. longipes*	*S. elegans*
April			
150–250 ($N=3$)	10.1±6.9	0.85±0.46	27.8±20.4
400–500 ($N=3$)	3.4±1.4	0.09±0.16	2.9±1.6
October			
150–250 ($N=5$)	7.1±13.8	0.04±0.07	5.0±6.7
400–500 ($N=5$)	6.1±4.2	1.3±1.0	7.4±6.8

Table 6. Comparison of individual wet weight (g) among three zooplankton prey in the habitat of walleye pollock (150–250 m in April and 400–500 m in October)

	Individual wet weight (Mean±SD)		
	T. japonica	*T. longipes*	*S. elegans*
April	0.007±0.005, $N=250$	0.063±0.026, $N=19$	0.051±0.019, $N=120$
October	0.009±0.010, $N=248$	0.076±0.051, $N=24$	0.033±0.020, $N=131$

Vertical Distributions of Zooplankton Prey for Walleye Pollock

Walleye pollock fed on *T. japonica* (4.3–17.2 mm in BL), *T. longipes* (14.6–38.1 mm in TL), and *S. elegans* (19.5–37.8 mm in BL, Fig. 5). The percentage of *T. japonica*≥5 mm, *T. longipes*≥15 mm, and *S. elegans*≥20 mm to the total number of each species in the stomach contents were 93.5–100%, 97.5–100%, and 88.9–100%, respectively. Vertical distribution patterns of zooplankton prey sampled with MTD nets were different between April and October (Fig. 6). The daytime *WMD* of *T. japonica*≥5 mm was between 200 and 264 m in April, and between 209 and 592 m in October. The daytime *WMD* of *T. japonica* tended to be greater in October than in April, but the difference was not significant (P-value was just 0.05). The daytime *WMD* of *T. longipes*≥15 mm was between 164 and 282 m in April, and between 346 and 618 m in October. The daytime *WMD* of *S. elegans*≥20 mm was between 172 and 283 m in April, and between 310 and 524 m in October. The daytime *WMD* of *T. longipes* and *S. elegans* were significantly greater in October than in April ($P=0.014$, in both species).

The nighttime *WMD* of *T. japonica*≥5 mm was between 131 and 246 m in April, and between 75 and 418 m in October. The difference between daytime and nighttime *WMD* for *T. japonica* was not significant in April ($P=0.12$), and was significant in October ($P=0.024$). The nighttime *WMD* of *T. longipes*≥15 mm was between 86 and 233 m in April, and between 189 and 370 m in October. The difference between daytime and nighttime *WMD* for *T. longipes* was not significant in April ($P=0.26$), and was significant in October ($P=0.030$). The nighttime *WMD* of *S. elegans*≥20 mm was between 121 and 302 m in April, and between 333 and 605 m in October. There were no significant differences between daytime and nighttime *WMD* for *S. elegans* in April ($P=0.80$) and October ($P=0.82$). In both daytime and nighttime, *T. japonica*<5 mm, *T. longipes*<15 mm, and *S. elegans*<20 mm were abundant in the top 10, 80, and 10 m depth layers, respectively, in April, and in the top 100 m depth layer in October.

Biomass and Individual Body Weight of Zooplankton Prey for Walleye Pollock

Although mean biomass (wet weight·1,000 m^{-3}) of *T. longipes* were significantly greater in the 150–250 m layer than the 400–500 m layer in April ($P=0.0092$, Table 5), no difference occurred between the layers for *T. japonica* or *S. elegans* ($P=0.12$ and 0.091, respectively). In October, the biomass of *T. longipes* was significantly greater in the 400–500 m layer than the 150–250 m layer ($P=0.031$). No difference in biomass occurred between the layers for *T. japonica* or *S. elegans* ($P=0.47$ and 0.18, respectively). Mean wet weight per individual of the three zooplankton prey in the habitat of walleye pollock were significantly different in both months ($P<0.0001$, Table 6). The results of multiple comparison indicated no significant difference

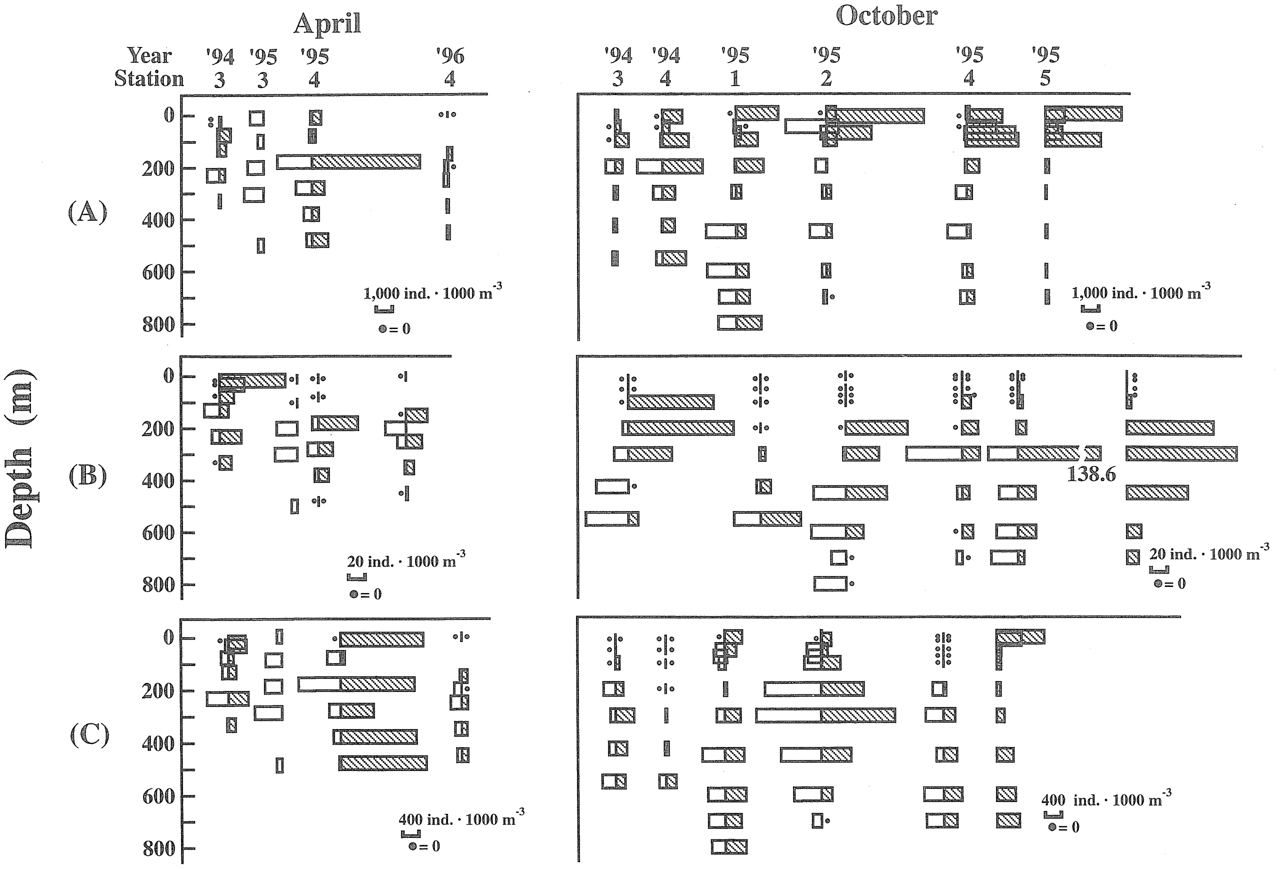

Fig. 6. Vertical distributions of zooplankton prey collected in daytime (open bars) and nighttime (shaded bars) with MTD nets in April and October. A: *Themisto japonica* ≥ 5 mm; B *Thysanoessa longipes* ≥ 15 mm; C: *Sagitta elegans* ≥ 20 mm.

of mean wet weight per individual between *T. longipes* and *S. elegans* in April ($P = 0.35$), significant differences between other pair-wise combinations in April ($P < 0.0001$), and significant difference between all pair-wise combinations in October ($P < 0.0001$).

Discussions

Previous studies have shown that walleye pollock feed from morning to evening in the North Pacific off Hokkaido,[12] continuously through the day and most actively at about sunset in the central Bering Sea,[13] and actively during the daytime in the eastern Bering Sea.[*2]

T. japonica and *T. longipes* showed DVM behavior in October (Fig. 6), while DVM behavior of walleye pollock was restricted to a small portion of schools (vertical migration distance: 50–200 m, Fig. 3) in both months. Both the presence[14] and absence[15,16] of DVM behavior for adult walleye pollock have been reported. DVM behavior of juvenile walleye pollock is well-known.[15,17–19] Bailey[15] suggested that DVM of age-0 pollock is related to food availability. If walleye pollock feed on zooplankton during the night, most of the pollock are expected to migrate upward during the night. Such vertical migration, however, was not recognized during continuous echogram observations. Thus, walleye pollock that remain in the same depth layer during the day and night presumably are visual predators during the daytime.

Walleye pollock were distributed deeper in October than in April (Fig. 3). Fish migration might be affected by various oceanographic conditions. Uda[20] reported that suitable ambient temperatures of walleye pollock range from 1 to 8°C. Other reports have shown that ambient temperature of walleye pollock in different study areas are 2.0–4.0°C,[21] about 2.0–3.0°C,[22] 1.4–2.4°C,[23] and 0.0–1.0 °C.[24] In this study, temperatures between 150 and 500 m depth (0.5–8.8°C) should be suitable for walleye pollock in October (Fig. 2). In addition, temperatures between 150 and 250 m depth in October are similar to those in April. Salinities below 150 m were fairly uniform in both months. There are few data regarding preferred dissolved oxygen levels for walleye pollock. Okada[14] and Yoshida[25] described that dissolved oxygen concentrations in walleye pollock habitats were 1.0–3.0 and 6.0 m*l*/*l*, respectively. Furuta and Kimura[26] suggested that dissolved oxygen concentrations from 2.1 to 2.8 m*l*/*l* is the lower limit where fish can survive. Dissolved oxygen concentrations between 150 and 500 m depth in October (4.7–6.4 m*l*/*l*) are greater than this threshold level, and dissolved oxygen levels between 150 and 250 m depth in October are similar to those in April. These suggest that walleye pollock neither avoid unsuitable temperature, salinity, and dissolved oxygen lev-

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[*2] K. Mito: Food relationships among benthic fish populations in the Bering Sea. M. S. thesis, Hokkaido University, Hakodate, Japan, 1974, p. 135 (in Japanese).

els nor follow the isoclines of these oceanographic conditions.

On the other hand, the spawning period of walleye pollock is between December and March.[2)] The results of comparison of *SCI* indicated that feeding intensity of walleye pollock in April was greater than in October (Fig. 4). This is the same result as the previous investigation.[6)] Walleye pollock may feed actively to recover their body condition in April (after spawning), and feed inactively in October (before spawning). To clarify the correspondence of vertical distribution between walleye pollock and their prey, the kind and vertical distribution of the main prey in April should be investigated. In April 1995–96, *T. japonica*, *T. longipes*, *T. inermis*, *N. cristatus*, and chaetognaths were important foods (Table 3). We previously reported that *T. japonica* (18.9% by weight) and chaetognaths (49.2%) were important foods in April 1993, and *T. japonica* (12.3%) and *T. longipes* (69.7%) were important foods in April 1994.[6)] Because *T. inermis* and *N. cristatus* little occurred in the diet in April 1993–94, *T. japonica*, *T. longipes*, and chaetognaths (maybe *S. elegans*) were thought to be important foods in April. *T. japonica* and *T. longipes* were also important foods in summer. It seems likely that the importance of *T. longipes* declines in autumn, and *T. japonica* is consistently important through spring-autumn.

Daytime *WMD* between April and October and biomass between 150–250 m and 400–500 m depth in both months of *T. japonica* were not significantly different (Fig. 6, Table 5). Biomass of *S. elegans* was not significantly different in both months, whereas daytime *WMD* in October was significantly greater than those in April. In contrast, the daytime *WMD* of *T. longipes* in October was significantly greater than those in April. Biomass of *T. longipes* between 150–250 m depth was significantly greater than those between 400–500 m depth in April, and it was the other way round in October. These results indicated that the abundant layer of this species was deeper in October than in April. Vinogradov[27)] described that the most abundant layer (modal depth of vertical distribution) of *T. longipes* is in the 200–500 m layer during the day in the northern Japan Sea in June. In our study, the most abundant layer of this species during the day ranged from 130 to 300 m depth in April and from 300 to 600 m depth in October (Fig. 6). *T. longipes* may gradually move to deeper layers from spring to autumn. The seasonal change in vertical distribution of walleye pollock is presumably related to those of *T. longipes*.

Walleye pollock is selective for *T. japonica* and *T. longipes* in April, and for *T. japonica* not *T. longipes* in October (Table 4). Nishiyama[28)] showed that the caloric value per wet body weight of amphipods is about 25% of that of euphausiids. Percy and Fife[29)] reported that the caloric value per dry body weight of chaetognaths were greater than hyperiid amphipods. The mean wet body weight per individual of *T. longipes* and *S. elegans* were greater than *T. japonica* (Table 6). Therefore, containing energy of *T. longipes* and *S. elegans* per individual may be much greater than *T. japonica*, and feeding success of walleye pollock to *T. longipes* and *S. elegans* may bring about their greater energy gain. On-board observation of live specimens of *T. japonica* showed that they were highly visible due to many dark pigments on body surface and showed continuous swimming behaviour. *T. longipes* were relatively difficult to spot except for the eyes and they showed quick swimming behaviour as known for tail swimming. Then walleye pollock may have greater visibility and catchability for *T. japonica* than *T. longipes*. *S. elegans* was very difficult to spot using on-board observation. Fraser[30)] reported that *S. elegans* would be lost to view in the grass dish due to their great difficulty to spot and sudden darts. Negative feeding selectivity for *S. elegans* in spite of high caloric contents per individual may be affected by these characteristics of this species.

In conclusion, seasonal vertical migration of walleye pollock is interpreted as follows: After spawning, walleye pollock begin to feed actively on euphausiids for their recovery. Then, walleye pollock gradually move to deeper layer to feed on euphausiids during spring-summer, because euphausiids is also important food for walleye pollock in summer. But, feeding activity of walleye pollock declines in October, and they depend on amphipods which are easy prey for walleye pollock.

In the Japan Sea, walleye pollock grow more slowly than in the southwestern Okhotsk Sea, the coastal area of the Pacific Ocean, and the Nemuro strait.*[1] Cannibalism by walleye pollock occurs near Funka Bay,[31)] off the eastern coast of Hokkaido,[32)] and the eastern Bering Sea.[15,22,33)] In the southwestern Okhotsk Sea, where walleye pollock have a higher growth rate than in the northern Japan Sea,[2)] adult pollock feed exclusively on euphausiids, while immature pollock feed mainly on amphipods.[34)] Walleye pollock feed mainly on zooplankton, and do not consume fishes (including juvenile pollock) in this study area (this study and Kooka *et al.*[6)]). The low growth rate of walleye pollock in the northern Japan Sea might be affected by the vertical distribution pattern and food utilization. Seasonal variation of water temperature and zooplankton prey biomass in the habitat of walleye pollock are necessary for further research in the other waters around Hokkaido.

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References

1) T. Maeda, T. Nakatani, T. Takahashi, S. Takagi, Y. Kajihara, and T. Meguro: Migration of walleye pollock in the coastal waters of Japan Sea of southwestern Hokkaido. *Bull. Japan. Soc. Fish. Oceanigr.*, **53**, 38–43 (1989) (in Japanese).

2) T. Ishigaki: Where does the Alaska pollock (*Theragra chalcogramma* PALLAS) after spawning go to? *Hokusuishi Geppo*, **17**, 351–363 (1960) (in Japanese).

3) S. Takagi, T. Maeda, Y. Kamei, T. Nakatani, T. Takatsu, and T. Takahashi: Distribution of walleye pollock *Theragra chalcogramma* off southwestern Hokkaido in the Japan Sea in spring. *Nippon Suisan Gakkaishi*, **62**, 205–212 (1996).

4) T. Ishida: On the age determination and morphometrical differ-

ences of the otolith of Alaska pollock in the Hokkaido coast. *Bull. Hokkaido Natl. Fish. Res. Inst.*, **11**, 36–67 (1954) (in Japanese).

5) R. J. Wootton: Ecology of Teleost Fishes, 1st ed., Chapman and Hall, London, 1990, pp. 133–144.

6) K. Kooka, T. Takatsu, Y. Kamei, T. Nakatani, and T. Takahashi: Food habits of walleye pollock inhabiting the mesopelagic zone in the northern Japan Sea in spring and autumn. *Nippon Suisan Gakkaishi*, **63**, 537–541 (1997).

7) S. Motoda: Devices of sample plankton apparatus. V. *Bull. Fac. Fish. Hokkaido Univ.*, **22**, 101–106 (1971).

8) T. Nakatani: Sampling techniques for fish eggs, larvae and juveniles, and their food organisms. *Aquabiology*, **9**, 108–110 (1987) (in Japanese).

9) J. Chesson: Measuring preference in selective predation. *Ecology*, **59**, 211–215 (1978).

10) S. Pearre: Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology*, **54**, 300–314 (1973).

11) K. E. Osgood and B. W. Frost: Ontogenetic diel vertical migration behaviors of the marine planktonic copepods *Calanus pacificus* and *Metridia lucens. Mar. Ecol. Prog. Ser.*, **104**, 13–25 (1994).

12) M. Mikawa: Walleye pollock. Annual report on the fish resources in Oct. 1953–Sept. 1954. Section 4 Bottom fish., Tohoku Regional Fisheries Research Laboratory Hachinohe Branch, 1956, pp. 27–31 (in Japanese).

13) H. Yoshida: Food and feeding habits of pelagic walleye pollock in the central Bering Sea in summer, 1976–1980. *Sci. Rep. Hokkaido Fish. Exp. Stn.*, **45**, 1–35 (1994).

14) K. Okada: Biological characteristics and abundance of pelagic walleye pollock on the Aleutian Basin. *I. N. P. F. C. Bull.*, **45**, 150–176 (1986).

15) K. M. Bailey: Interaction between the vertical distribution of juvenile walleye pollock *Theregra chalcogramma* in the eastern Bering Sea, and cannibalism. *Mar. Ecol. Prog. Ser.*, **53**, 205–213 (1989).

16) T. Suzuki: Biological characteristics of the walleye pollock *Theragra chalcogramma* (Pallas) distributed at surface layer in the central area of the Bering Sea as observed by fish finder. *Bull. Fac. Fish. Hokkaido Univ.*, **27**, 137–144 (1976) (in Japanese).

17) R. D. Brodeur and M. T. Wilson: Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Can. J. Fish. Aquat. Sci.*, **53** 1951–1963 (1996).

18) R. D. Brodeur: A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fish. Oceanogr.*, **5**, 148–166 (1996).

19) T. Nakatani and T. Maeda: Distribution and movement of walleye pollock larvae *Theragra chalcogramma* in Funka Bay and adjacent waters, Hokkaido. *Nippon Suisan Gakkaishi*, **53**, 1585–1591 (1987).

20) M. Uda: A consideration on the long years trend of the fisheries fluctuation in relation to sea conditions. *Nippon Suisan Gakkaishi*, **23**, 368–372 (1957).

21) G. Swartzman, W. Stuetzle, K. Kulman, and M. Powojowski: Relation the distribution of pollock schools in the Bering Sea to environmental factors. *ICES J. mar. Sci.*, **51**, 481–492 (1994).

22) D. A. Dwyer, K. M. Bailey, and P. A. Livingston: Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. *Can. J. Fish. Aquat. Sci.*, **44**, 1972–1984 (1987).

23) K. Watanabe, K. Yabuki, T. Hamatsu, O. Yamamura: Distribution of walleye pollock *Theragra chalcogramma* along the coast of southern Hokkaido, in the early summer. *Bull. Hokkaido Natl. Fish. Res. Inst.*, **57**, 53–61 (1993) (in Japanese).

24) T. Maeda : Subpopulations and migration pattern of the Alaska pollock in the eastern Bering Sea. *Bull. Japan. Soc. Fish. Oceanogr.*, **19**, 15–32 (1971) (in Japanese).

25) H. Yoshida: Ecological study on pelagic walleye pollock in the Bering Sea in summer. Ph. D. thesis, University of Hokkaido, Hakodate, 1984, p. 202 (in Japanese).

26) Y. Furuta and S. Kimura: On the vertical distribution of fishes and limnological conditions in Lake Kizaki and Lake Nakatsuna in summer. *Bull. Freshwater Fish. Res. Lab.*, **19**, 103–111 (1969) (in Japanese).

27) M. E. Vinogradov and A. F. Sazhin: Vertical distribution of the major groups of zooplankton in the northern part of the Sea of Japan. *Oceanology*, **18**, 205–209 (1978).

28) T. Nishiyama: Energy requirement of Bristol Bay sockeye salmon in the central Bering Sea and Bristol Bay, in " Oceanography of the Bering Sea" (ed. by D. W. Hood and E. J. Kelley), Institute of Marine Science University of Alaska, Fairbanks, 1974, pp. 321–343.

29) J. A. Percy and F. J. Fife: Distribution of biomass and caloric energy in the macrozooplankton community of Frobisher Bay, N. W. T. *Can. Data Rep. Fish. Aquat. Sci.*, **387**, 1–42 (1983).

30) J. H. Fraser: Experimental feeding of some medusae and chaetognath. *J. Fish. Res. Bd. Canada*, **26**, 1743–1762 (1969).

31) T. Maeda, T. Takahashi, M. Ueno: Annual life period of the adult Alaska pollock in the adjacent waters of the Funka Bay, Hokkaido. *Nippon Suisan Gakkaishi*, **47**, 741–746 (1981).

32) O. Yamamura: Ecological study on demersal fish community off Sendai Bay, northern Japan, with special reference to niche dynamics among dominant fishes. Ph.D. thesis, University of Hokkaido, Hakodate, 1994, p. 245.

33) K. Bailey and J. Dunn: Spring and summer foods of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea. *Fish. Bull., U.S.*, **77**, 304–308 (1979).

34) U. Suzuki and K. Kuroshima: Investigation of walleye pollock in the southeast part of the Okhotsk Sea. *Hokusuishi Geppo*, **29**, 17–31 (1972) (in Japanese).