ISSN 0032-9452, Journal of Ichthyology, 2025, Vol. 65, No. 3, pp. 488–494. © Pleiades Publishing, Ltd., 2025.
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Mass Occurrence of Walleye Pollock *Gadus chalcogrammus* (Gadidae) in the Surface Layer of the Oyashio Basin (Western North Pacific): Possible Benefit from Abundant Copepods

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Received September 16, 2024; revised December 3, 2024; accepted December 5, 2024

Abstract—A total of 2999 individuals of walleye pollock *Gadus chalcogrammus* was caught by a surface trawling net covering the 0—ca. 30 m depth layer during May 2022, at two sites, 36 and 172 km off the southern coast of Hokkaido Island. The fact that no fish was caught at a station further south suggested that the pollock originated from the coastal area of Hokkaido Island rather than Honshu Island. Although the body length of the fish from both sites was similar, ranging ca. 35–45 cm standard length, fish condition differed significantly with fish from the southern (offshore) station having stouter bodies. Stomach contents analysis revealed that the fish from the southern station ingested 2.1 times more prey (measured as stomach contents index) consisting mainly of copepods (86% in dry weight) than those from the northern station. Because the southern station was in a more advanced condition of phytoplankton blooming, it has been suggested that the walleye pollock migrated south to utilize the abundant copepods in the surface layer during the blooming.

Keywords: migration, North Pacific Basin, body condition, blooming, copepods, *Neocalanus*

DOI: 10.1134/S0032945224602471

INTRODUCTION

Migration is the mass directional movement of a large number of species from one location to another (Begon et al., 2006). For marine fishes, such activities have different purposes, including spawning, wintering, summering, feeding etc. (Secor, 2015). In the temperate and subarctic areas, seasonality is pronounced, and the annual temperature range on the coastal shelf can exceed 15°C even in the bottom layer (Yamamura and Kooka, 2023). Such changes not only cause metabolic stress but also lead to large changes in food availability and interspecific interactions, with considerable effects on fish growth and survival. To avoid or utilize such fluctuations, fish sometimes undergo large-scale migrations (Beamish et al., 2005; Muhling et al., 2019).

Walleye pollock is distributed throughout the Subarctic North Pacific (Bakkala et al., 1986) and is one of the most important demersal fish both ecologically and commercially in the western Subarctic Pacific, including waters off northern Japan Archipelago (Masuda et al., 1984; Ikeda et al., 2008). It is prey for higher trophic levels (Tamura et al., 1998; Goto et al., 2017; Wang et al., 2022) and a driver of the ecosystem as a pivotal intermediate predator, having the potential to affect lower trophic levels through its feeding impact (Ciannelli et al., 2004; Yamamura, 2004). Along the Pacific coasts of Hokkaido Island, the known migration of walleye pollock was the eastward ontogenetic migration by pre-settlement juveniles beyond Cape Erimo (Honda et al., 2004).

In the present study, we report an unexpected mass occurrence of adult and subadult walleye pollock in the surface layer of the Oyashio Basin far offshore of the previously known limit of the species distribution and infer the factor of the migration using the stomach contents analysis and environmental measurements.

MATERIALS AND METHODS

The data used in the present study was obtained onboard T/S Oshoro-maru of Hokkaido University.

At each sampling station, water temperature, salinity, and fluorescence were measured at depths from ca. 30 m above the sea floor to 1 m below the sea surface using a conductivity-temperature-depth sensor (SBE 911 Plus, Sea-Bird Electronics, Bellevue) and a fluorometer (Sea-point Chlorophyll Fluorometer, Seapoint Sensors, Exeter). The fluorescence (unitless value) was summed for depths 5 to 150 m to assess the primary production at each station. Zooplankton samples were collected at each station by vertical tows

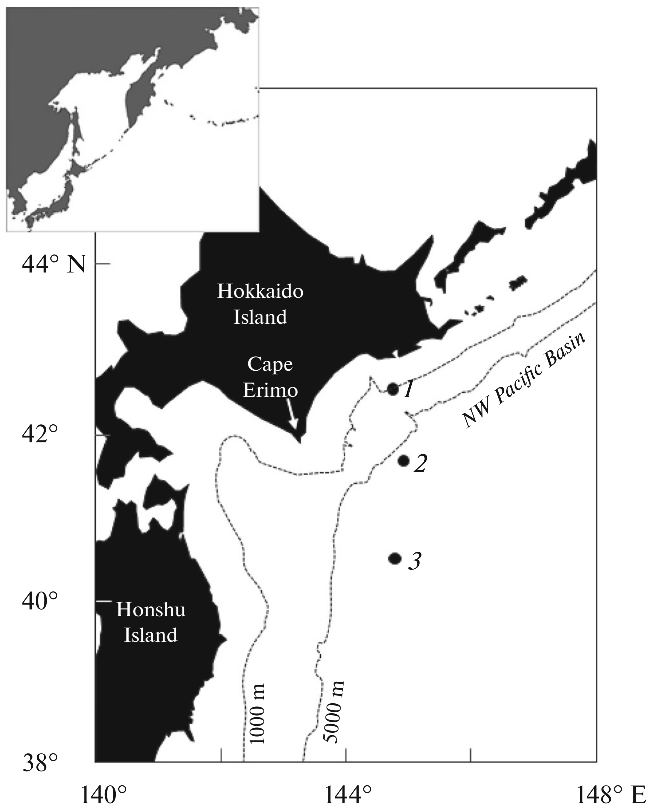

Fig. 1. Map showing sampling stations (*1–3*) in relation to the western North Pacific (inset).

of a NORPAC net attached with a flowmeter to a depth of 50 m. After fixation with 10% formaldehyde-seawater solution, they were sorted to the major taxonomic groups and were measured with wet weight. Of these, copepods were further classified into species level although *Neocalanus flemingeri* and *N. plumchrus* were treated as a species complex (*N. flemingeri/plumchrus*) because these species were not distinguishable without dissection in the C1 stage (Miller and Clemons, 1988) or detailed body measurements in the C2–C5 stages (Tsuda et al., 1999).

Nekton distributed in the surface layer was sampled at the three stations 36, 172, and 261 km from the nearest shoreline (Fig. 1, Table 1) using a surface trawling net (NST-340-SS, Nichimo Co. Ltd., Tokyo) with a head rope length of 41 m, a graded mesh of 15.2 m (net mouth)[1] to 45 mm (cod end), and attached with a cod end liner of 17.5 mm mesh. During the tow, the head rope was sustained on the sea surface by canvas kites and buoys. The vertical extent of the mouth opening was monitored using an acoustic sensor attached to the bottom of the mouth during each tow. The towing duration (from the time of wire-set to the time of commencing heaving in) was 1 h for each tow. The ship speed was targeted at 4 knots (7.4 km/h) but varied between 3.7–4.2 knots (6.9–7.8 km/h) according to towing conditions. The towing depth varied by station, and the bottom of the net mouth reached up to a maximum depth of 34 m. The average net depths (i.e. bottom of the net mouth) were 32.7, 24.0, and 34.3 m, respectively, for the three stations.

The trawling catches were identified, counted, and weighed for each species. A total of 60 individuals were randomly selected, and measured for standard length (*SL*) to the nearest mm and body weight (*BW*) to the nearest 5 g on board. Of these, 30 were dissected, and their stomachs were preserved in ethanol. The protocol of stomach contents identification followed that described in Yamamura et al. (2002). In the laboratory, stomachs were opened, and food items were sorted to the lowest possible taxon after removing excess water by suction. Each prey item was dried at 52°C in a drying oven for 24 h and in a desiccator for 36–48 h and then weighed to the nearest 1 mg.

The body condition of fish was assessed by Fulton's body condition index: $K = BW/SL^3 \times 10^6$. To reduce the effect of feeding conditions when comparing *K* by site, the average wet weight of stomach contents at each station was reduced from *BW* in the calculation. Fish diet was assessed by frequency of occurrence (*F*) and dry weight composition (*W*). The feeding intensity of fish at each station was assessed by stomach contents index ($SCI = SCW/BW \times 10^2$), where *SCW* indicates total wet weight of stomach contents for each individual.

RESULTS

Sea surface temperatures were comparable at 8.9 and 8.6°C at stations 1 and 2, respectively, whereas it raised to 12.6°C at station 3. Fluorescence (unitless value) was 95.9 and 159.7 at the first and second stations, respectively, while it showed a far lower value (16.1) at station 3 (Table 1). Zooplankton biomass showed a similar pattern to fluorescence with higher values at stations 1 and 2 (1.3 and 2.5 g/m^{-3}, respectively) and a lower value at station 3 (0.3 g/ m^{-3}) (Fig. 2). The highest biomass was recorded at station 2, but sampling appears to have been incomplete as the net was clogged with large amounts of diatoms. At this station, "other organisms," consisting of small copepods, appendicularians, and the gastropod *Limacina helicina*, made up >50% of the biomass. These organisms could not separate further because of either too small body sizes or sticky and mucous properties. Copepods was the most abundant taxa in stations 1 and 2, with densities of 0.75 and 0.53 g/m^{-3}, respectively. However, the biomass of copepods decreased rapidly at station 3 to 0.06. *Neocalanus plumchrus/flemingeri* (0.34 g/m^{-3}) was dominant in copepods at station 1 whereas *Eucalanus bungii* was dominant at stations 2 and 3 (0.20 and 0.04 g/m^{-3}, respectively).

[1] Author confirmed the specification of the net by a document provided from the manufacturer.

Table 1. List of sampling stations for T/S Oshoro-maru cruise May 2022 and measurements of environmental variables

Station	1	2	3
Date	23/05/2022	24/05/2022	25/05/2022
Time (LMT)	07:29–08:28	09:00–10:00	07:08–08:07
Latitude (N)	42°36′29″	41°41′48″	40°30′05″
Longitude (E)	144°25′34″	144°33′36″	144°27′36″
Distance from shore, km	35.7	171.7	261.0
Bottom depth, m	1873	5513	5985
Sea surface temperature, °C	8.9	8.6	12.6
Ship speed (average ± *SD*)	3.7 ± 0.3	4.2 ± 0.5	3.9 ± 0.4
Net depth (average ± *SD*)	28.1 ± 2.2	16.8 ± 1.9	18.8 ± 5.1
Net depth (min–max)	23.1–32.7	13.3–24.0	13.3–34.3
Fluorescence (unitless)	95.9	159.7	16.1
Zooplankton biomass, g/m^{-3}	1.3	2.5	0.3

LMT, local mean time. Locations and other values refer to the point where the tows were commenced. "Net depth" refers to the depth of the net mouth bottom, and "fluorescence" is the summed value for measurements at 5–150 m depths; here and in Table 3: *SD*, standard deviation.

Table 2. Catch of fish in number at each surface trawling station

Common name	Scientific name	Station		
		1	2	3
Salmon shark	*Lamna ditropis*	0	1	0
Pink salmon	*Oncorhynchus gorbuscha*	13	12	0
Chum salmon	*Oncorhynchus keta*	0	1	0
Walleye pollock	*Gadus chalcogrammus*	2159	840	0

No invertebrate was sampled by the net.

A total of 2172 and 854 fish were collected at stations 1 and 2, respectively, whereas no fish was caught at station 3 (Table 2). Of these, walleye pollock was most dominant at both stations 1 and 2 accounting for 99.4 and 98.6% of the total number of catches, respectively. Pink salmon *Oncorhynchus gorbuscha* were also caught at stations 1 and 2, but their contribution to the total number was trivial constituting only 0.6 and 1.4%, respectively. Other fish species present included salmon shark *Lamna deitopis* and chum salmon *Oncorhynchus keta*; one individual of each was caught at station 2.

The body length of walleye pollock sampled at stations 1 and 2 were in similar ranges at 353–459 and 350–446 mm, respectively (Fig. 3). The average values (± *SD*, standard deviation) were also close to each other at 395 ± 22 and 392 ± 20, with no significant difference by station. The length–weight relationship of walleye pollock differed by site (Fig. 4). The fish sampled at station 2 showed higher body weights compared to those from station 1, resulting in a higher average in condition factor than station 1 (7.85 ± 0.78 *vs.* 7.32 ± 0.71, Student *t*-test: $p = 0.001$).

Of the 60 stomachs examined for contents, none was empty. The wet weight of contents averaged 3.90 and 10.97 g at stations 1 and 2, respectively. Thus, the fish at the latter site ingested 2.8 times more content

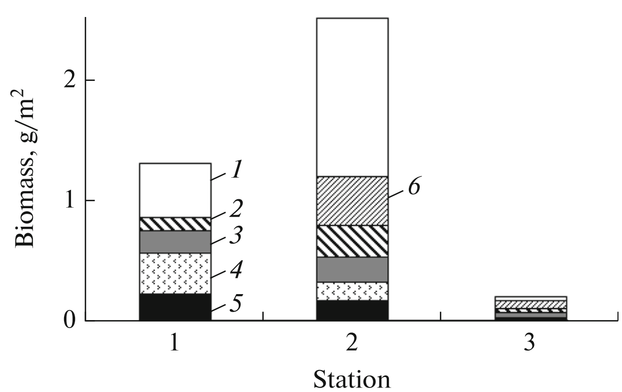

Fig. 2. Biomass of zooplankton sampled at each station collected by NORPAC net: (*1*) other organisms; (*2*) Chaetognatha; (*3*) *Eucalanus bungii*; (*4*) *Neocalanus plumchrus*/*flemingeri*; (*5*) *Neocalanus cristatus*; (*6*) Medusae.

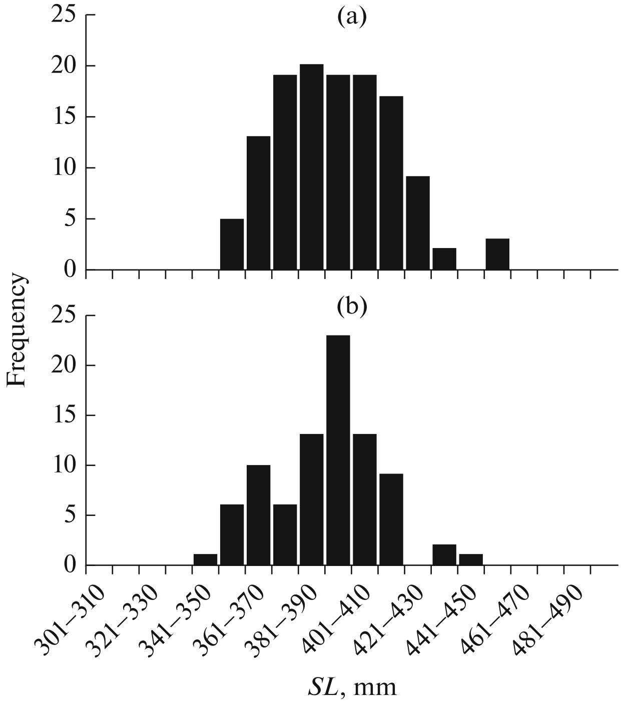

Fig. 3. Body standard length (SL) frequency distribution of walleye pollock collected at stations 1 ((a) $\bar{x} = 395 \pm 22$) and 2 ((b) $\bar{x} = 392 \pm 20$); the value ($\pm$ standard deviation) for each station.

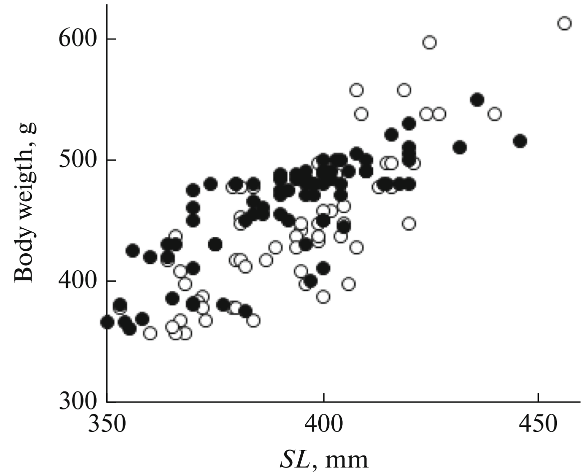

Fig. 4. Relationship between body length (*SL*) and body weight for individual fish collected at stations 1 (○) and 2 (●). Body weight was adjusted by the average wet weight of stomach contents at each station (Table 3) to reduce the effect of feeding intensity.

than those at the former. The stomach contents index at these stations were 0.94 ± 0.56 and 2.26 ± 0.95, respectively (Table 3). From the stomachs, at least 15 species from seven orders and five phyla were identified (Table 3). Of these, Calanoida was the most diverse order, containing five species, followed by Euphausiacea, which comprised four species. The diets differed by station; while copepods and euphausiids shared similar proportions at station 1 (43.6 and 45.2%, respectively), copepods (mainly *Neocalanus plumchrus/flemingeri* and *Eucalanus bungii*) was exclusively dominant (85.7%) at station 2. Due to the limited extent of the body size range, dietary differences by the body length of the predator were very limited (Fig. 5). Other noticeable prey items were *Themisto japonica* (Amphipoda), which occurred at station 1, and appendicularians, which occurred at both stations.

DISCUSSION

Three distinct stocks of walleye pollock are known to be distributed around Hokkaido: the Japan Pacific, the Sea of Japan, and the Sea of Okhotsk (Tsuji, 1990; Ando et al., 2024). Although walleye pollock is also distributed along the northeastern coast of Honshu Island, it has been regarded as part of the Japanese Pacific stock (JPS), which is mainly distributed along the Hokkaido coast (Honda et al., 2004). Therefore, the walleye pollock that occurred in the present study is concluded to comprise the JPS, regardless of whether their origin was Hokkaido or Honshu coast. Of the three stations sampled, pollock were caught at two stations in the north, and the largest number occurred at station 1, located at the continental slope off the Hokkaido coast. These facts suggest that the pollock originated on the southern coast of Hokkaido.

Although walleye pollock is a demersal species, its occurrence in the surface layer is not a novel discovery. In the Aleutian Basin of the Bering Sea, called Donut

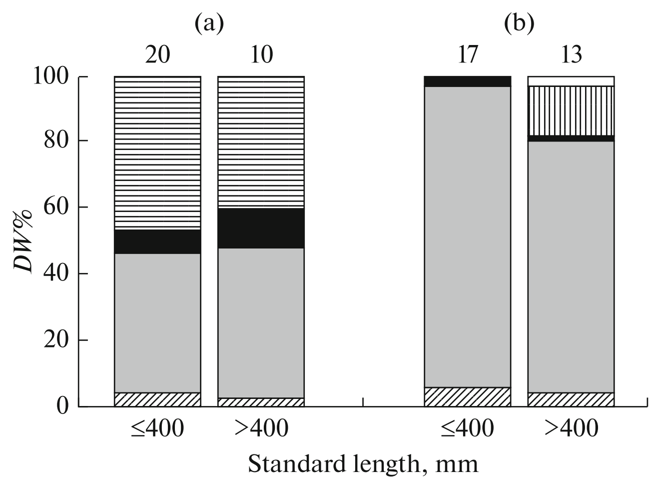

Fig. 5. Dry weight percentage composition (*DW%*) of stomach contents of walleye pollock for different body size classes and stations 1 (a) and 2 (b): (⊟) Euphausiids, (■) *Themisto japonica*, (▩) Copepoda, (▨) Appendicularians, (▥) Myctophidae, (□) other organisms. Numerals above the bars indicate the number of stomachs examined.

Table 3. Percent frequency of occurrence (*FO*) and dry weight percentage (*DW*) of prey items of walleye pollock collected at Stations 1 and 2 (number of stomachs examined = 30)

Prey taxa	Station 1		Station 2	
	FO	*DW*	*FO*	*DW*
Gastropoda: *Limacina* sp.	6.67	0.01	36.67	1.42
Copepoda:				
unidentified	20.00	5.49	26.67	21.14
Neocalanus cristatus	16.67	1.71	10.00	1.01
N. plumchrus/flemingeri	56.67	34.01	93.33	53.78
Eucalanus bungii	13.33	2.42	70.00	9.77
Euchaeta sp.	3.33	+	0	0
Candacia sp.	6.67	0.01	0	0
Amphipoda: *Themisto japonica*	66.67	7.84	40.00	1.12
Euphausiacea:				
unidentified	6.67	0.43	0	0
Euphausia pacifica	96.67	43.37	23.33	0.28
Thysanoessa inermis	0	0	3.33	0.06
Th. longipes	6.67	0.24	0	0
Th. raschii	16.67	1.12	0	0
Chaetognatha	6.67	0.02	3.33	0.02
Protochordata: Appendicularia	26.67	3.29	53.33	4.57
Pisces: *Stenobrachius leucopsarus*	0	0	3.33	6.82
Cottidae (unidentified juvenile)	3.33	0.04	0	0
Total *DW* of stomach contents, g	21.88		64.27	
Average *WW* of stomach contents, g	3.904		10.967	
SCI ± *SD*	0.95 ± 0.56		2.26 ± 0.95	

Average wet weight (*WW*) of stomach contents examined and stomach contents index (SCI) for both stations are also shown; "+", the percentage was < 0.01.

Hole, there were once huge aggregations of walleye pollock supporting annual catches of over one million tons (Nishimura et al., 2001; Bailey, 2011). These aggregations have been considered to migrate during periods of population expansion from the eastern or western Bering Sea (Shuntov et al., 1993; Bailey et al., 2000). Although walleye pollock played a pivotal role in the ocean basin ecosystem of the Bering Sea during the period of high abundance, its importance in the food web became trivial after its depletion in the 1980s (Zavolokin et al., 2016; Gorbatenko et al., 2024). On the other hand, there have been few reports of the distribution of walleye pollock in the upper epipelagic zone in the ocean basins of the western North Pacific, especially in the Oyashio region, in spite of the intensive research efforts by Russian scientists. For instance, although Ovsyannikova et al. (2021) reported a distribution pattern of walleye pollock Kuril Island waters, they covered depths ≥ 86 m, while there was no mention of walleye pollock in the trophic structure of the upper epipelagic fish community in the northwestern Pacific Ocean during the 1980s and 2000s (Zavolokin et al., 2016).

Off the southeastern coast of Hokkaido, some studies reported the epipelagic distribution of juvenile (ages 0 and 1) walleye pollock migrating upward during nighttime (Honda et al., 2004; Miyashita et al., 2004). The body length of walleye pollock sampled in this study ranged between 350–459 with modes around 390 mm. According to the age-length key (Sakai et al., 2023), this size range refers to ages 3–5, indicating that they were subadult and adult fish. Because subadult and adult walleye pollock are generally distributed within the 300 m bathymetry (i.e., ca. ≤ 30 km from the coastline) off the southeastern coast of Hokkaido (Shida, 2002), the present study is firstly reporting the far offshore distribution of subadult/adult walleye pollock in the northwestern Pacific Basin (ca. 170 km from the coastline).

There should be some factors that promote the far offshore distribution of walleye pollock in the Oyashio Basin beyond their normal habitat. Based on the result of the stomach contents analysis, we suggest that this factor should be prey availability. Although fewer pollock were collected at station 2, which was located in the northwestern Pacific Basin, they consumed > 2 times as much prey as measured by SCI. This station exhibited 1.7 times higher fluorescence values than station 1, indicating it was in a more advanced blooming condition. Copepods comprised 87% of the prey ingested, indicating that walleye pollock utilized copepods at station 2. Although copepods were less abundant in the NORPAC sample (Fig. 2), this inconsistency would have reflected either reduced sampling efficiency due to densely occurring diatom or the feeding impact by pollock as has been shown in the eastern Bering Sea (Ciannelli et al., 2004).

In observing the body condition of walleye pollock in the Oyashio region over a year, they rapidly recovered their nutritional status during May after their winter leaning condition. Because walleye pollock heavily ingested copepods comprising mainly *Neocalanus cristatus* during spring, it has been concluded that the superabundance of this species was essential for their spring recovery of body condition in the Oyashio region (Yamamura et al., 2002). However, in the present study, walleye pollock ingested far more amounts of *N. plumchrus/flemingeri* than *N. cristatus* (Table 3). This inconsistency is elusive by the difference in vertical distributions; while *N. cristatus* is distributed mainly in the epipelagic layer below the surface layer (i.e. > 50 m depths), *N. plumchrus* occurs in the surface layer explosively during the spring bloom (Tsuda et al., 1999). In this study, our sampling covered the surface layer only, so it still remains unclear whether dependence on *N. plumchrus/flemingeri* is ubiquitous to offshore walleye pollock and to what depth walleye pollock are distributed.

The sea surface temperature at station 3, where no pollock was collected, was 12.6°C. Although the hypothesized southward migration of walleye pollock may have been restricted by water temperature, a more plausible interpretation is that they remained in areas of high productivity due to blooming for effective feeding and nourishment. A similar migration pattern has been found in post-spawning Pacific herring *Clupea pallasii* in Prince William Sound, which persisted there for extended days to feed on the *Neocalanus* "bloom" (Bishop and Eiler, 2018). Because the area of high production moves northward with the progress of the season (Kasai et al., 1997), it should also be hypothesized that the offshore pollock will return to their original distribution area along the coast of Hokkaido.

CONCLUSIONS

The present study is the first to report the presence of walleye pollocks in the surface layer of the Oyashio Basin, which is far from the coastal area. We also suggest that they migrate southward from the Hokkaido coast to utilize the high productivity of spring bloom and abundant copepods, and then go back northward as the the season progresses. To confirm these hypotheses, a wide-area acoustic survey covering the entire blooming season would be needed. Such a study will enhance our understanding of the trophodynamics of walleye pollock in the Oyashio waters.

ACKNOWLEDGMENTS

The authors are grateful to the officers and crews of T/S Oshoro-maru for their cooperation at sea.

FUNDING

This work was supported by ongoing institutional (Hokkaido University) funding. No additional grants to carry out or direct this particular research were obtained.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The fish collection was reviewed and ruled exempt by Japan Fishery Agency. Our study did not kill excess fish following Hokkaido University's guideline for experimental animal welfare (https://www.kokudoukyou.org/index.php?page=kisoku_index) (accessed on 13 Sept. 2024).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

Ando, K., Yokoyama, Y., Miyairi, Y., et al., Otolith radiocarbon signatures provide distinct migration history of walleye pollock around Hokkaido, Japan in the North-Western Pacific, *Ecol. Evol.*, 2024, vol. 14, no. 7, Article e11288. https://doi.org/10.1002/ece3.11288

Bailey, K.M., An empty donut hole; the great collapse of a North American fishery, *Ecol. Soc.*, 2011, vol. 16, no. 2, Article 28.
https://doi.org/10.5751/es-04124-160228

Bailey, K.M., Quinn, II, T.J., Bentzen, P., and Grant, W.S., Population structure and dynamics of walleye pollock, *Theragra chalcogramma, Adv. Mar. Biol.*, 2000, vol 37, pp. 179–255.
https://doi.org/10.1016/S0065-2881(08)60429-0

Bakkala, R., Maeda, T., and McFarlane, G., Distribution and stock structure of pollock (*Theragra chalcogramma*) in the North Pacific, *Bul. Int. Nort. Pac. Fish. Comm.*, 1986, vol. 45, pp. 3–20.

Beamish, R.J., McFarlane, G., and King, J.R., Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America, *Deep-Sea Res. Part II,* 2005, vol. 52, no. 5, pp. 739–755.
https://doi.org/10.1016/j.dsr2.2004.12.016

Begon, M., *C., Ecology: From Individuals to Ecosystems*, Oxford: Townsend and J. Harper, 2006.

Bishop, M.A. and Eiler, J.H., Migration patterns of post-spawning Pacific herring in a subarctic sound, *Deep-Sea Res. Part II*, 2018, vol. 147, pp. 108–115. https://doi.org/10.1016/j.dsr2.2017.04.016

Ciannelli, L., Brodeur, R., and Napp, J., Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea, *Mar. Biol.*, 2004, vol. 144, pp. 515–526. https://doi.org/10.1007/s00227-003-1215-4

Gorbatenko, K.M., Melnikov, I.V., and Sheibak, A.Y., Feeding of walleye pollock *Gadus chalcogrammus* (Gadidae) in the epipelagic zone of the Bering Sea, *J. Ichthyol.*, 2024, vol. 64, no. 3, pp. 452–463. https://doi.org/10.1134/S0032945224700127

Goto, Y., Wada, A., Hoshino, N., et al., Diets of Steller sea lions off the coast of Hokkaido, Japan: An inter-decadal and geographic comparison, *Mar. Ecol.*, 2017, vol. 38, no. 6, Article e12477-n/a. https://doi.org/10.1111/maec.12477

Honda, S., Oshima, T., Nishimura, A., and Hattori, T., Movement of juvenile walleye pollock, *Theragra chalcogramma*, from a spawning ground to a nursery ground along the Pacific coast of Hokkaido, Japan, *Fish. Oceanogr.*, 2004, vol. 13, no. s1, pp. 84–98. https://doi.org/10.1111/j.1365-2419.2004.00318.x

Ikeda, T., Shiga, N., and Yamaguchi, A., Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific, *J. Oceanogr.*, 2008, vol. 64, no. 3, pp. 339–354. https://doi.org/10.1007/s10872-008-0027-z

Kasai, H., Saito, H., Yoshimori, A., and Taguchi, S., Variability in timing and magnitude of spring bloom in the Oyashio region, the western subarctic Pacific off Hokkaido, Japan, *Fish. Oceanogr.*, 1997, vol. 6, no. 2, pp. 118–129. https://doi.org/10.1046/j.1365-2419.1997.00034.x

Masuda, H., Amaoka, K., and Araga, C., *The Fishes of the Japanese Archipelago*, Tokyo: Tokai Univ. Press, 1984.

Miller, C.B. and Clemons, M.J., Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean, *Prog. Oceanogr.*, 1988, vol. 20, no. 4, pp. 293–313. https://doi.org/10.1016/0079-6611(88)90044-4

Miyashita, K., Tetsumura, K., Honda, S., et al., Diel changes in vertical distribution patterns of zooplankton and walleye pollock (*Theragra chalcogramma*) off the Pacific coast of eastern Hokkaido, Japan estimated by the volume backscattering strength (Sv) difference method, *Fish. Oceanogr.*, 2004, vol. 13, no. s1, pp. 99–110. https://doi.org/10.1111/j.1365-2419.2004.00313.x

Muhling, B., Brodie, S., Snodgrass, O., et al., Dynamic habitat use of albacore and their primary prey species in the California current system, *CalCOFI Rep.*, 2019, vol. 60, pp. 79–93.

Nishimura, A., Yanagimoto, T., Mito, K., and Katakura, S., Interannual variability in growth of walleye pollock, *Theragra chalcogramma*, in the central Bering Sea, *Fish. Oceanogr.,* 2001, vol. 10, no. 4, pp. 367–375.

Ovsyannikova, S., Ovsyannikov, E., and Novikov, Y.V., The distribution of walleye pollock, *Theragra chalcogramma*, and conditions of its habitat off the southern Kuril Islands, *Russ. J. Mar. Biol.*, 2021, vol. 47, no. 7, pp. 548–562. https://doi.org/10.1134/S106307402107004X

Sakai, O., Chimura, M., Chiba, S., et al., Stock assessment and evaluation for the Japanese Pacific stock of walleye pollock (fiscal year 2023), *Marine Fisheries Stock Assessment and Evaluation for Japanese Waters (Fiscal Year 2022/2023), Version 09/2024*, Tokyo: Japan Fish. Agency; Japan Fish. Res. Education Agency, 2023. https://abchan.fra.go.jp/wpt/wp-content/uploads/2024/03/details_2023_12.pdf.

Secor, D.H., *Migration Ecology of Marine Fishes*, Baltimore: JHU Press, 2015.

Shida, O., Age-dependent bathymetric pattern of walleye pollock, *Theragra chalcogramma*, off the Pacific coast of eastern Hokkaido, *Sci. Rep. Hokkaido Fish. Exp. Stn.*, 2002, vol. 63, pp. 9–19.

Shuntov, V.P., Volkov, A. F., Temnykh, O.S., and Dulepova, Y.P., *Mintai v ekosistemakh dal'nevostochnykh morei* (Walleye Pollock in the Ecosystems of the Far-Eastern Seas), Vladivostok: TINRO, 1993.

Tamura, T., Fujise, Y., and Shimazaki, K., Diet of minke whales *Balaenoptera acutorostrata* in the northwestern part of North Pacific in summer 1994 and 1995, *Fish. Sci.*, 1998, vol. 64, no. 1, pp. 71–76. https://doi.org/10.2331/fishsci.64.71

Tsuda, A., Saito, H., and Kasai, H., Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific, *Mar. Biol.*, 1999, vol. 135, pp. 533–544. https://doi.org/10.1007/s002270050654

Tsuji, S., Alaska pollock population, *Theragra chalcogramma*, of Japan and its adjacent waters, II: reproductive ecology and problems in population studies, *Mar. Behav. Physiol.*, 1990, vol. 16, no. 1, pp. 61–107. https://doi.org/10.1080/10236249009378744

Wang, R., Chimura, M., Sadayasu, K., et al., Summer diet and feeding strategy of Pacific cod (*Gadus macrocephalus*) inhabiting the southern coast of Hokkaido, Japan, *Mar. Biol. Res.*, 2022, vol. 18, nos. 7–8, pp. 435–447. https://doi.org/10.1080/17451000.2022.2147948

Yamamura, O., Trophodynamic modeling of walleye pollock in the Doto area, northern Japan: model description and baseline simulations, *Fish. Oceanogr.*, 2004, vol. 13, no. s1, pp. 138–154. https://doi.org/10.1111/j.1365-2419.2004.00319.x

Yamamura, O. and Kooka, K., Community structure of demersal fish over the continental shelf off the southeastern coast of Hokkaido Island: The effect of eurythermy in dominant species, *J. Sea Res.*, 2023, vol. 195, Article 102418. https://doi.org/10.1016/j.seares.2023.102418

Yamamura, O., Honda, S., Shida, O., and Hamatsu, T., Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: Ontogenetic and seasonal variations, *Mar. Ecol. Prog. Ser.*, 2002, vol. 238, pp. 187–198. https://doi.org/10.3354/meps238187

Zavolokin, A.V., Radchenko, V.I., and Naydenko, S.V., Changes in the trophic structure of an epipelagic community in the western Bering Sea and western North Pacific Ocean with an emphasis on Pacific salmon (*Oncorhynchus* spp.), *N. Pac. Anadr. Fish Comm. Bull.*, 2016, vol. 6, pp. 259–278.

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