Journal of
Marine Science and Technology

Volume 31 | Issue 4 Article 14

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Recommended Citation
Li, Xinyi; Yamaguchi, Hiroshi; Shirakawa, Hokuto; Minami, Kenji; Sato, Nobuhiko; Zhu, Yanhui; Miyakoshi, Yasuyuki; and Miyashita, Kazushi (2023) "Impact of Multiple Water Temperature Structures on the Behavioral Pattern of Chum Salmon (*Oncorhynchus keta*) on the Coast of the Shiretoko Peninsula," *Journal of Marine Science and Technology*: Vol. 31: Iss. 4, Article 14.
DOI: 10.51400/2709-6998.2721
Available at: https://jmstt.ntou.edu.tw/journal/vol31/iss4/14

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RESEARCH ARTICLE

Impact of Multiple Water Temperature Structures on the Behavioral Pattern of Chum Salmon (*Oncorhynchus keta*) on the Coast of the Shiretoko Peninsula

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Abstract

During the migration of chum salmon (*Oncorhynchus keta*) towards the Shiretoko Peninsula in Hokkaido, Japan, the convergence of coastal currents results in the formation of intricate water temperature structures. However, the impact of this phenomenon on the behavioral tendencies of chum salmon remains largely unexplored. In 2012 and 2013, we conducted a study to document the vertical water temperature profiles and uninterrupted swimming patterns of homing chum salmon in the coastal waters surrounding the Shiretoko Peninsula. The results indicated that chum salmon exhibited a preference for avoiding thermoclines characterized by rapidly decreasing water temperatures. They were predominantly observed swimming either in the surface or deep seawater layers (210−230 m), away from the thermocline. This finding demonstrates that homing chum salmon adapt their behavioral patterns in response to the vertical temperature distribution in the water. The findings presented in this study contribute to our understanding of the swimming behavior of chum salmon, providing valuable insights that can be utilized to develop effective management strategies aimed at enhancing sustainability.

Key words: Chum salmon, Behavioral pattern, Water temperature, Data logger

1. Introduction

Chum salmon (*Oncorhynchus keta*) is one of seven Pacific salmon species, with a global annual catch of 32,300 t [1]. It is an ecologically [2,3] and economically [4] important species in the North Pacific. As one of Japan's most important fishery resources, chum salmon return to their natal river in northeastern Japan from September to November of annually [4]. Returned chum salmon are primarily caught using salmon trap nets (96 %) [5]. The Shiretoko Peninsula in Hokkaido, Japan, has the highest chum salmon yield area in Japan, and salmon trap net fisheries are highly developed [6]. However, in recent decades, there has been a significant decline in the catch of chum salmon in Japan, from 70 % of the total catch in the North Pacific in 1991 to 40 % at present [7]. To maintain the sustainable development

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Received 28 June 2023; revised 3 November 2023; accepted 7 November 2023.
Available online 15 December 2023

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https://doi.org/10.51400/2709-6998.2721

of chum salmon fishery resources, there is an urgent need to investigate the behavioral pattern of homing chum salmon along the coast of the Shiretoko Peninsula and the factors that may cause changes in the regional catch.

In nature, climate change [8,9], density dependence [10], and artificial release [11,12] are crucial factors affecting fish population dynamics. Beamish [13] and Eriyama et al. [14] suggested that artificial release and hatchery technologies are the main catalysts for chum salmon return. However, between 1990 and 2022, the number of releases of chum salmon in Hokkaido, Japan, was generally consistent [15] but catch recurrence changed and gradually decreased. Beamish et al. [16] and Hare et al. [17] investigated the combined effects of density dependence, climate change, and artificial releases on chum salmon population dynamics and suggested that the changes in catches could be largely explained by climate change. However, there have been cases where different patterns of catch variation have occurred in different areas of the same sea. According to statistical data from 2012, the catch of the Utoro Fishing Association on the west side of the Shiretoko Peninsula was 80 % that of the previous year, while that of the Abashiri Fishing Association in the same marine waters was 10 % higher than the previous year [18], the discrepancy suggests that factors beyond climatic conditions may also be influencing the catch volume.

Salmon trap nets are usually set up in shallow waters, waiting for salmon to enter [19,20]. This method utilizes the behavioral ecology of the target species for net fishing [21]. In other words, changes in the behavioral patterns of chum salmon could directly lead to changes in the salmon trap net catch. Chum salmon is a typical cold water fish, surviving at optimum water temperatures ranging from 13 to 15 °C [22,23]. As a temperature-changing animal, the temperature of seawater determines the temperature of salmon and affects them at all stages of life [24]. High water temperatures alter the growth rate and migration period of chinook (*Oncorhynchus tshawytscha*) [25,26] and pink salmon (*Oncorhynchus gorbuscha*) [26]. Sockeye (*Oncorhynchus nerka*) [27] and chinook salmon [26] use cold water blocks in the ocean for behavioral thermoregulation under high water temperatures. Adult chum salmon are believed to adapt their behavioral strategies according to the water temperature structure [28] to achieve a balance between utilizing directional cues about their natal rivers and temperature regulation [29-31]. In other words, water temperature affects the behavioral patterns of chum salmon.

The Shiretoko Peninsula bordering the Sea of Okhotsk, is a major producer of chum salmon in Japan. The Soya Warm Current (SWC), Eastern Sakhalin Current Water (ESCW), and Coastal Oyashio Water (COW) converge [32-34] along the Shiretoko Peninsula, and the variable sea conditions have been well-established [35]. The SWC exhibits its strongest interaction with ESCW from September to October [36,37], during which the SWC leads to the formation of surface cooling zones and subsurface dome structures, significantly impacting the coastal water temperature structure [38,39]. This period coincides with the return period of chum salmon; at that time, the homing chum salmon will be in a multilayered water temperature structure. The complex structure of multiple water temperatures may alter the behavioral patterns of chum salmon. To verify this, we attached micro data loggers to homing chum salmon in the coastal waters around the Shiretoko Peninsula to record their behavioral patterns in 2012 and 2013. The vertical water temperature structure and salinity distributions in the same water were extrapolated using a conductivity-temperature-depth (CTD) profiler. We concurrently collected water temperature and salinity data from both the eastern and western coasts. The primary aim of this study was to explore the effects of vertical changes in water temperature on the behavioral patterns of chum salmon by comparing swimming behavior profiles under different water temperature structures.

2. Materials and methods

2.1. Study area

This study was conducted in the Shiretoko Peninsula, Hokkaido, Japan (43°6′−44°6′N, 144°3′−145°8′E) (Fig. 1). The experiments were conducted between September 2012 and September 2013. Considering that the SWC extends from the Sea of Japan to the northeastern part of Hokkaido, the marine environment on the western side of the peninsula, which is directly affected by the SWC, differs from that on the eastern side of the peninsula, which is indirectly affected. In this study, the coast of the Shiretoko Peninsula was bounded by Cape Shiretoko and divided into western and eastern sides (Fig. 1).

2.2. Environmental data collection

On September 22−23, 2012, and September 18−19, 2013, we measured vertical water temperature and salinity using a CTD profiler (19plus V2 SeaCAT;

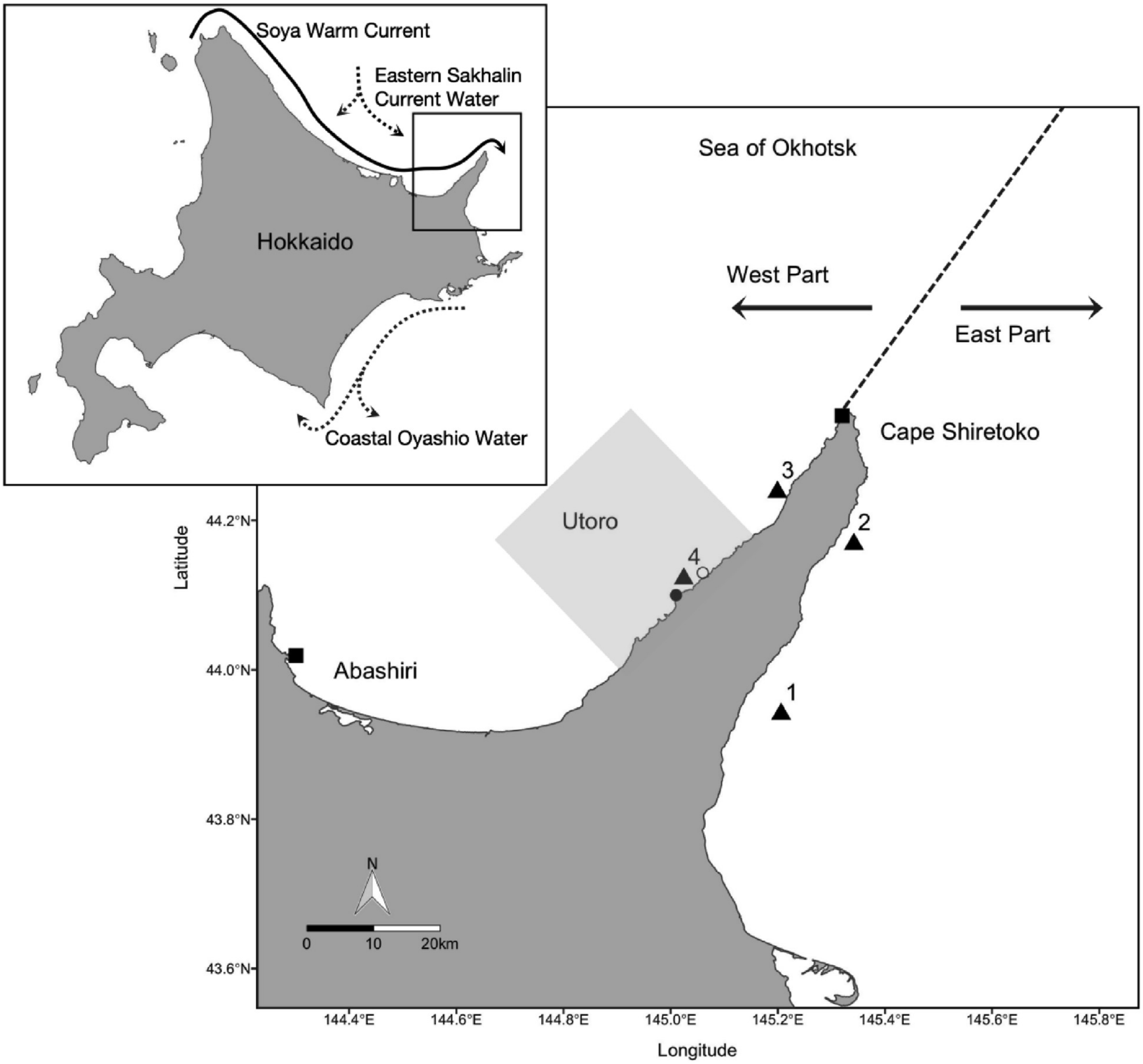

Fig. 1. Schematic diagram of the ocean currents around Hokkaido and geographic location of surveys (upper left corner). The larger map shows the study area of this study around the Shiretoko Peninsula (43°6′–44°6′N, 144°3′–145°8′E), Hokkaido, Japan. The broken line extending from Cape Shiretoko divides the Shiretoko Peninsula into 'West Part' and 'East Part.' The solid and hollow circles indicate the release points in 2013 and 2012, respectively. The black triangles are the four measured points of the CTD profiler.

Sea-Bird Scientific, Bellevue, WA, USA) aboard the 'Ushio-maru' (179t, a practice ship attached to Hokkaido University, Faculty of Fisheries); the measurement points are shown in Fig. 1. The vertical swimming depth of adult chum salmon generally does not exceed 200 m [40-42], and the maximum drop depth of the CTD was set to 500 m in this study.

2.3. Logger experiments on salmon

Adult chum salmon homing from the Bering Sea toward their natal river in Japan first reach the Shiretoko Peninsula [43,44]. The release experiments were conducted on September 3, 2012, and September 6, 2013, and the release point was set to the west side of Shiretoko Peninsula, as shown in Fig. 1. The chum salmon used for the release experiment were caught in the Utoro Sea (Fig. 1); injured and bled individuals were excluded. All remaining individuals were placed in 2-phenoxyethanol diluted to 0.04 % with seawater for anesthesia for approximately 3 min 2-phenoxy ethanol appears to have no adverse effects on the homing behavior of chum salmon [45]. After anesthesia came into effect, we attached a micro data logger to the fish just below the anterior segment of the dorsal fin. A nylon strap was passed through the fish via a perforated tube, and the micro data logger was sutured to the left side of the fish. Finally, the fork length, weight, sex, and maturity of the fish were recorded. The entire process of anesthesia and data logger attachment took approximately 5 min. The marked individuals were allowed to recover in a seawater tank for 10–30 min and were released sequentially until the effect of anesthesia passed. Eight and twenty individuals were released in 2012 and 2013, respectively. Swimming depth and ambient temperature were monitored simultaneously using the micro data logger (Lat 1400; Lotek, Newmarket, ON, Canada). Each data logger was 35 mm in length and 11 mm in diameter, weighed 5.1 g in air and 1.5 g in seawater, had a resolution of 0.25 m, an observed water temperature range of −5 to 35 °C, and the maximum range of the depth channel was 2000 m. The data loggers were set to record empirical data at intervals of 1 min. Similar to tagging, externally attached data loggers may reduce the swimming performance of salmonids [46,47]. However, a tag load of less than 2 % (i.e., tag mass/body mass; [48]) does not significantly affect swimming behavior [49]. The minimum weight of the released individuals in this study was 2.9 kg, and the tag load was far less than 2 %. Therefore, the results of this experiment are credible. Furthermore, The CTD profiler recorded vertical water temperature and salinity simultaneously. Released individuals were recovered with the assistance of fishing associations and anglers. All animal handling, anesthesia, and surgical procedures followed the University of Nebraska–Lincoln Institutional Animal Care and Use Committee-approved protocol no. 1691.

2.4. Statistical analyses

The Shiretoko Peninsula was divided into east and west sides by Cape *Shiretoko* (Fig. 1), and the released individuals were labeled according to their recapture locations. For example, 'West' and 'East' mean individuals were recaptured on the west and east sides, respectively. Because chum salmon show reduced activity and passive sinking for 6–8 h after being marked [50], data from 8 h after the release experiment were excluded. In addition, marked individuals were mainly recovered by salmon trap nets, which were usually collected once a day between 4:00 and 6:00 am, meaning that marked individuals were in the salmon trap nets for a maximum of 24 h. Therefore, data collected within 24 h before net collection were excluded. If the day before the net collection was a fishing-off day, the

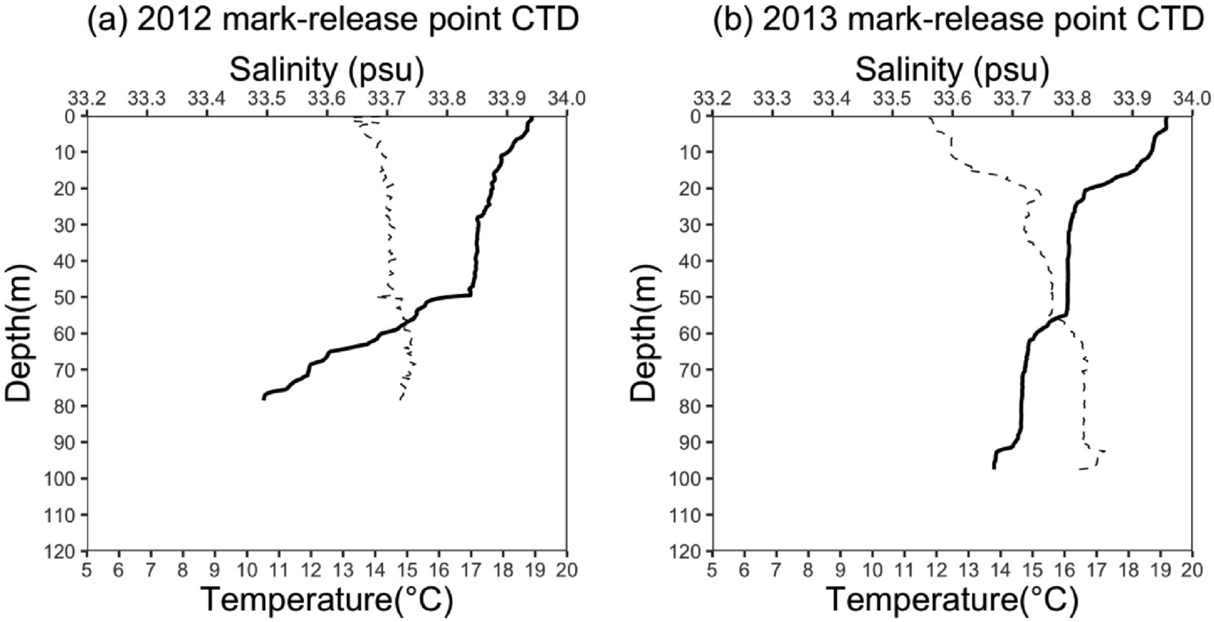

Fig. 2. Vertical distribution of water temperature and salinity at the release points. The ordinate represents water depth; water salinity is indicated on the upper abscissa, and water temperature on the lower abscissa. Water temperature is represented as a solid line and salinity as a broken line. (a) Vertical distribution of water temperature and salinity at the release points on September 3, 2012. (b) Vertical distribution of water temperature and salinity at the release points on September 6, 2013.

exclusion time became 24 h to accommodate the fishing-off day time. After processing the data as described above, individuals with insufficient recording times were excluded from the analysis. According to the definition provided by Tanaka [51], chum salmon dropping below 10 m and rising again to 10 m at shallow depths was defined as one vertical movement. We recorded the number of vertical movements, frequency of vertical movements per unit time (times/h), and maximum and minimum swimming depths (m). Statistical analyses were conducted using 'Ethographer,' a suite of functions designed for visualizing and analyzing bio-logging data within IGOR Pro ver9.0 (WaveMetrics Inc., Portland, OR, USA). Various statistical metrics for the time series data can be obtained via the graphical user interface, including event ID, start time, end time, average swimming depth, minimum swimming depth, maximum swimming depth, duration, standard deviation, and sum of diving events. In addition, if a thermocline is detected, the number of individuals passing through the thermocline will be calculated using R Statistical Software (v4.1.2; [52]). Assuming a thermocline depth is X meters, the number of points where the swimming depth-time series graph intersects with y = X can represent the number of times individuals pass through the thermocline. A thermocline is a transition layer between warmer mixed water on the ocean surface and colder deep water [53], and the temperature changes rapidly with depth [54]. This study used the definition suggested by Gray [55], who defined a thermocline as a water layer with a temperature change greater than 0.5 °C within a depth interval of 1 m.

3. Results

3.1. Vertical changes in water temperature at the release point

Fig. 2 shows the water temperature and salinity obtained using the CTD at the release points in 2012 and 2013. At the release point in 2012, the water temperature from the surface to a 50-m depth slowly decreased from 19 to 17 °C, and below 50 m, the water temperature sharply decreased from 17 to 10.5 °C at a depth of 80 m (Fig. 2a). The salinities at the surface and bottom were 33.63 and 33.72 PSU, respectively. At the release point in 2013, the sea surface temperature was approximately 19.2 °C, decreasing phasically to 13.5 °C at a depth of 100 m. The sea surface salinity was 33.55 PSU, with a phased increase to 33.83 PSU from the sea surface to the bottom (Fig. 2b). One of the most prominent differences was the presence of a well-mixed water mass in 2013, whereas the water temperature dropped rapidly at a depth of 50 m in 2012.

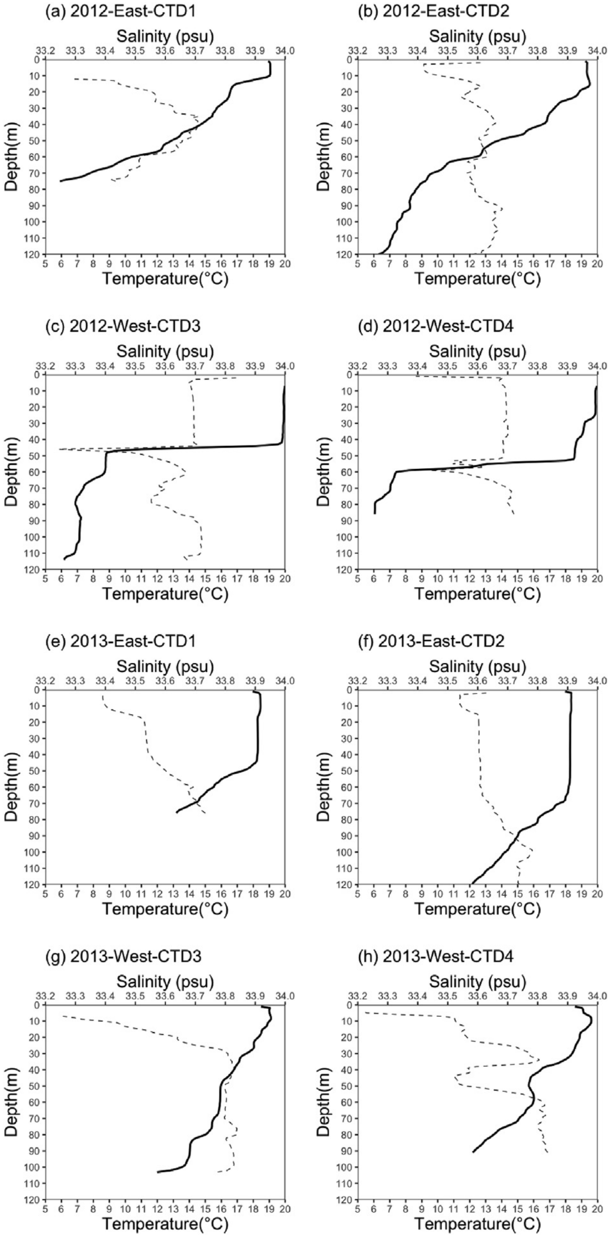

Fig. 3. Vertical distribution of water temperature and salinity at four CTD profiler observation points on September 22–23, 2012, and September 18–19, 2013. The ordinate represents water depth, water salinity is indicated on the upper abscissa, and water temperature is indicated on the lower abscissa. Water temperature is represented as a solid line and salinity as a broken line. (a) Observations at point 1 in the 'East Part' in 2012. (b) Observations at point 2 in the 'East Part' in 2012. (c) Observations at point 3 in the 'West Part' in 2012. (d) Observations at point 4 in the 'West Part' in 2012. (e) Observations at point 1 in the 'East Part' in 2013. (f) Observations at point 2 in the 'East Part' in 2013. (g) Observations at point 3 in the 'West Part' in 2013. (h) Observations at point 4 in the 'West Part' in 2013.

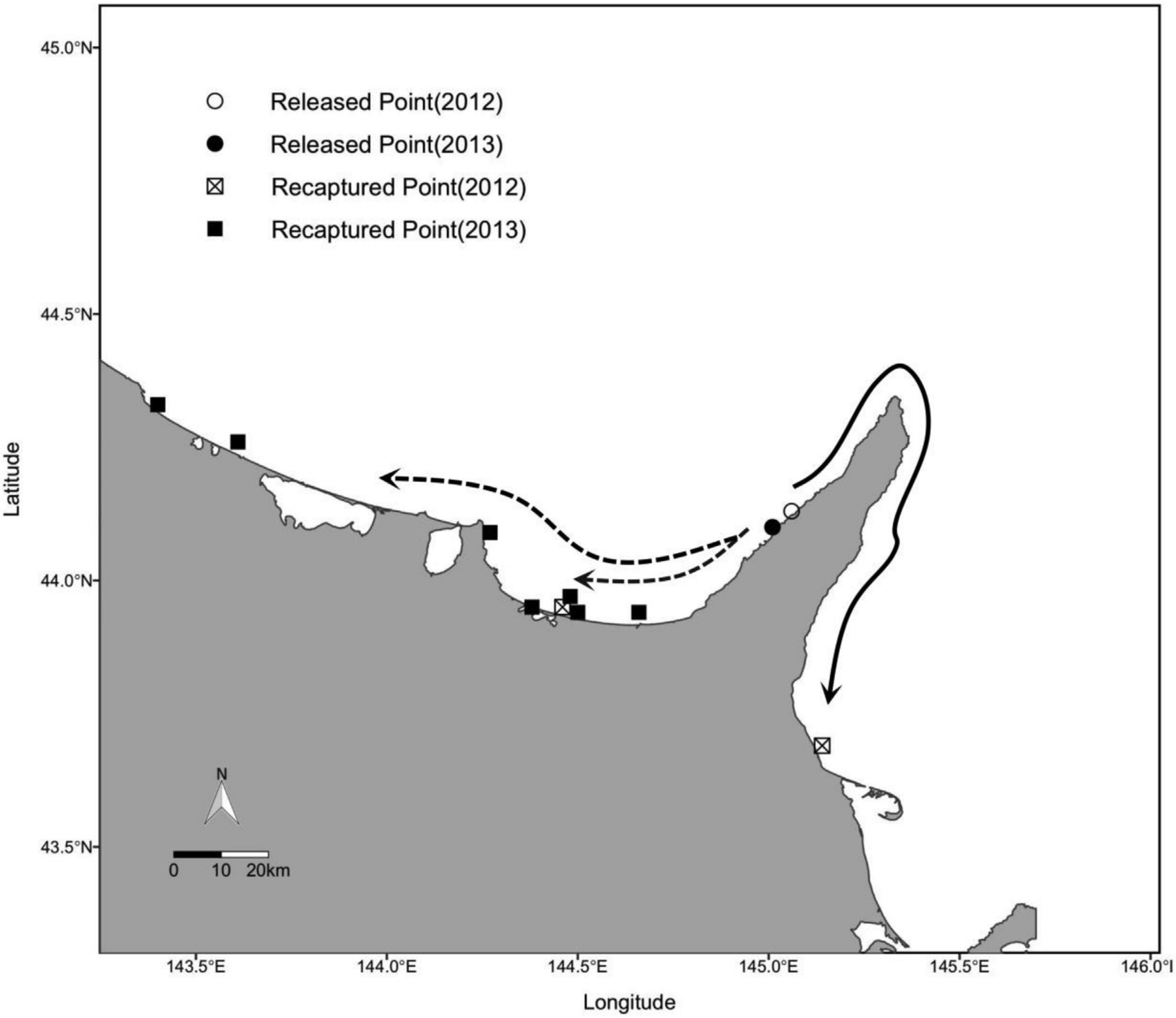

Fig. 4. Release and retrieval points in 2012 and 2013. Solid and hollow circles represent the release points in 2013 and 2012, respectively. Solid and hollow rectangles represent the retrieval points in 2013 and 2012, respectively. The solid line illustrates the anticipated swimming route of individuals retrieved on the west side of the Shiretoko Peninsula, whereas the dashed line illustrates the anticipated swimming route of individuals retrieved on the east side.

3.2. Vertical changes in the water temperature in the coastal waters around Shiretoko Peninsula

On the east side of the peninsula on September 22–23, 2012, the water temperature slowly decreased from 19 to 6 °C from the sea surface to the seafloor. At observation point 1, the salinity was 33.4 PSU at the sea surface, rose to 33.7 PSU at a depth of 40 m, and then dropped back to 33.4 PSU. At observation point 2, the variation in salinity was minimal at approximately 33.4 PSU at the sea surface and 33.6 PSU at the bottom (Fig. 3ab). The water

Table 1. Data of retrieved individual chum salmon

	Logging duration (h)	Depth (m)		Temperature (°C)			Diving events (10 m)			50- m depth passage
		Median	Maximum	Median	Minimum	Maximum	Number (*n*)	Frequency (*n*/h)	Mean dive duration (minutes)	Frequency (n/h)
West'12	76	41.3	362.4	12.3	−0.2	20.4	35	0.46	59.7	0.17
East'12	60	14.6	144.3	16.6	4.1	19.4	100	1.67	20.4	0.65
West'13	614	44.8	258.7	15.6	1	20.6	1099	1.79	25.4	0.63

From left to right: logger recording time (h), median swimming and maximum diving depth (m), median experienced water temperature (°C), maximum and minimum ambient temperature (°C), number of diving events (times), frequency of diving (times/h), mean diving duration (minutes), and frequency of 50-m depth passage (times/h).

temperature and salinity distribution on the western side significantly differed from those on the eastern side. On the west side of the peninsula, the water temperature was unchanged at 20 °C from the water surface to a depth of 50 m. In parallel, seawater salinity remained at 33.7 PSU. There was a strong decrease in salinity and temperature at a water depth of 50 m; the water temperature dropped to less than 8 °C, and the salinity dropped sharply to approximately 33.4 PSU (Fig. 3cd).

On the east side of the peninsula on September 18–19 2013, the water temperature was approximately 18 °C from the surface to a 40-m depth, decreasing slowly to 12 °C from 40 m to the seafloor at observation point 1. The salinity at the sea surface was recorded at 33.4 PSU, with a gradual increase to 33.75 PSU at the seafloor (Fig. 3e). At observation point 2, the water temperature varied from approximately 18 °C at the surface to a 60-m depth, gently decreasing to 12 °C between 60 m and the seafloor. Sea surface salinity measured 33.55 PSU, with a gradual rise to 33.73 PSU at the seafloor (Fig. 3f). On the west side of the peninsula, the sea surface temperature was approximately 19 °C, gradually decreasing to 12 °C on the seafloor. The sea surface salinity was 33.2 PSU, increasing to 33.8 PSU on the seafloor (Fig. 3gh). According to the CTD data, the structure of seawater temperature and salinity on the west side of the peninsula in 2012 considerably differed from that on the east side in 2012 and on both sides in 2013. From at least September 3 to 23, 2012, a thermocline in water temperature at a 50-m depth formed two stratified water masses, with water temperature suddenly dropping to approximately 10 °C.

3.3. Retrieved individuals

Four of the eight individuals released in 2012 were recaptured. After removing the data loggers 8 h after the release experiment and 24 h before recapture, two individuals were excluded because of insufficient recording times. The remaining two individuals were marked as West’12 (ID3211) and East’12 (ID2081) according to their retrieved location and year of release (Fig. 4). Twelve of the twenty individuals released in 2013 were recovered, and five individuals with insufficient recording times were excluded. The remaining seven individuals (ID2221, ID2206, ID2609, ID2610, ID3385, ID3377, and ID2561) were all recaptured on the west side of the Shiretoko Peninsula and were marked as West’13 for analysis (Fig. 4). The total analysis time was 76 h for West’12 (76 h for each individual), 60 h for East’12 (60 h for each individual), and 614 h for West’13 (87.7 h for each individual) (Table 1).

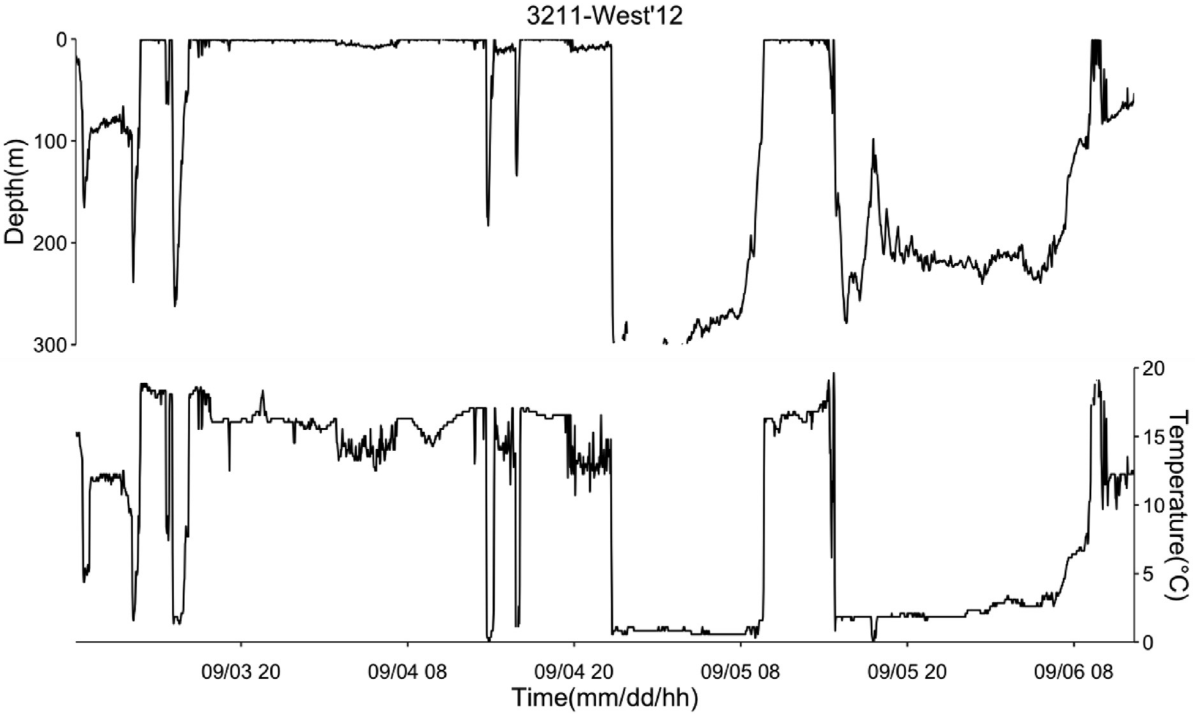

Fig. 5. Swimming depth and ambient temperature profiles of homing chum salmon retrieved on the west side of the Shiretoko Peninsula in 2012. The vertical axis on the left represents the swimming depth (m), while the right vertical axis represents the ambient temperature (°C).

West’12 more frequently swam on the sea surface and at a 210–230-m depth (Fig. 5), with a bimodal swimming depth distribution. The swimming depth for West’12 was negatively correlated with ambient temperature. Most of the time, the ambient temperature decreased as the depth increased; however, there were shallow swimming depths with low water temperatures (Fig. 6). West’12 had a bimodal swimming depth distribution. The median swimming depth for West’12 was 41.3 m, and the maximum swimming depth was 362.4 m (Table 1). The ambient temperature for West’12 also showed a bimodal distribution, being mostly 1, 2, and 16 °C (Fig. 6). The median, minimum, and maximum ambient temperatures for West’12 were 12.3, −0.2, and 20.4 °C, respectively. The hourly diving frequency was 0.46/h, and the mean dive duration was 59.7 min. In addition, West’12 had a passage frequency of 0.17/h at a depth of 50 m, where a thermocline appeared on the west side of the Shiretoko Peninsula in 2012 (Table 1).

East’12 more frequently swam in shallow water below 100 m (Fig. 7), with a median swimming depth of 14.6 m and a maximum swimming depth of

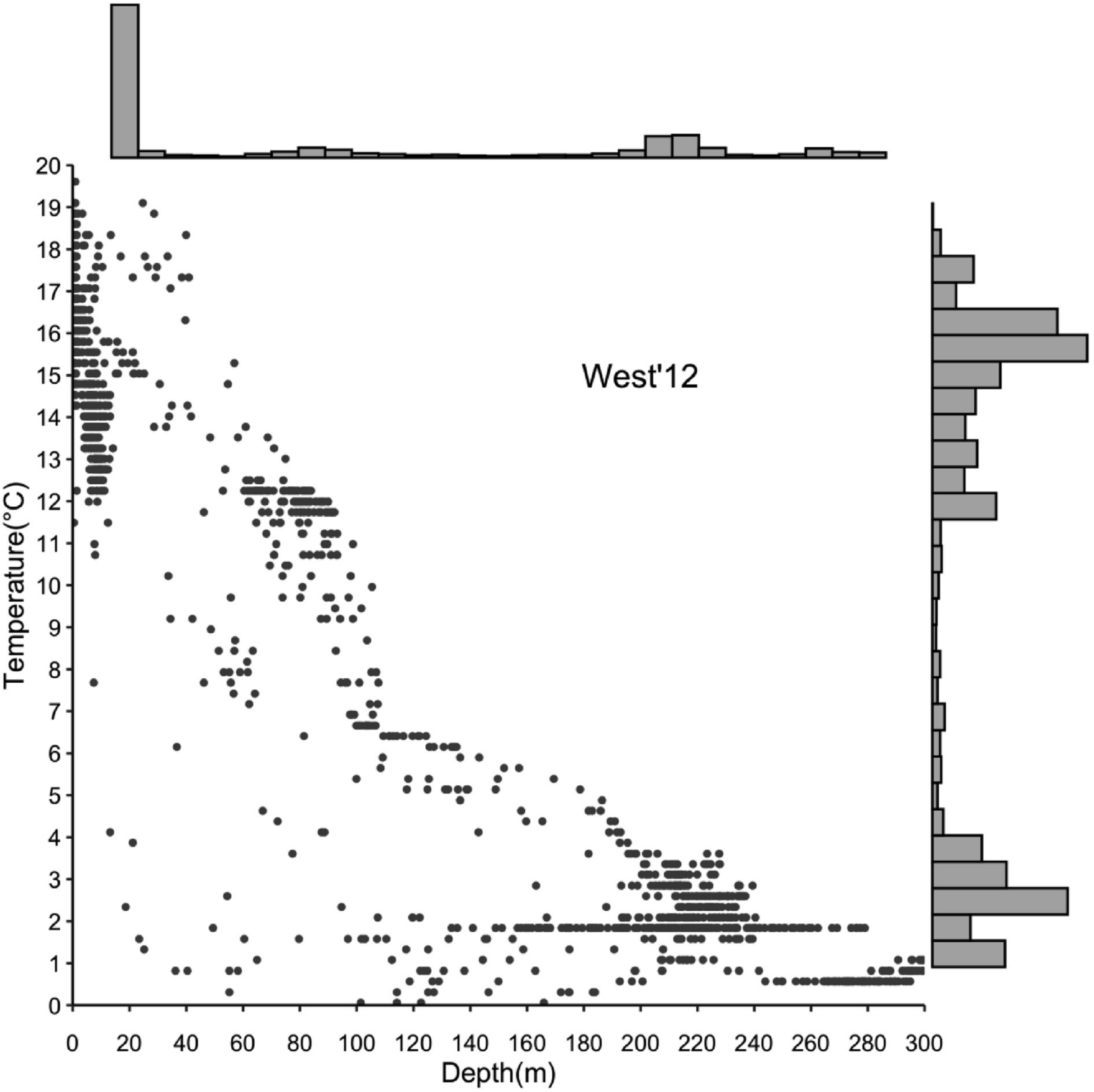

Fig. 6. Relationship between the ambient temperature and swimming depth of West’12. The vertical axis represents the ambient temperature (°C), while the right vertical axis represents swimming depth (m). The upper and right histograms show the frequency distributions of swimming depth and ambient temperature for West’12, respectively.

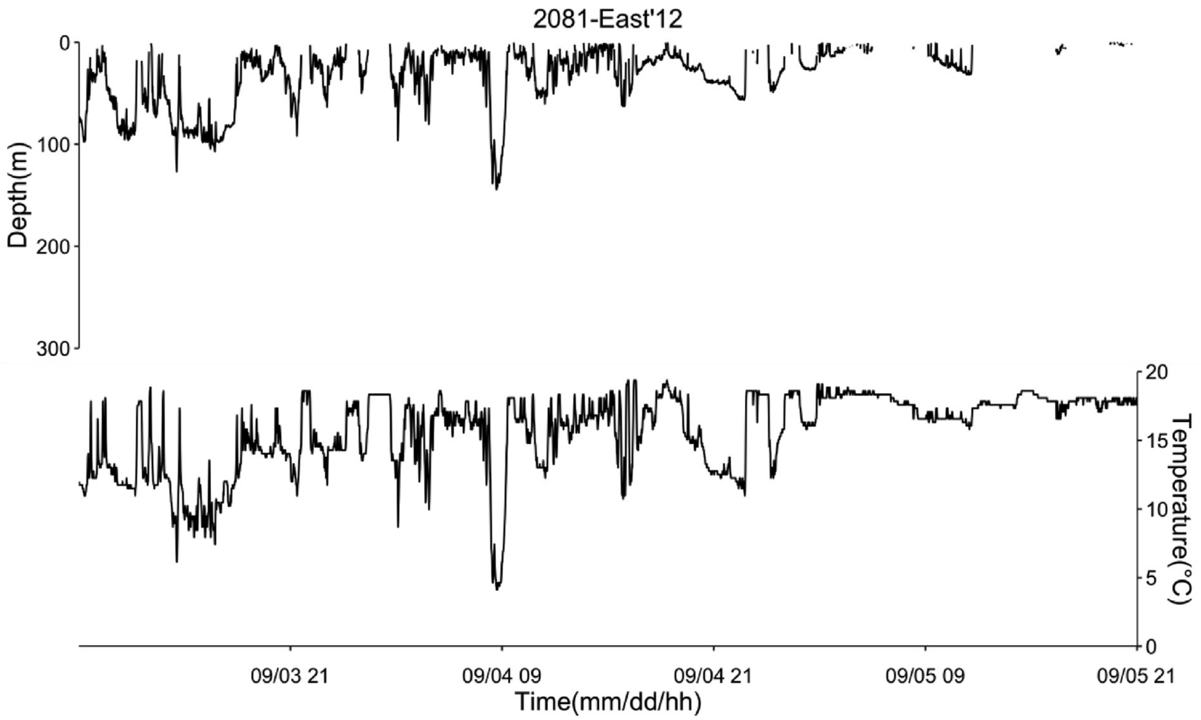

Fig. 7. Swimming depth and ambient temperature profiles of homing chum salmon retrieved on the east side of the Shiretoko Peninsula in 2012. The vertical axis on the left represents the swimming depth (m), while the right vertical axis represents the ambient temperature (°C).

144.3 m (Table 1). The swimming depth for East'12 was negatively correlated with ambient temperature, and ambient temperature decreased with increasing swimming depth (Fig. 8). The ambient temperature for East'12 was concentrated from 12 to 18 °C (Fig. 8), with median, minimum, and maximum ambient temperatures of 16.6, 4.1, and 19.4 °C, respectively. The diving frequency was 1.67/h, which was 3.7-fold higher than that for West'12. The mean dive duration was 20.4 min, significantly shorter than that for West'12. The 50-m depth passage frequency was 0.65/h, 3.8-fold that of West'12 (Table 1).

Seven recaptured West'13 individuals showed similar swimming patterns; ID3385 is a typical example (Fig. 9). Both West'13 and East'12 spent most of their time swimming in the shallow layer below 100 m. The swimming depth for West'13 was negatively correlated with ambient temperature, and the ambient temperature decreased with an increase in swimming depth (Fig. 10). West'13 exhibited a median dive depth of 44.8 m and a maximum depth of 258.7 m (Table 1).

The ambient temperature for West'13 was concentrated from 11 to 19 °C (Fig. 10), with median, minimum, and maximum ambient temperatures of 15.6, 1, and 20.6 °C, respectively. The diving frequency was 1.79/h, 3.9-fold that of West'12. The average single diving dwell time was 25.4 min (Table 1), significantly shorter than that of West'12. The 50-m depth passage frequency was 0.63/h, approximately 3.7-fold that of West'12.

Since swimming depth and ambient temperature are not normally distributed, separate Kruskal–Wallis tests were conducted for swimming depth and ambient temperature in West'12, East'12, and West'13 using the R. The test results reveal significant differences among West'12, East'12, and West'13 in terms of swimming depth (Kruskal–Wallis chi-squared = 2503, df = 2, p-value <2.2e-16). Likewise, significant differences were also observed in ambient temperature (Kruskal–Wallis chi-squared = 1316.2, df = 2, p-value <0.01). These findings suggest notable variations in swimming patterns among West'12, East'12, and West'13.

4. Discussion

CTD data revealed that (Figs. 2 and 3), only in 2012, a thermocline was formed at a 50-m water depth on the west side of the Shiretoko Peninsula, where the water temperature was approximately 18 °C and salinity was approximately 33.7 PSU from the surface to a 50-m depth. At a depth of 50 m, the water temperature rapidly decreased to approximately 8 °C, and seawater salinity dropped to 33.3 PSU. Because the salinity of ESCW is 32.0–33.0 PSU and that of the SWC is more than 33.6 PSU [37], the thermocline in 2012 is thought to have been formed by the confluence of the SWC and ESCW.

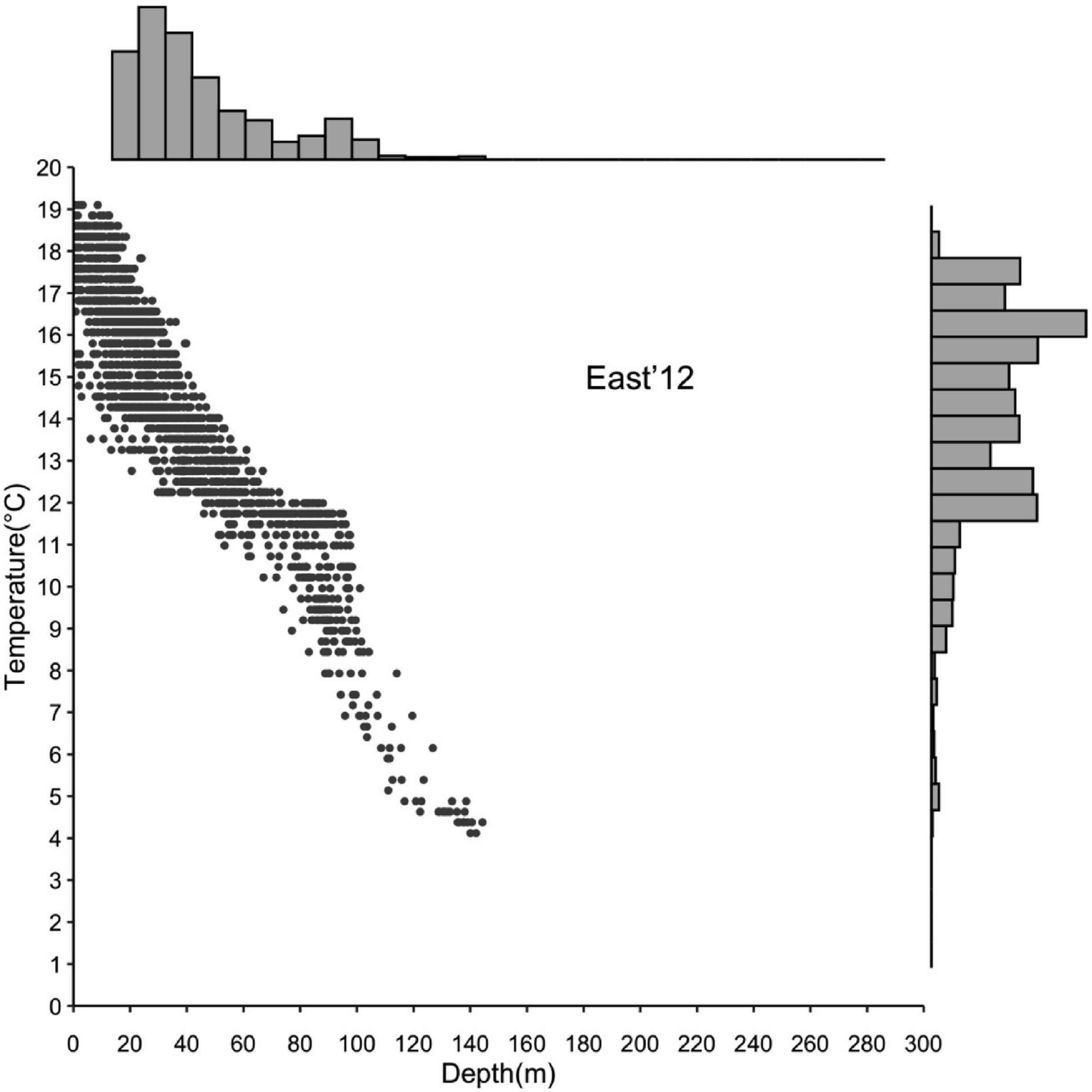

Fig. 8. Relationship between the ambient temperature and swimming depth of East'12. The vertical axis represents ambient temperature (°C), while the right vertical axis represents swimming depth (m). The upper and right histograms show the frequency distribution of swimming depth and ambient temperature for East'12, respectively.

Based on the results of the release experiments, the swimming patterns of homing chum salmon could be divided into two main patterns. The first pattern involves swimming at a shallow depth of 100 m and making frequent vertical movements similar to East'12 and West'13. This behavioral pattern is similar to that observed in homing chum salmon [51] in September 1994 [41] and December 1997 on the coast of Sanriku, Japan, and can be considered the general behavioral pattern of homing chum salmon. The second pattern, exhibited by West'12, involves swimming in shallow seawater or at depths of 210–230 m with low diving activity. The vertical movement frequency of East'12 and West'13 was 3.71- and 3.98-fold that of West'12. It can be considered that these individuals inhibited body temperature increases through frequent vertical movement. The reason West'12 could stay in shallow water for a long time when the ambient temperature was considerably lower than that of East'12 and West'13 is probably the appearance of low-temperature water blocks on the surface of the swimming area of West'12 (Fig. 6) [51,56].

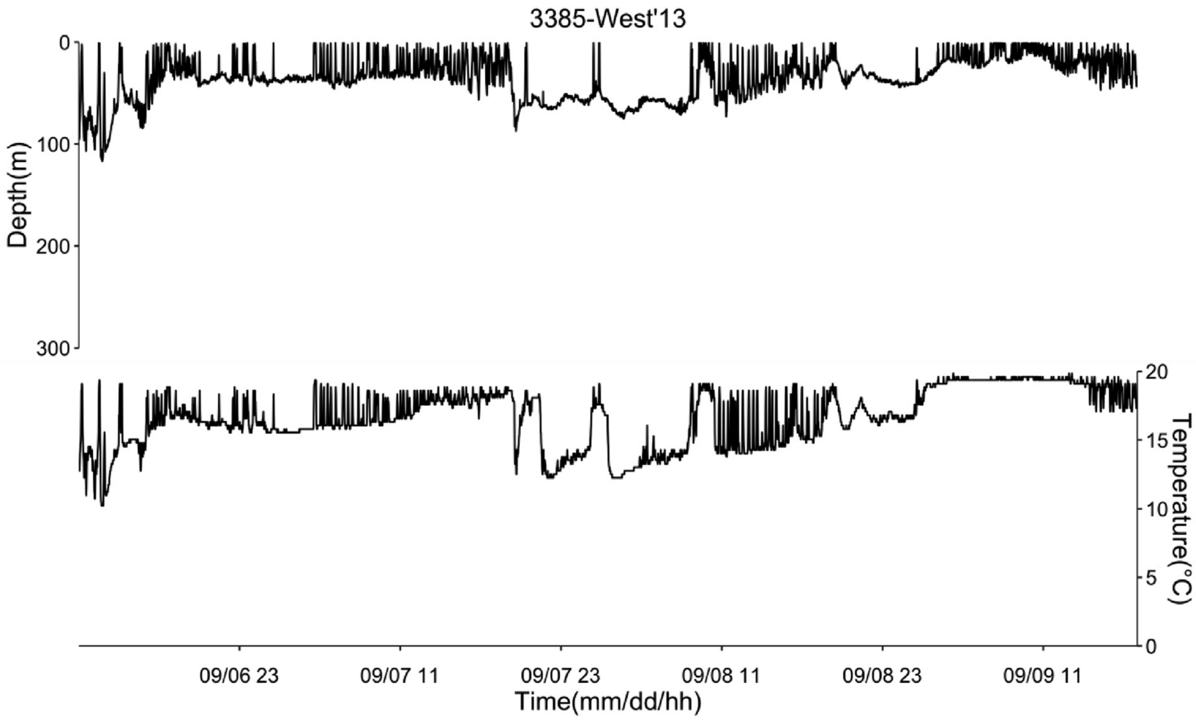

Fig. 9. Typical swimming depth and ambient temperature profiles of homing chum salmon number 3385 retrieved on the west side of the Shiretoko Peninsula in 2013. The vertical axis on the left represents the swimming depth (m), while the right vertical axis represents the ambient temperature (°C).

We calculated the passage frequency of the released individuals based on a depth of 50 m where the thermocline appeared. West'13 and East'12 passed through the thermocline at frequencies of 0.65 and 0.63/h, respectively, 3.8- and 3.7-fold that of West'12, respectively. Chum salmon is an ectotherm with a narrow temperature tolerance [23], and its body temperature changes in response to changes in water temperature. A dramatic drop in water temperature (e.g., thermocline) as a stressor can cause many physiological, behavioral, and health effects in fish [57], including cold shock, which, in extreme cases, can even lead to fish death [58]. Fish often show avoidance tendencies when they encounter a thermocline; this tendency has also been observed in both Atlantic cod (*Gadus morhua*) [59] and Atlantic bluefin tuna (*Thunnus thynnus*) [60]. The low passage rate and distinct swimming pattern of West'12 at a depth of 50 m appeared to be influenced by the thermocline. In addition, among the individuals used for analysis in the present study, two individuals were recovered from the west and east sides of the Shiretoko Peninsula in 2012; however, at the same time, all seven individuals in 2013 were recovered from the west side of the Shiretoko Peninsula. We speculate that some of the homing chum salmon in 2012 changed their homing paths to avoid the thermocline that appeared on the western side of the Shiretoko Peninsula.

Although classified as having similar behavioral patterns, East'12 and West'13 dove to depths >50 m more often than the homing chum salmon on the coast of Sanriku in 1994 [41] and 1997 [51]. This could be due to the greater thermal difference in seawater as the sea surface warms [61]. The deep-diving behavior of East'12 and West'13 minimized metabolic energy costs [51] while searching for their natal rivers [30,31] or regulated body temperature before spawning [62]. In fact, the surface temperature of the coastal waters of the Shiretoko Peninsula during this experiment was approximately 20 °C, while that along the Sanriku coast was 10.5–12.5 °C in 1994 and 12 °C in 1997, much lower than that during the present study.

Salmon trap nets passively trap fish, and catches depend on how often the target fish appear around the nets. Salmon trap nets in the Shiretoko Peninsula typically extend from the surface to a depth of approximately 30 m. In other words, the catch increases when the frequency of chum salmon swimming in waters shallower than 30 m increases. As mentioned above, chum salmon prefer shallow water when the surface temperature decreases and the thermal difference between surface and deep water becomes smaller [63]. Under these circumstances, the frequency of chum salmon occurring around the salmon trap net increases, which is in agreement with Yatsu [64] and Kubo [65], who

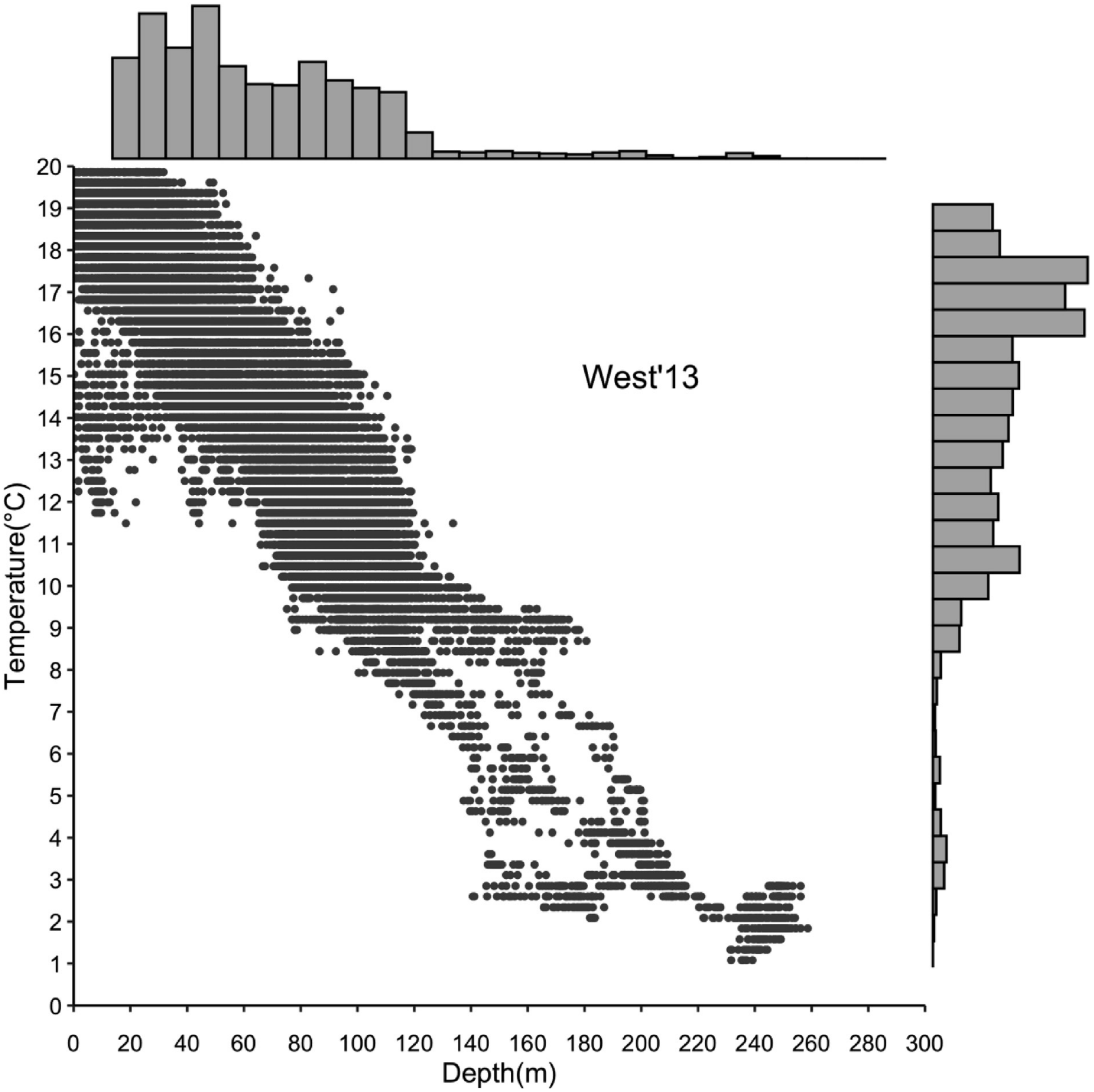

Fig. 10. Relationship between the ambient temperature and swimming depth of West'13. The vertical axis represents ambient temperature (°C), while the right vertical axis represents swimming depth (m). The upper and right histograms show the frequency distribution of swimming depth and ambient temperature for West'13, respectively.

argued that catch increases when low sea surface temperatures occur. Comparing the two behavioral patterns of homing chum salmon observed in this study, it is easily seen that East'12 and West'13 spent most of their time moving at depths shallower than 100 m. Conversely, West'12, which preferred to be active at the surface and in deeper waters from 210 to 230 m, will less frequently be around the nets, as shown in Figs. 6, 8 and 10. This suggests that the behavioral patterns and surface occurrences of chum salmon during their homing migration have been altered due to the influence of the thermocline. The formation of a thermocline due to the confluence of currents is likely one of the reasons for regional variations in catch in the coastal areas of the Shiretoko Peninsula.

In conclusion, our study clearly demonstrated that homing chum salmon adjust their behavioral patterns according to the vertical water temperature structure. Multiple water temperature structures alter the behavioral patterns of chum salmon along the coast of the Shiretoko Peninsula. Moreover, this study provides evidence of homing chum salmon avoiding thermoclines. Chum salmon tended to move in the surface layer of seawater or deeper waters away from the thermocline, which decreased the frequency of their appearance around the salmon trap nets, which may be one of the reasons for the decrease in catch. One limitation of this study is that the data logger recorded the continuous swimming behavior of East’12 from the time it was released on the west side of the Shiretoko Peninsula until it was retrieved on the east side, but due to the absence of location tracking experiments, we cannot determine when East12 entered the eastern waters of the Shiretoko Peninsula. Another limitation is that due to a limited number of released individuals and a short data collection period, we couldn't establish the behavioral patterns of chum salmon with varying caudal fork length, weight, sex, and maturities. It's currently unclear whether salmon with these differences exhibit distinct behaviors when encountering a thermocline, a question we will explore in future research.

Funding

Funding acquisition for this research was provided by Kazushi Miyashita, one of the authors.

Conflict of interest

The authors declare there are no competing interests.

Acknowledgments

The authors would like to express their gratitude to the individuals who have supported and assisted in the development of this paper. Specifically, we would like to acknowledge the staff of the Abashiri Fishery Cooperative, Utoro Fishery Cooperative, and Shari Fishery Cooperative for their valuable support of our study. We also extend our recognition to the ‘Ushio-maru’ research vessel affiliated with Hokkaido University, Faculty of Fisheries, for their assistance in conducting logger experiments and collecting environmental data. Additionally, we would like to express our appreciation to the fishermen and anglers who recaptured marked salmon, as their participation was crucial to the success of our research. Lastly, we would like to thank Editage (www.editage.com) for their professional assistance in editing the English language of the manuscript.

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