Optimum timing and size at release of chum salmon: Improving survival by modifying hatchery practices

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Optimum timing and size at release of chum salmon: Improving survival by modifying hatchery practices

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Abstract

An existing conceptual model that assessed the timing of and size at release of juvenile Japanese chum salmon in Japanese waters is modified using data obtained from young salmon collected in coastal waters off Kombumori, eastern Hokkaido, Japan. The early life histories of Tokachi River late-migrating chum salmon are estimated based on microstructural analysis of thermally marked otoliths from recaptured fish. A revised model is presented that reveals the optimal timing of and size at release of chum salmon juveniles to be dependent upon their size at sea entry and sea surface temperature (SST) near Tokachi River mouth. Juvenile salmon are assumed to grow at a fixed rate after sea entry and to reach a target fork length upon arrival in Kombumori waters when SST conditions are within a specific optimal range. However, because of annual variation in SST, the size at and timing of juvenile chum salmon sea entry following their release from hatcheries represents a moving target, which flexible hatchery release practices are required to meet. Return rates of adult chum salmon to Tokachi River correlate positively with the number of days elapsed between the period when SST is suitable near the river mouth where they enter the sea, and SST conditions in Kombumori waters, which suggests that in years when SST increases rapidly the survival of salmon tends to decline. Windows of optimal times of and sizes at release are proposed for juvenile chum salmon to improve their survival and hatchery success.

KEYWORDS
chum salmon, hatchery, juvenile, migration, otolith, recruitment, release

1 | INTRODUCTION

Chum salmon (*Oncorhynchus keta*) stocks have been supported by intensive hatchery programs in Japan for more than 40 years (Mayama & Ishida, 2003; Miyakoshi et al., 2013). While studies have demonstrated non-negligible quantities of naturally spawned chum salmon occur in Japanese waters (Iida et al., 2018; Miyakoshi et al., 2012; Morita et al., 2013), no quantitative estimates of their population sizes exist throughout their recognized distribution (Miyakoshi et al., 2013).

Hatchery programs have contributed to increased chum salmon stocks in Japan from the 1970s to 1990s (Beamish & Bouillon, 1993; Kaeriyama, 1998; Mayama & Ishida, 2003), but catches began to decline from the mid-2000s, and have continued to do so to present. Catches in 2016 were reduced to levels experienced in the late 1970s to the early 1980s, at a time when annual numbers of released chum fry (1.8–2 $\times$ 10^9) were about the same as at present (Saito & Miyakoshi, 2018).

Coastal oceanic sea surface temperature (SST) and ocean currents around Japan may affect survival of chum juveniles during their early ocean life, contributing to poor recent adult returns (Kitada, 2018; Nagata et al., 2016; Saito & Miyakoshi, 2018; Wagawa et al., 2016). Exactly how coastal conditions affect the survival of these juveniles off Japan is, however, not clear. The Fisheries Agency of Japan, in response to requests from stakeholders (e.g., fishery cooperatives and salmon hatchery associations) and northern prefectural governments, organized several projects from 2013 to promote catch recovery. Increasing chum salmon survival by improving hatchery release techniques is an expectation of these programs.

The size at and timing of release of juvenile salmonids from hatcheries influences their post-release growth and/or survival, in addition to future year-class strengths of catchable fish (Honda et al., 2020; Karppinen et al., 2014; Satterthwaite et al., 2014; Weitkamp et al., 2015; Wertheimer & Thrower, 2007; Zeug et al., 2020). Many studies on hatchery-reared and naturally spawned salmonids have examined the effects of size at and/or timing of sea entry on survival (Bilton et al., 1982, 1984; Claiborne et al., 2011, 2014; Henderson & Cass, 1991; Holtby et al., 1990; Irvine et al., 2013; Jonsson et al., 2016; Karppinen et al., 2014; Morley et al., 1988, 1996; Scheuerell et al., 2009; Ward et al., 1989; Ward & Slaney, 1988; Zabel & Achord, 2004). Based on studies performed in coastal Hokkaido waters, Nogawa (1992) proposed a conceptual model that identified the optimal size at and timing of release of chum salmon in Japan.

An explanation for and background to Nogawa's model is provided by Seki (2013), so it is not repeated here. However, in brief, this model is two-dimensional with an x-axis represented by coastal SST and a y-axis by size at hatchery release (Figure 1). SSTs are used to appraise the timing of release, with 5–13°C considered an appropriate range for juvenile chum salmon to reside in coastal Japanese waters. Size at release along the y-axis ranges 50–80 mm fork length (FL) based on Kaeriyama (1986), who determined that juveniles ≥50 mm FL commenced coastal residency and those ≥80 mm FL

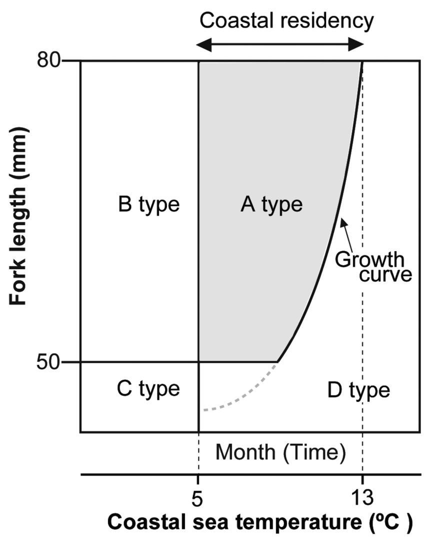

FIGURE 1 Conceptual model depicting the optimal size at and timing of release of juvenile chum salmon. Release is related to coastal sea temperature and occurs at preferred fork lengths (FL) of 50–80 mm. After release, juveniles are expected to grow to an FL exceeding 80 mm FL before coastal sea temperatures reach 13°C. Releases are categorized into Types A–D, with Type A releases (shaded) deemed preferred in Japanese hatcheries

commenced offshore migration. Thus, juvenile chum salmon should be at least 80 mm FL by the time SSTs reach 13°C, about the empirical upper SST limit for their distribution in Japanese coastal waters. To incorporate growth in coastal waters, a specific growth rate (SGR) which enabled fish to attain 80 mm FL by the time coastal SST reached 13°C was assumed. Mark–recapture studies on hatchery-reared chum salmon revealed a coastal SGR to average 0.01 (Seki, 2013). In general, SGR $= (\ln FL_2 - \ln FL_1)/(t_2 - t_1)$, where FL_1 and FL_2 are fork lengths at the time of t_1 and t_2, respectively (Wootton, 1998). When the FL_1 is set to 50 mm FL (the FL at the start of coastal residency ($t = t_1$)), the growth curve after sea entry of chum salmon juveniles can be described as $FL_t = 50 \exp(SGR\ (t - t_1))$. Therefore, by incorporating 0.01 into the SGR of the equation above, Nogawa's model (Figure 1) was constructed.

Four categories of juvenile chum salmon are recognized in Nogawa's model (Figure 1): (a) fish released at FL ≥ 50 mm when coastal SSTs range 5–13°C, and expected to grow to FL ≥ 80 mm until coastal SST reaches 13°C; (b) fish released at FL ≥ 50 mm when coastal SST is below 5°C; (c) fish released at FL < 50 mm when coastal SST is below 5°C; and (d) released fish that do not fit any of Categories A–C (National Salmon Resources Center, 1998). Based on these categories, Nogawa (1992) appraised the proportion of chum salmon releases in Category A (regarded as suitable for release for coastal survival) to total release numbers of chum released into the Honshu Sea of Japan, in 1987 and 1988.

While Nogawa's original model is simple, difficulties arise in its application to individual hatcheries. Because Japanese juvenile chum salmon migrate along coasts and over long distances toward the Sea of Okhotsk (Irie, 1990; Urawa, 2000), it is unclear which coastal SSTs (e.g., those near the river mouth or during the migration) should be considered in the model. Additionally, juvenile SGRs in coastal waters vary between years and are also dependent on hatchery locations (stock origin) (e.g., Honda et al., 2017; Saito et al., 2009), but the SGR in the concept model is generally fixed at 0.01. Finally, according to Kaeriyama (1986), juveniles of FL ≥ 80 mm actively migrate offshore, but juveniles may depart coastal waters near natal rivers from about 70 mm FL (Mayama et al., 1982). Thus, in the concept model, a FL of 80 mm does not necessarily dictate commencement of offshore migration. To efficiently use the concept model in actual hatcheries, model parameters (e.g., SSTs, size at release, and SGR) must be adjusted for each hatchery. Furthermore, results from appraising release lots using Nogawa's concept model should be compared with adult return numbers to identify the optimal size at and timing of release of juvenile chum salmon that can be expected to increase adult returns.

To adapt Nogawa's model to a specific hatchery, as a case study, it is herein modified to include size at sea entry, SSTs at the time of sea entry, SSTs during migration, and SGR for late-migrating Tokachi River chum salmon propagated after November. Model parameters are estimated from daily increment analysis (Honda et al., 2017, 2020; Saito et al., 2009) of thermally marked otoliths of Tokachi River juvenile chum salmon recaught in Kombumori coastal waters, about 80 km from the mouth of Tokachi River. Based on these recaught individuals, a suitable size at release and timing of sea entry are estimated which would enable juveniles to migrate to Kombumori waters in the 2004–2013 brood years (BYs). Release conditions are then examined to determine how coastal SSTs affect adult returns during their early ocean life.

2 | METHODS

2.1 | Tokachi River chum salmon

Five salmon hatcheries occur within the Tokachi River watershed. Of these, the Tokachi Salmon Hatchery Station (TSHS) is owned by the Japan Fisheries Research and Education Agency (Figure 2); the other four are owned by the Tokachi Kushiro Salmon Enhancement Program Association. From 1997 to 2016, an average of 61.8×10^6 chum salmon juveniles were released from these hatcheries annually into Tokachi River (Japan Fisheries Research and Education Agency, "Numbers of in-river catch, egg collection and juvenile releases by salmon rivers," http://salmon.fra.affrc.go.jp/zousyoku/river/river.html, accessed January 13, 2021). An annual average of 15.3×10^6 of these juveniles were liberated from the TSHS (Japan Fisheries Research and Education Agency, unpubl. data). Since brood year (BY) 2004, otoliths of all TSHS chum juveniles have been thermally marked.

Adult chum salmon returning to Tokachi River are caught for hatchery brood stock during the months of August and December either from a tributary in the lower part of Sarubetsu River where a weir has been installed 40 km upstream of the Tokachi River mouth or from below the Chiyoda Dam on the mainstream, 43 km upstream from the river mouth (Figure 2). Although potential natural spawning habitat for chum salmon exists in this river, few of them naturally spawn here, which suggests that this population is largely maintained by hatchery-reared fish (Urabe et al., 2013).

Late-migrating chum salmon returning to Tokachi River after November have relatively low in-river return rates compared with earlier-migrating fish (Figure S1). To relate the size at and timing of juvenile release to adult returns, the otoliths of TSHS chum salmon juveniles produced from late-migrating adults have been thermally marked for BYs 2004–2014 (excluding BYs 2010–2012) (Table 1).

2.2 | Juvenile surveys and checking otolith thermal marks

The Japan Fisheries Research and Education Agency (formerly National Salmon Resources Center) has performed juvenile salmon monitoring surveys in coastal waters off Kombumori (Figure 2) since 1997. Each year surveys have been carried out six or seven times at 7- to 10-day intervals in June–August. On each survey day, sampling has occurred at stations 0.6, 1.2, 4.0, 8.0, and 12 km from shore, where juvenile chum salmon have been collected by surface trawl nets with 4–38-mm mesh, of length 20–25 m, depth 2–4 m, with a central 3-m bag, deployed between two boats. At each station nets were towed for 10–30 min at 2–3 km/h. Catch was placed into an icebox, transported to a laboratory, and then stored at −18°C until analysis. See Honda et al. (2017) for survey details.

Thawed fish were measured for fork length (FL) to the nearest 0.1 mm before their otoliths (sagittae) were removed beneath a stereoscopic microscope using fine-tipped forceps. After flushing extraneous tissue with water drops, otoliths were individually stored in multi-well plastic plates and allowed to dry at room temperature. One of each otolith pair per fish was then mounted onto a glass slide with thermoplastic cement (Buehler, https://www.buehler.com) and polished with Buehler FibrMet abrasive discs (0.3–12-μm grind sizes) until the core appeared. The otolith thermal-mark hatch code was read at 200× by at least two experts, and the fish origin (river and/or region, release lot) then identified from a hatch code database (similar to that on the NPAFC website, http://wgosm.npafc.org) maintained by the Salmon Research Department, Fisheries Resources Institute, Japan. From 2005 to 2015, 79 juvenile chum salmon originating from late-migrating adults were recaught during these surveys (Table 2).

2.3 | Otolith daily increment analysis

Size at and timing of sea entry and days of coastal residency were estimated from otolith daily increment analysis of these juveniles (Table 2). If an otolith was missing, composed of vaterite, or lost in processing, the individual from which it came was excluded from analysis (thus, there are fewer sample numbers than captured individuals in Table 2). Individual otoliths were glued to glass slides using

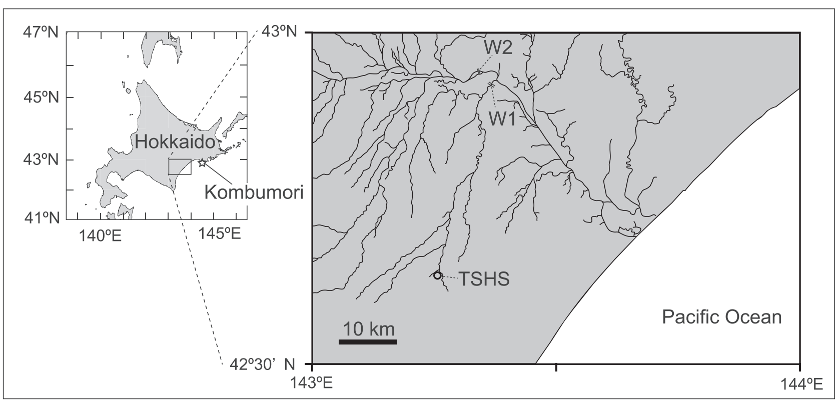

FIGURE 2 Study sites. The star in the left panel marks Kombumori coastal waters where juvenile chum salmon are collected. The right panel shows the Tokachi River system, with the Tokachi Salmon Hatchery Station (TSHS) from where juvenile chum salmon with otolith thermal marks are released. Adult chum salmon migrating upriver are collected each year at locations W1, a fish weir in Sarubetsu River, and W2, near Chiyoda Dam

TABLE 1 Release data for chum salmon juveniles produced from eggs collected in November, identifiable with thermally marked otolith in Tokachi River

Brood year	Otolith mark	Nov date eggs collected	Date of release	Number released × 10^3	Average fork length at release (mm)
2004	2,4n-3nH	17, 2004	May 31, 2005	1507	50.9
		27, 2004		1514	54.1
2005	2,4n-3nH	20, 2005	May 29, 2006	1540	54.7
		30, 2005		1541	52.8
2006	2–5-4H	14, 2005	May 22, 2007	1550	55.2
		24, 2005	May 24, 2007	1540	51.5
2007	2–5-4H	14, 2007	May 22, 2008	1550	59.0
		24, 2007		1432	52.0
2008	2–5-4H	14, 2008	May 29, 2009	1500	63.0
		28, 2008		1514	64.0
2009	2–5-4H	16, 2009	May 24, 2010	1487	57.0
		26, 2009		1492	57.0
2013	2,5,2H	15, 2013	May 23, 2014	1600	57.0
		28, 2013	May 26, 2014	1379	56.0
2014	2–5,2H	5, 2014	May 18, 2015	1333	57.0
		10, 2014		1335	58.0
	2,5-2H	17, 2014	May 25, 2015	1435	60.0
		27, 2014		1506	59.0

TABLE 2 Number of chum salmon juveniles with otolith thermal marks collected in coastal waters off Kombumori, eastern Hokkaido, Japan, and results of their otolith microstructure analyses

				Results of otolith microstructure analysis				
Brood year	Otolith mark	# of juveniles caught off Kombumori	FL at capture[a] (mm)	# fish in sample	Date of sea entry[b]	FL at sea entry[a] (mm)	SGR[a] (× 10^{-3})	Days of coastal residency[b]
2004	2,4n-3nH	23	78.2 ± 3.5	18	May 28, 2005 (May 20–June 2)	54.4 ± 3.4	9.67 ± 1.76	38 (33–46)
2005	2,4n-3nH	0	-	0	-	-	-	-
2006	2–5-4H	9	78.6 ± 4.2	5	May 26, 2007 (May 20–June 1)	59.4 ± 4.2	7.88 ± 1.18	35 (30–44)
2007	2–5-4H	7	84.4 ± 4.5	7	May 27, 2008 (May 17–June 3)	59.9 ± 2.4	7.77 ± 1.25	44 (37–50)
2008	2–5-4H	21	82.3 ± 7.2	18	June 7, 2009 (May 28–June 12)	63.2 ± 4.6	9.53 ± 2.11	27 (15–40)
2009	2–5-4H	17	76.5 ± 2.9	15	June 4, 2010 (May 21–June 13)	58.1 ± 6.3	11.03 ± 2.57	25 (15–39)
2013	2,5,2H	0	-	0	-	-	-	-
2014	2–5,2H	0	-	0	-	-	-	-
	2,5-2H	2	88.0 ± 1.8	0	-	-	-	-
Total		79	79.8 ± 5.6	63	June 1 (May 17–June 13)	58.8 ± 5.6	9.60 ± 2.22	32 (15–50)

Abbreviations: -, no data; FL, fork length; SD, standard deviation; SGR, specific growth rate.
[a]Mean ± SD.
[b]Mean (range).

thermoplastic cement and polished as described previously for hatch code determination until increments around the otolith margin were clearly visible. When juvenile chum salmon migrate from fresh to salt water and remain there for some time, a "sea entry check" forms on their otolith (Saito et al., 2007). Although this sea entry check can be difficult to identify, using light microscopy, a difference can be observed in the increments formed in fresh and salt waters (Saito et al., 2007), especially if a fish has been in salt water for 5–7 days or more (Saito, unpubl. data).

The number of daily increments and their widths from the sea entry check to the otolith edge were measured on each otolith using an ARP/W + RI measurement system (Version 5.30; Ratoc System Engineering Co. Ltd., Tokyo, Japan). An axis passing through the otolith core was drawn in either the dorsal or ventral direction, depending on increment readability. The sea entry check was then specified on a computer screen, and each daily increment was specified along the measurement axis to the otolith edge at 200× or 400×. From this measurement, the otolith radius from the core to sea entry check (R_{se}), total otolith radius from the core to the otolith edge (R_t), and number of daily increments formed during coastal residency (ND) were calculated.

Fork length at sea entry (FL_{se}) was back-calculated from each R_{se} in the same method used by Honda et al. (2020). The assumed relationship between total otolith radius (OR) and FL for salmon juvenile is $FL = a \times OR^{\wedge}b$, where a and b are parameters to be estimated for each fish, and determined so as to pass two points—one at hatch (OR_H or FL_H) and the other at capture (OR_C or FL_C)—minimizing the sum of squared residuals of both points using Microsoft Excel Solver. OR_H and FL_H are fixed for all individuals at 111.11 μm and 20.44 mm or 143.13 μm and 20.44 mm, depending on whether a measurement axis extended dorsally or ventrally, respectively. For OR_C and FL_C, actual measured values for each fish (R_t, FL at capture) were used. Once parameters of a and b were obtained, FL_{se} was calculated by substituting R_{se} for OR in the equation. For each fish, the days of coastal residency and date of sea entry were calculated from ND and date at capture.

To modify Nogawa's model for optimal size at and timing of chum salmon release from a hatchery, SST at sea entry was used as an index of timing of sea entry. Because the date of sea entry for each fish was estimated from otolith daily increment analysis, daily mean SST on the date of sea entry in the area nearest Tokachi River mouth was selected from merged satellite and in situ Global Daily Sea Surface Temperature (MGDSST) data sourced from the NEAR-GOOS Regional Real Time Database (http://ds.data.jma.go.jp/gmd/goos/data/database.html, accessed on July 17–18, 2019). MGDSST is provided for each 0.25° × 0.25° grid from 89.875°S to 89.875°N and 0.125°E to 359.875°E. For daily mean SST on the date of sea entry, SSTs for a 0.25° grid centered on 42.625°N, 143.875° E were used; the Tokachi River mouth is at 42.693°N, 143.664°E (Saito et al., 2015).

Some estimated sea entry dates predated actual release dates (range −1 to −11 d, average −3.6 d, n = 19). This suggests that some TSHS juveniles escape before release dates and/or that estimates for days of sea entry contain errors. When differences of −4 d (rounded to the nearest whole day from 3.6) occurred, estimate errors of +4 d are also probable; accordingly, estimates for days of sea entry contain (on average) errors of ±4 days. To accommodate this error, the average SST over a 9-d period centered on the estimated sea entry date for each fish was taken as the SST at sea entry for that fish. SST at capture in Kombumori waters was similarly prepared from MGDSSTs. Because dates at capture were exact (not estimated), SST was selected from the SST database for the capture date of each fish on a 0.25° grid centered on 42.875°N, 144.375°E.

SGR was calculated as SGR = (ln (FL at capture) − ln (FL_{se}))/days of coastal residency (Wootton, 1998), with variables based on individually measured FL at capture and estimated FL_{se} and days of coastal residency.

2.4 | Adult returns to Tokachi River

Adult chum salmon returning to Tokachi River are monitored at approximately 10-d intervals during their upriver migration from September to November for body size (FL, body weight), age based on scales, and otolith thermal mark hatch codes in a process reviewed by Saito (2015). On each monitoring day, about 50 adult males and 50 adult females were randomly sampled at the weir and measured. Some scales removed from each fish from body areas posterior to the dorsal and anterior to the anal fins, and from upper and lower lateral lines, were placed between holding papers, then later glued onto gummed cards, and pressed onto acetate slides to make impressions. Scale impressions were then read by two or more experts with a reflex projector to determine age. Otoliths were stored individually in multi-well plastic plates and then prepared as described for juvenile hatch code detection.

Once fish age and hatch-code compositions were determined for males and females for a given monitoring day, their compositions were extrapolated to the total in-river catch numbers for each sex for that 10-d interval including the monitoring day. These estimates of total in-river catch by sex, age, and hatch code were then summed for the entire upriver season to generate total numbers of in-river catch by age and hatch codes for each year.

Although chum salmon returning to Tokachi River are caught at two sites, fish with otolith thermal marks were released only from the Sarubetsu River TSHS site (Figure 2). According to Kusumo (2017), estimates of chum salmon with otolith thermal marks (from the TSHS) to total in-river catch ranged 24.7%–41.2% at the Sarubetsu River weir from 2013 to 2014, but below the Chiyoda Dam, these estimates ranged 1.1%–1.8% for this same period. The Chiyoda Dam is 5 km upstream of the point where the Sarubetsu River and mainstream converge, with the weir on Sarubetsu River built 1 km upstream from this. Despite these two locations being close, adult chum salmon released from the TSHS were mainly caught in their natal Sarubetsu River tributary. Thus, estimates of in-river catch by age and hatch code are made based on catches solely from the Sarubetsu River weir. In-river return rate (%) for each hatch code was calculated based on the sum of numbers of in-river catch of age 2–5 fish/the total release number × 100.

2.5 | Data analyses

Annual differences in FL at sea entry, SGR, and FL at capture among BYs were examined by analysis of variance (ANOVA). Because days are discrete variables, annual differences in days of coastal residency among BYs were assessed by nonparametric Kruskal–Wallis tests. To compare FL at sea entry to FL at release for each BY, average FL at sea entry and average FL at release (Table 1) were tested by one-tailed *t*-test; it was evident at the time average FL at sea entry was calculated if the former was greater or smaller than the latter, in which case I used a one-tailed *t*-test instead of two-tailed one. Instead of incorporating interannual variability in FL at sea entry, SGR, and FL at capture into Nogawa's original model (Figure 1), overall mean values are used. Before using overall mean values, normality for FL at sea entry, SGR, FL at capture, SST at sea entry, and SST at capture were first evaluated using the Shapiro–Wilk test, and a coefficient of variation (CV) was also calculated for FL at sea entry, SGR, and FL at capture. Correlations between in-river return rates by hatch code and potential drivers affecting salmon survival, such as date and FL at release, and several outputs from the revised model were tested with Spearman's rank correlation. All statistical analyses were performed using R Version 3.5.2 (R Core Team, 2018).

3 | RESULTS

3.1 | Interannual variability in FL at capture and sea entry, timing of sea entry, days of coastal residency, and growth rates of juvenile chum salmon

Some 79 juveniles sourced to late-migrating adult salmon with otolith thermal marks were caught from 2005 to 2015 off Kombumori (Table 2). Despite 3081×10^3 (2005) and 2979×10^3 (2013) BY juveniles being released from the TSHS (Table 1), none was caught off Kombumori. Additionally, no BY 2014 juveniles with a 2–5,2H hatch code were caught (Table 2).

Mean FL at capture (±SD) ranged 76.5 ± 2.9 to 84.4 ± 4.5 mm (Table 2), with a statistically significant difference among BYs (Figure S2a). Based on Table 1, average FLs of released juveniles for each hatch code weighted by the number of fishes released are 52.5 mm (BY 2004), 53.8 mm (BY 2005), 53.4 mm (BY 2006), 55.6 mm (BY 2007), 63.5 mm (BY 2008), 57.0 mm (BY 2009), 56.5 mm (BY 2013), and 57.5 mm (BY 2014, 2–5,2H hatch code) and 59.5 mm (BY 2014, 2,5-2H hatch code). If this average represents the population mean for each BY group (because variance data for FL at release are unavailable), the average FL at sea entry of juveniles in BYs 2004, 2006, and 2007 was significantly greater than the average FL when they were released (one-tailed *t*-test: [BY 2004] $t = 2.386$, df = 17, $p < 0.05$; [BY 2006] $t = 3.255$, df = 4, $p < 0.05$; [BY 2007] $t = 4.632$, df = 6, $p < 0.01$). Differences in FL at sea entry and FL at release were 1.9 mm for BY 2004, 6.0 mm for BY 2006, and 4.3 mm for BY 2007. No statistically significant differences in FL at release or FL at sea entry were found for BYs 2008 and 2009 (one-tailed *t*-test: [BY 2008] $t = -0.308$, df = 17, $p > 0.05$; [BY 2009] $t = 0.673$, df = 14, $p > 0.05$).

Average FL at sea entry differed among BYs (Figure S2b). FL at sea entry for BY 2008 appeared greater than for other BYs (Table 2), probably because of the greater FL at release for BY 2008 (Table 1). On average, juvenile chum salmon recaught in Kombumori coastal waters spent 32 days at sea (Table 2). Average days of coastal residency differed significantly among BYs (Kruskal–Wallis test; $\chi^2 = 39.018$, df = 4, $p < 0.0001$, Figure S2c). Average SGR ± SD during coastal residency was $9.60 \times 10^{-3} \pm 2.22 \times 10^{-3}$ for all juveniles (Table 2). Average SGR also differed significantly among BYs (ANOVA; df = 4; 58, $F = 4.246$, $p < 0.001$, Figure S2d).

Although statistically significant differences were detected among BYs for FL at capture, FL at sea entry, days of coastal residency, and SGR, these estimates are not available for some BYs (2005, 2013, and 2014) because no or too few samples were available. Additionally, these estimates were obtained from only 63 fishes. Because of this, based on these estimates, no attempt is made to incorporate interannual variability in FL at sea entry, FL at capture, and SGR into a revised model. Instead, overall mean estimate values are used, where necessary.

3.2 | Frequency distribution of juvenile chum salmon FL at sea entry and capture, SGR, and SST at sea entry and capture

Histograms for FL at sea entry, SGR, and FL at capture in otolith increment analyses ($n = 63$) are presented in Figure 3. Estimates follow normal distributions (Shapiro–Wilk test: [FL at sea entry] W = 0.978, $p = 0.321$; [SGR] W = 0.971, $p = 0.149$; [FL at capture] W = 0.975, $p = 0.218$). FL at capture for all juveniles ($n = 79$) also followed a normal distribution (Shapiro–Wilk test: $W = 0.982$, $p = 0.327$). The CV of SGR (0.231) was greater than those for FL at sea entry (0.095) and FL at capture (0.071). The frequency distribution of SSTs at sea entry and capture were not normally distributed (Shapiro–Wilk test: [SST at sea entry] W = 0.935, $p = 0.002$; [SST at capture] W = 0.841, $p < 0.0001$). Quartiles 1 and 3 (the 25th–75th percentile values) for SST at sea entry (6.7–8.7°C) and SST at capture (11.0–12.8°C) (Figure 4) incorporate half of the juveniles in this study; these values for SST at sea entry are hereinafter referred to as the "Window for SST at sea entry" (WSSTse), and those for SST at capture the "Window for SST at capture" (WSSTca).

3.3 | Modifying Nogawa's model for optimal size at and timing of release

Juvenile chum salmon migrating from Tokachi River and caught in Kombumori coastal waters grew on average 79.8 mm FL, with a mean SGR of 9.60×10^{-3}, so the revised model incorporates these values when Kombumori SST conditions are within the WSSTca range. In Figure 5, the revised model is presented using average SST for

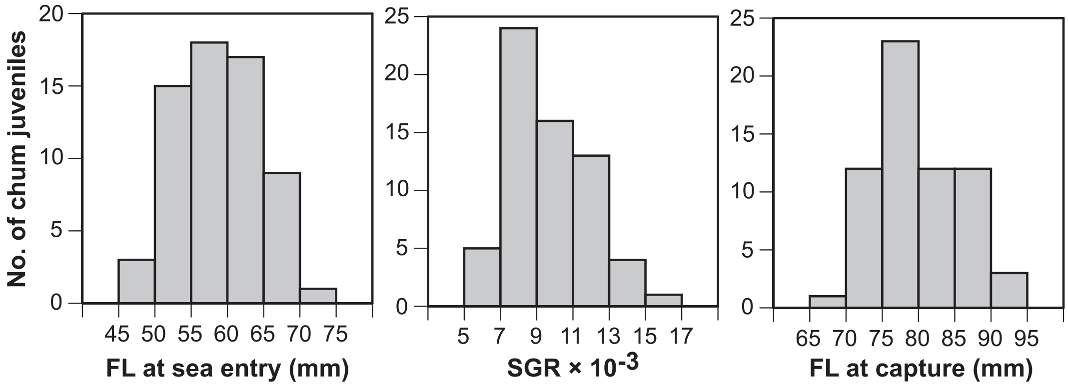

FIGURE 3 Histograms of fork length (FL) at sea entry, specific growth rate (SGR), and FL at capture of juvenile chum salmon from coastal waters off Kombumori. FL at sea entry and SGR are estimated from otolith microstructure analyses

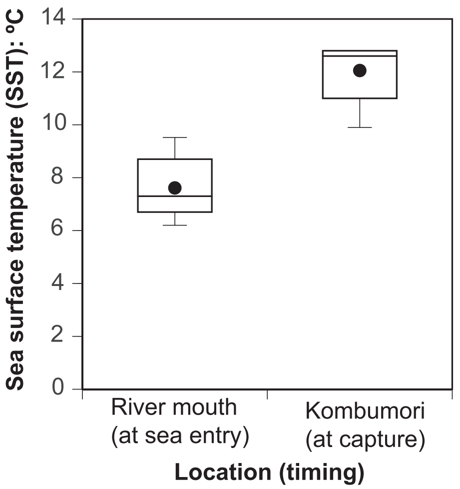

FIGURE 4 Boxplots of sea surface temperature (SST) experienced by juvenile chum salmon at sea entry near the Tokachi River mouth and from where they were caught in coastal Kombumori waters. Boxes represent 75th and 25th percentiles, bars in boxes represent medians, whiskers represent 90th and 10th percentiles, and dots represent means. WSSTse = 25th to 75th percentiles of SST at sea entry, and WSSTca = SST at capture from 25th to 75th percentiles

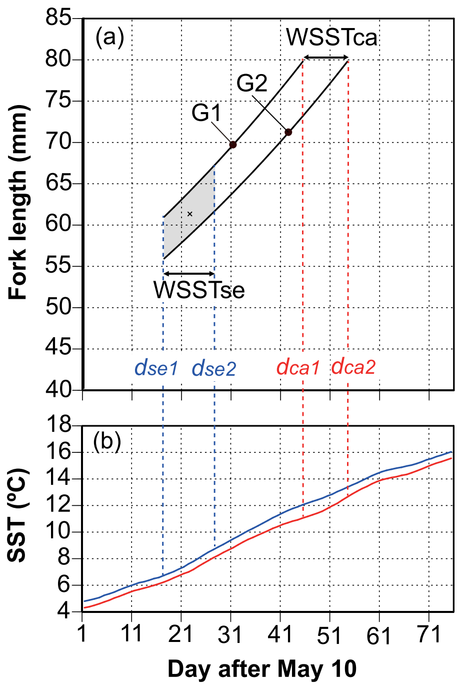

FIGURE 5 (a) Revised model for optimal size at and timing of releases of the late-migrating Tokachi River chum salmon and (b) averaged daily sea surface temperature (SST) from 2005 to 2015 near the Tokachi River mouth (blue) and in Kombumori waters (red). In the upper panel (a), the x- and y-axes indicate the date after May 10 and the fork length at sea, respectively. WSSTca = window of SST at capture; WSSTse = window of SST at sea entry; d_{se1} and d_{se2} = the first and last days of the WSSTse, respectively; d_{ca1} and d_{ca2} = the first and last days of the WSSTca, respectively; G1 and G2 = growth curves drawn suing the equations FL (t) = 79.8 exp(−SGR (d_{ca1} − t)) and FL (t) = 79.8 exp(−SGR (d_{ca2} − t)), respectively, where SGR and t mean specific growth rate (= 9.60 × 10^{-3}) and date after May 10, respectively; shaded area = optimal area of size at and timing of sea entry of late-migrating Tokachi River chum salmon; "×" marks the center of the optimal area

2005–2015. First, a duration of the WSSTca is determined on the x-axis based on daily SST at Kombumori; the first and last days of the WSSTca are defined as d_{ca1} and d_{ca2}, respectively. Using 79.8 mm FL for arrival of Kombumori and an SGR of 9.60 × 10^{-3}, the growth of a fish arriving at Kombumori at time d_{ca1} can be expressed as FL(t) = 79.8 exp (−9.60 × 10^{-3} (d_{ca1} − t)). Similarly, the growth of a fish arriving at Kombumori at time d_{ca2} and 79.8 mm FL can be expressed as FL (t) = 79.8 exp (−9.60 × 10^{-3} (d_{ca2} − t)). The two growth curves, G1 and G2, are drawn backward, one from d_{ca1} (at a temperature of 11°C, 45 days after May 10) and one from d_{ca2} (at a temperature of 12.8°C 54 days after May 10) on the y-axis at FL of 79.8 mm. Because half of all juveniles also experienced WSSTse conditions, the WSSTse values are also plotted on this graph, based on daily SST at the mouth of Tokachi River. The first and last days of the WSSTse are defined as d_{se1} and d_{se2}, respectively; d_{se1} is the day when 6.7°C temperatures are first experienced (17 days after May 10), and d_{se2} is the day when 8.7°C temperatures are reached and not exceeded (27 days after May 10). The gray-shaded area within the two growth curves bound by this temperature range then represents the size at and timing (after May 10) of sea entry required for juvenile chum salmon to have attained an FL of 79.8 mm upon arrival in Kombumori coastal waters in WSSTca conditions. This gray-shaded area is hereinafter referred to as the "optimal area."

For each BY from 2004 to 2014, the optimal area varies (Figure 6). Optimal areas for BYs 2008 and 2014 extend over a longer time than those for other BYs. In years in which the WSSTse is protracted, the optimal area also increases. From the definition for modifying the conceptual model, when the WSSTca is short, the range of FL at sea entry is also narrower. The optimal area for BY 2013 has a FL that is almost 65 mm at sea entry. When the interval between the WSSTse and WSSTca was shorter, FL at sea entry for the optimal area increased, such as for BY 2013.

3.4 | Effects of release practice and coastal SST on in-river return rates of Tokachi River chum salmon assessed using the revised model

Neither date of release expressed in days from May 1 in each release year nor size at release was correlated with in-river return rates for BYs 2004–2009, or BYs 2013–2014 (Spearman rank correlation: [date of release] $\rho = 0.202$, $p > 0.05$; [size at release] $\rho = -0.033$, $p > 0.05$). Mean SST at sea entry, mean SST at capture, and mean SGR were also not correlated with in-river return rates (Spearman rank correlation: [SST at sea entry] $\rho = 0.6$, $p > 0.05$; [SST at capture] $\rho = -0.1$, $p > 0.05$; [SGR] $\rho = -0.1$, $p > 0.05$). Coordinates of center points in optimal areas for BYs in Figure 6 are not correlated with in-river return rates (Spearman rank correlation: [date of sea entry] $\rho = -0.092$, $p > 0.05$; [FL at sea entry] $\rho = -0.460$, $p > 0.05$). The number of days from the start of the WSSTse to the end of the WSSTca does not correlate with in-river return rates (Spearman rank correlation: $\rho = 0.460$, $p > 0.05$). Neither WSSTse duration nor WSSTca duration correlates with in-river return rates (Spearman rank correlation: [WSSTse duration] $\rho = 0.261$, $p > 0.05$; [WSSTca duration] $\rho = -0.483$, $p > 0.05$). The number of days between the WSSTse and WSSTca are positively correlated with in-river return rates (Spearman rank correlation: $\rho = 0.792$, $p < 0.05$; Figure 7). Although a significant relationship was not observed, a tendency for the CV of FL at capture to increase (Spearman rank correlation: $\rho = 0.667$, $p > 0.05$, Figure 8) is apparent when the number of days between the WSSTse and WSSTca increases.

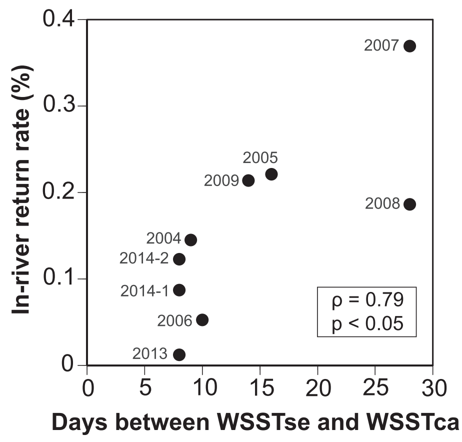

FIGURE 7 Relationship between the WSSTse and WSSTca time intervals and in-river return rates for late-migrating Tokachi River chum salmon with thermally marked otoliths. Years = brood years (BY); BY juveniles in 2014 were released with two different otolith thermal marks, expressed here as 2014–1 and 2014–2, respectively

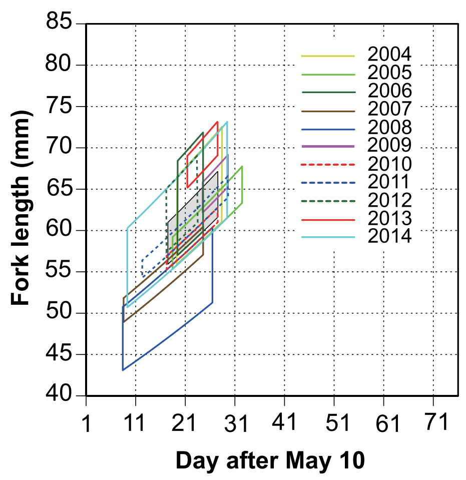

FIGURE 6 Estimated optimal areas for late-migrating Tokachi River chum salmon based on sea surface temperatures. Colors indicate brood years. The optimal areas for 2010–2012 brood years are shown as dotted lines, because late-migrating Tokachi River chum salmon from these brood years lack thermally marked otoliths, and were excluded from analyses

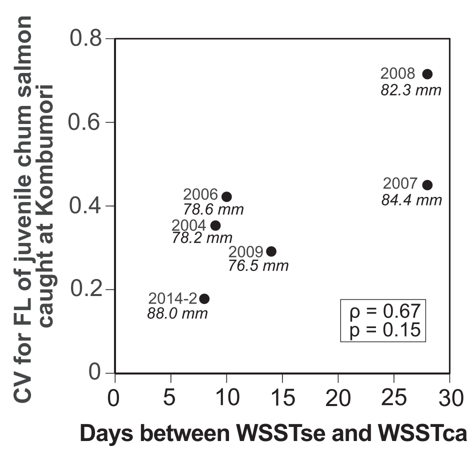

FIGURE 8 Relationship between WSSTse and WSSTca time intervals and coefficient of variation for fork length of juvenile chum salmon at capture in Kombumori waters. Regular and italic letters near filled circles in the graph indicate brood years and mean fork lengths, respectively

4 | DISCUSSION

A methodology modifying Nogawa's conceptual model for the optimal size at and timing of release of chum salmon fry is proposed that uses data obtained from microstructure analysis of otoliths from thermally marked chum juveniles recaught in coastal waters. Using Tokachi River late-migrating chum salmon with otolith thermal marks for BYs 2004–2009 and 2013–2014 as a testbed, the window of optimal size at and timing of fry release in relation to coastal SST is visualized graphically. This information is very useful for appraising hatchery release practices. In addition, optimal areas in Figure 6 indicate that the optimal size at and timing of sea entry varied year to year, reflecting variation in coastal SST. This indicates that the size at and timing of sea entry represents a moving target, as reported by Mathews and Ishida (1989) and Irvine et al. (2013). Therefore, predicting fixed optimal release dates is impractical, especially in an increasingly variable environment.

The position and size of optimal areas in Figure 6 differs among BYs. Generally, in years when the WSSTse was protracted (or brief), optimal areas were extended (or shortened), and in years when the WSSTca was protracted (or short), the range of FL at sea entry increased (or decreased), respectively. When both the WSSTse and WSSTca were short, the optimal areas decreased, such as in BYs 2009 and 2013. When intervals between the WSSTse and the WSSTca were short, the upper sides of the optimal areas (indicating the upper limits of FL at sea entry) were vertically higher. The BY 2013 optimal area was the most extreme, with juvenile salmon of almost 65 mm FL required at sea entry. Because no BY 2013 juvenile chum salmon were caught in Kombumori coastal waters (Table 2), FL at sea entry for BY 2013 could not be estimated. However, it was likely that FLs at sea entry for BY 2013 were much lower than 65 mm FL.

FL at sea entry for each BY was equal to or exceeded FL at release. In cases where FL at sea entry exceeded FL at release, the difference was at most 6 mm (BY 2006). Because the FL at release for BY 2013 was 56.5 mm, the FL at sea entry for this year could not attain 65 mm, even if FL at sea entry exceeded FL at release by 6 mm (as in BY 2006). Using the revised model, it is apparent that juvenile BY 2013 salmon were too small at release to have attained 79.8 mm FL upon arrival in Kombumori coastal waters, and they likely perished. Because BY 2013 had the lowest in-river return rate, the survival of juvenile salmon could be influenced by whether they did or did not enter the window of optimal area. In this sense, visualizing optimal areas provides a tool to investigate the survival processes of juvenile salmon during their early marine life.

Biological traits measured or estimated for juvenile chum salmon, such as FL at capture, FL at sea entry, days of coastal residency, and SGR, vary between years. The causes for this variability remain unknown. Data for FL at capture, FL at sea entry, and SGR for all juveniles are normally distributed, which suggests that each measurement (estimate) is symmetrical around a mean. Thus, as a first step, the use of mean values for FL at capture, FL at sea entry, and SGR is probably reasonable in a revised model.

The CV for SGR (0.231) is greater than that for FL at capture (0.071) and FL at sea entry (0.095). Although growth during coastal residency is variable, juvenile salmon may need to attain a certain average FL to reach Kombumori coastal waters, because FL at capture showed a normal distribution with a small CV. FL at sea entry also followed a normal distribution with a small CV, implying there might be an optimal size at sea entry to reach Kombumori coastal waters. However, FL at sea entry might be affected by FL at release, because the former increases when the latter increases (see BY 2008). Although there is little control over SGR and FL at capture once juveniles have been released, FL at sea entry could be controlled by adjusting FL at release.

Weitkamp et al. (2015) reported the size at and timing of ocean entry of hatchery-reared Chinook salmon (*O. tshawytscha*) and steelhead trout (*O. mykiss*) into Columbia River estuary to be determined by hatchery practices, such as the timing of and size at which juveniles were released. Thus, the concept model proposed by Nogawa (1992) is modified so that juveniles reach a target FL (79.8 mm FL) in Kombumori coastal waters during the WSSTca period. Alternatively, FL at sea entry could be fixed as a target (e.g., 58.8 mm FL), with SGR growth curves of 9.60×10^{-3} then drawn forward from those days when the WSSTse begins and ends (the duration) to obtain an area bound by growth curves and WSSTca. While this option indicates a range of FL at capture for juveniles arriving in Kombumori coastal waters during the WSSTca, the requirement is to develop conceptual models of optimal size at and timing of release to improve hatchery practices.

Hatchery managers have been advised to stagger juvenile release dates through the natural outmigration period of wild coho salmon (*O. kisutch*) smolt (Irvine et al., 2013). Staggering releases is a bet-hedging strategy that reduces the risk of all fish in any release cohort experiencing the same harsh environment during sea entry and possibly perishing (Satterthwaite et al., 2014). Conversely, if overlap exists in the optimal areas of multiple years, this overlap area might provide a target for size at and timing of sea entry to reduce temporal variability in juvenile mortality. Whichever strategy (staggered or target) is superior, visualizing optimal areas as shown in this study will facilitate conceptualization and development of future hatchery release strategies.

Many studies have dealt with the optimal size at and timing of sea entry or release for Pacific *Oncorhynchus* species (Bilton et al., 1982, 1984; Claiborne et al., 2011, 2014; Henderson & Cass, 1991; Holtby et al., 1990; Irvine et al., 2013; Morley et al., 1988, 1996; Scheuerell et al., 2009; Ward et al., 1989; Ward & Slaney, 1988; Zabel & Achord, 2004). Even within a species (coho salmon), the optimal size at and timing of sea entry or release can differ over small scales, such as occurs among rivers and creeks on Vancouver Island (British Columbia). For example, the optimal release size in Rosewall Creek progressively increased through the release season (Bilton et al., 1982). The effects of timing of release on adult returns were stronger than those of size at release in Quinsam River, with effects of the latter being minor (Bilton et al., 1984; Morley et al., 1988). While larger smolt size in Carnation Creek conferred no consistent survival advantage, larger smolts survived better in years when marine survival was otherwise relatively poor (Holtby et al., 1990). For steelhead trout (*O. mykiss*), smolt-to-adult survival was also not always related to smolt size in Keogh River (Ward, 2000). These findings suggest that optimal release strategies may differ, even in closely located hatcheries or rivers (Irvine et al., 2013).

In addition to potential site-specific optimal release strategies, earlier versions of optimal size at and timing of release models were constructed based on experimental releases for few BYs (Bilton et al., 1982, 1984; Morley et al., 1988). However, effects of size at and timing of sea entry or releases on marine survival differ among years and are related to variability in the marine environment (Holtby et al., 1990). Thus, the optimal size at and timing of sea entry or release should be monitored and adjusted to take environmental variability into consideration (Morley et al., 1996).

Coastal SSTs are used to determine the timing of sea entry and juvenile occurrence in Kombumori coastal waters. Various studies have reported SSTs at sea entry or during coastal residency to affect salmonid growth and survival (e.g., Friedland et al., 2000; Honda et al., 2020; Hvidsten et al., 2009; Mortensen et al., 2000; Mueter, Peterman, & Pyper, 2002; Mueter, Ware, & Peterman, 2002; Nagata et al., 2016; Saito et al., 2011, 2016; Saito & Nagasawa, 2009; Ward & Slaney, 1988). Water temperature directly influences growth and survival through physiological processes (Weatherley & Gill, 1995) and indirectly by changing food resources (zooplankton communities), the numbers of each species in communities, and their phenology (i.e., bloom timing) (Chittenden et al., 2010; Willette et al., 1999; Yamada et al., 2019). Water temperature also affects the temporal and spatial distributions of predatory fishes and juvenile salmon in coastal waters, which may be linked to salmon mortality (Emmett et al., 2006) and migration (Bøe et al., 2019; Byron & Burke, 2014). In coastal waters off Abashiri and Kushiro, eastern Hokkaido, juvenile chum salmon residing within 1 km of shore commence their offshore migration when SST exceeds 8°C (Kasugai et al., 2016; Nagata et al., 2007). The potential effects of sea temperature on salmon survival are so many and varied, and they probably work in conjunction with other factors such as metabolism, food supply, and predator encounters. However, SST may be a proximate cue that in favorable conditions synchronizes juvenile chum salmon migration. In terms of optimal sea entry timing, differences in river temperature and coastal SST may also relate to salmon survival as Miller et al. (2012) mentioned.

In-river return rates of late-migrating Tokachi River chum salmon tend to decrease when the number of days between the WSSTse and WSSTca decreases (Figure 7). This suggests that the rapid increase in coastal SST experienced during juvenile migration may reduce their survival. Although no significant correlation was detected, a tendency was apparent for the CV of FL at capture to increase with an increase in days between WSSTse and WSSTca (Figure 8). Additionally, when the number of days between WSSTse and WSSTca increased, mean FL at capture also increased (i.e., BYs 2007 and 2008), excepting BY 2014. Accordingly, juvenile chum salmon could arrive at Kombumori with a larger (or smaller) mean size and with more (or less) size variation, when coastal SST increases slowly (or rapidly). Honda et al. (2019) demonstrate that growth rates of juvenile Japanese chum salmon captured in offshore waters of the Sea of Okhotsk, where juveniles reside after leaving Japanese coastal waters, were much higher than those reported previously for coastal resident or migrant juvenile chum salmon along the coast of Japan. Taking this result of Honda et al. (2019) into consideration, the size variation among brood years upon arrival at Kombumori might influence their survival following departure, which may affect brood-year abundance as adult fish. Conversely, BY 2014 showed the largest mean FL with the least size variation among examined brood years (Figure 8). This may mean that only fish growing to a much larger size could successfully arrive at Kombumori when coastal SST increased rapidly. Because the window of optimal area for BY 2014 shown in Figure 6 is much larger than that for other brood years, fish could potentially grow larger than those from other brood years. However, such larger fish upon arrival off Kombumori may be less abundant, resulting in poorer adult returns. Size-selective mortality is known for early marine chum salmon life stages, with greater survival of faster-growing and consequently larger juveniles than smaller ones (Honda et al., 2017). Under severe coastal conditions, such as those experienced during rapid seasonal increases in SST, size-selective mortality might act more strongly in coastal waters, where in normal years, size selectivity would be less detectable.

Relatively few late-spawning Tokachi River adult chum salmon returned to Tokachi River compared with earlier-spawning salmon. For this reason, TSHS staff began monitoring salmon returns using thermal marks for BYs 2004–2009, 2013, and 2014. Phenological events such as the timing of spawning are important traits that are closely linked to a species' fitness, and these traits reflect thermal conditions in rivers and oceans experienced by salmon populations (Kovach et al., 2012; Quinn, 2005). Microevolutionary changes in the timing of migration may be one mechanism that enables salmon populations to persist in changing climates (Kovach et al., 2012). Under the actual thermal conditions in Tokachi River and coastal waters adjacent to the river, the survival of juveniles of late-spawning chum salmon may be lower than those of earlier-spawning salmon, like reported for other salmon species (e.g., Kovach et al., 2012; Quinn & Adams, 1996; Scheuerell et al., 2009; Taylor, 2008). Additionally, the timing of migration of chum salmon populations in Hokkaido has changed through hatchery selection (Miyakoshi et al., 2013).

Should coastal SST forecasts be available several months in advance, and predictions of WSSTse and WSSTca be available prior to juvenile chum salmon release, the methodology described herein could be used by hatchery managers to determine an optimal size at and timing of sea entry for chum juveniles, thereby increasing the probability of their reaching Kombumori coastal waters. At some Japanese salmon hatcheries, development of egg-to-alevin chum salmon stages is regulated by heating or cooling of the water, or by transplanting, for example, eggs from one hatchery to another with different water temperatures. This process enables the size at and timing of release of fry to be controlled (Fujise et al., 2003). Additionally, growth control of chum salmon fry is to an extent performed by mixing different water sources of different temperature, such as warm spring and cold river waters. If the window of optimal size at and timing of release can be predicted before release, the post-release growth control and survival of chum salmon may increase. Several nowcast and forecast systems now exist to describe or predict ocean conditions (Kuroda et al., 2017 and references therein), and a method for predicting coastal SSTs a month earlier has been developed to estimate the timing of release of juvenile chum salmon into coastal Sanriku (Japan) waters (Kuroda et al., 2018). In conjunction with this prediction, adjusting the size at and timing of sea entry for juvenile chum salmon might improve their early marine survival.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

T. Saito conceived the manuscript, analyzed the data, and drafted the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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