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Genetic Variation in Early Survival of Chum Salmon Families with Respect to Seawater Temperature

Mi-Kyung Choe[1] and In-Kyu Yeo*
[1]Marine Research Institute, Cheju National University, Cheju 695-810, Korea
Department of Marine Biotechnology, Cheju National University, Cheju 690-756, Korea

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The present study estimated the variation of early survival of chum salmon families with respect to temperature and size after transfer to seawater. Heritability for seawater tolerance of half-sib families was also estimated at 45 days after hatching. Gametes were collected from 6 male and 18 female chum salmon to make 18 paternal half-sib families. Seawater tests were carried out at 3, 7 and 12 ℃ of 32‰ seawater and compared with freshwater. Survival was significantly affected by seawater temperature. The highest seawater tolerance was obtained in 45-day old chum salmon at 7 ℃ seawater and the lowest seawater tolerance was obtained at 3 ℃. Overall survivals in seawater tolerance at 32‰ varied among families. There were significant variance in fry survival among females (P=0.0001), and among males (P=0.0001). The heritabilities of survival in seawater in chum salmon were estimated to be 0.32~0.34 for the sire components at 45 days after hatching in 1998.

Key words: chum salmon, *Oncorhynchus keta*, heritability, seawater tolerance, genetic variation

Introduction

Salmonid propagation is dependent on a greater or lesser degree on artificially reared juveniles for reproduction and early development and releasing. The artificial propagation of salmon has been regarded as a promising way to enhance salmon stocks. In recent years, in order to increase the returning population of salmonids many efforts have also been regarded. Seawater tolerance has been considered effect on survival after releasing in seawater, and has been examined in many salmon species. Size-related salinity tolerance, however, has also been mostly reported for salmonids.

Among the Pacific salmon, chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*), in contrast to masu salmon (*O. masou*) fry are unique in the ecology of their early life at ages (Iwata et al., 1982), and known for exhibiting remarkably efficient hypoosmoregulate ability in their early life stages (Black, 1951; Houston, 1961; Parry, 1960; Weisbart, 1968).

However, chum and pink salmon have been reared for extensive periods in freshwater and can grow in a freshwater (Senn and Buckley, 1978; Kwain and Lawrie, 1981; Iwata et al., 1982).

Early survival rates in marine environment may be dependent upon size at saltwater entry, with smaller fish more prone to predation than larger ones from the same stock (Parker, 1971). When stocks are artificially enhanced, increasing juvenile size before release could therefore increase survival rates in ocean. Initial rearing in marine environment has been reported to enhance juvenile growth and survival (Martin et al., 1981; Higgs et al., 1985).

However, the various studies have been carried out to investigate the hypoosmoregulatory capacity in salmonids recently. The osmoregulatory ability of the fry in seawater gradually decreased with an increase in body weight or in the time spent in freshwater (Iwata et al., 1982). Varnavsky (1991) showed that large (360~500 mg) pink salmon fry are more sensitive to temperature during seawater

*To whom correspondence should be addressed.

adaptation than small (180~280 mg) fry. Kojima et al. (1993) reported that the seawater adaptability of chum alevins develops rapidly after hatching and reaches a climax at the stage of yolk absorption; the adaptability of juveniles slightly decrease with growing from 0.4 to 3~4 g body weight, but then recovers. However, seawater tolerance of chum and masu salmon after releasing in seawater are not well known in detail yet.

On the other hand, Murray et al. (1993) studied on growth and survival of juvenile coho salmon (*O. kisutch*) reared at different salinities. They reported that growth and survival were, on average, higher in freshwater than in seawater, but juveniles from some families had higher or equivalent rates than in seawater than in freshwater. These differences are possible due to genetic difference of fry. The salinity tolerance is related to the effects of temperature, photoperiod, and stages of parr-smolt transformation (Adams et al., 1973; Wagner, 1974; Zaugg and Wagner, 1973; Zaugg and Mclain, 1976; Ewing et al., 1979, 1980).

In the present study, we examined the effect of genetic variation of transferring juveniles to seawater at different temperatures after hatching on their survival.

Materials and Methods

Fish

Chum salmon were obtained from the Yakumo Branch of Hokkaido Salmon Hatchery about 70 km north of Hakodate, Japan in 1997. Gametes were collected from 6 male and 18 female chum salmon. Eggs and sperm were stripped at the Yakumo Branch of the Hokkaido Salmon Hatchery and transported to a laboratory on ice and eggs subsequently fertilized. In a mating system, the eggs from 18 females were separately fertilized with sperm from six males to produce six pairs of paternal half-sib on 2 December 1997.

The fertilized eggs were incubated in a 254 ℓ (290 ×35×25 cm) tank. Each of the 18 families was separately stocked within stainless baskets (19×15 ×6 cm) in the tank. The water was circulated and maintained at 10 ℃. The incubated eggs of each family hatched in late January 1998. At 38 days after hatching, the fry of each family were separated into three lots. Each lot (20 fish were randomly chosen from each of 18 families) was kept in an indoor tank which was supplied with 10 ℃ freshwater. Fish were starved during the experimental period. Each lot was directly transferred from freshwater to 3, 7 and 12 ℃ seawater (32‰) at 45 days after hatching in the tank.

Seawater tolerance test

Salinity was measured by using a Inductively Coupled Salinometer (Model 601 MK III, Watanabe keiki MFG, Co., LTD.). Seawater tolerance was determined by exposing fish to a test seawater and mortalities were recorded periodically during the experimental period. Body weights were also recorded at the start of the experiment. Lighting was under natural photoperiod conditions. Fish were not fed during tests.

In the laboratory, seawater tolerance tests were carried out at salinity of 32‰ and compared with freshwater as control. Test fish were removed from the rearing and transferred to 185 ℓ tanks where the temperature was gradually increased or decreased to approximate the desired temperature for seawater tolerance tests. After 24 hr, fish were placed into 23 ℓ containers immersed in a controlled water bath to regulate and maintain temperature (Neslab Model 10399 Temperature Control Unit). Water was continuously aerated during the 96 hr tests (24 hr, 72 hr for groups).

Analysis

During incubation, dead eggs were removed and stored in Stockard's solution and later inspected to remove unfertilized eggs. Survival rates of egg were then calculated based on the number of eggs initially stocked. After hatching, body weight of fry was measured to the nearest mg. The number of dead fish in each tank was daily recorded.

The effect of transfer temperature in chum salmon fry was considered to be fixed with other random effects. The effects of different temperatures of transfer to seawater on fish weight and survival after 24, 72 and 96 hr of testing were investigated with the analysis of variance model

$$Y_{ijkl} = \mu + S_i + D_{ij} + E_k + SE_{ik} + DE_{ijk} + e_{ijkl}$$

where Y_{ijkl}=observed character; μ=mean; S_i=

effect of male ($i=1\sim6$); Dij=effect of female with male ($j=1\sim3$); Ek=effect of transfer temperature; DEijk=interaction between female and transfer time; e$ijkl$=the uncontrolled environmental and genetic deviations attributable to individuals within progeny.

On the data of survival, analysis of variance was performed in which the phenotypic variance was divided into several observation components: between-male component, σ^2_S, between-female component within male, σ^2_D, between-pair component, σ^2_{SD}, and within-progeny component, σ^2_W, among individuals within a family. Analysis of variance for survival was conducted using binary data (0=dead, 1=alive), and estimated by nested ANOVA.

Heritabilities for salinity tolerance of half-sib families were estimated by the following formula using the variance components described above. Furthermore, standard errors on heritabilities were determined as described by Becker (1984) for equal numbers of progeny in respective mating system.

The heritability for half-sib is expressed as:

$h^2_S=4\sigma^2_S/(\sigma^2_S+\sigma^2_D+\sigma^2_W)$ for sire;

$h^2_D=4\sigma^2_D/(\sigma^2_S+\sigma^2_D+\sigma^2_W)$ for dam;

$h^2_{SD}=2\sigma^2_{SD}/(\sigma^2_S+\sigma^2_D+\sigma^2_W)$ for parent.

Variation in fry weight and survival rates were examined by using analysis of variance (females nested within males). The relationship between fish weight and survival and between transfer time and survival in seawater tolerance tests was examined by testing for independence of survival and weight using the G-test incorporating Williams correction (Sokal and Rohlf, 1981). The Kruskal-Wills test was used to compare fish weight between families, and survival (in hour) between families. Phenotypic correlations between survival and survival related-treats were estimated based on family means by ANOVA.

Results

There was no significant difference in egg weight among females in chum salmon. Survival rate of embryos was above 95% for all but one family, with significant differences observed between females and males ($P<0.005$), but not among males. Survival rates in alevin were above 99% for all families. Means and coefficients of variation (CV=100·SD/mean) for body weight of chum salmon were calculated (Table 1). Chum salmon fry body weight ($P=0.0001$) varied between females within males, and among males ($P=0.0001$).

Table 1. Means and coefficients of variation (CV) for body weight (mg) of chum salmon, *Onchorhynchus keta*

Trait	45 days after hatching
Mean	353.0
CV	11.9
No.	18.0

No.= number of families studied

Seawater tolerance test

In 24 hr tolerance tests, the highest seawater tolerance of chum salmon was observed at 7 ℃ and lowest at 3 ℃. However, intermediate seawater tolerance was observed at 12 ℃ (Fig. 1). This phenomenon was no exception in this experiment. The seawater tolerance of 45 day old chum salmon was varied depending on temperatures.

Interactions between temperature and families were significantly different. Fry survival at 45 day old after hatching of chum salmon was significantly affected by males ($P=0.0001$) and females ($P=0.0001$). There were interactions between males and temperature in transferring of juveniles to sea water,

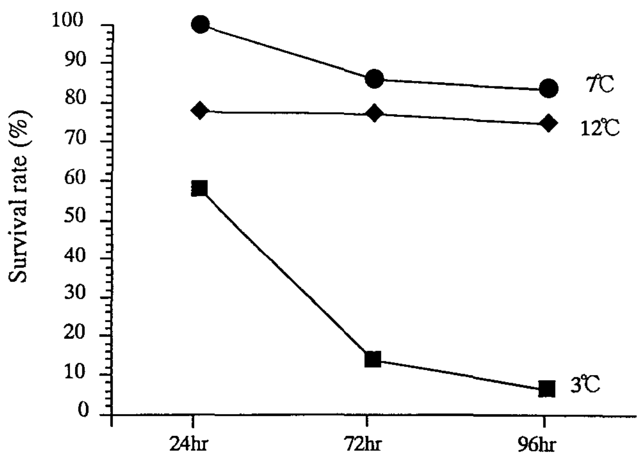

Fig. 1. Changes in survival rate of chum salmon fry at various temperatures after direct transfer from freshwater to seawater. Seawater adaptability of fry of different lots (3, 7 and 12℃ of temperature) were examined simultaneously on March 8, 1998.

and also between females and temperature. Into 7 and 12 ℃ temperatures at transfer, fry had lower mortality than into 3 ℃ transferred for the same time period in seawater. Mortality markedly increased in 3 ℃ after transferring to seawater. Changes in survival rate of chum salmon families at various temperatures after direct transfer from freshwater to seawater were shown in figure 2. Various survival rate (%) for seawater tolerance was obtained with the same families of fry in chum salmon at the different temperatures. In 24 hr tolerance test, survival rates of chum salmon families were extremely various at 3 ℃ and similar to at 12 ℃. In 7 ℃, there was no significant difference in mean survival rate of fry based on period of transfer to seawater, or between females or among males.

As indicated above, survival of fish in seawater tolerance tests at 32‰ was different among families in each water temperature. There were variance in fry survival among females ($P=0.0001$), and among males ($P=0.0001$). For 18 families in 3 ℃ (32‰) water, only one or zero fish in each family survived for the 96 hr period. Mean fry weight at 45 day old of chum salmon was significantly affected by males ($P<0.005$). There was interaction between males and temperatures at transfer of fry to seawater, and also between females and temperatures (Table 2).

Sample size for any single test for families at 32 ‰ was small. Re-analysis of data pooled into 3, 7 and 12 ℃ families in each temperature indicated that survival was significantly affected by temperature ($P=0.0001$), with a highest proportion of fish surviving in 7 ℃ water lot.

Heritability

Heritability estimates for seawater tolerance tests at 45 days after hatching are shown in Table 3. At 45 days after hatching, heritabilities was estimated for survival trait of 18 half-sib families for 3 and 7 ℃, and of 9 half-sib families for 12 ℃ were 0.32~0.34 (h^2_S), 0.73~0.79 (h^2_D), and 0.32~0.57 (h^2_{SD}).

Phenotypic correlations

The phenotypic correlations between egg size, egg weight, body weight of fry, body weight of dam, and survival rate after transfer to seawater (32‰) for chum salmon are shown in Table 4. Significant correlation was not found in growth traits and reproductive traits, but positive except for body weight (BW) of fry at 3 ℃. Phenotypic correlations

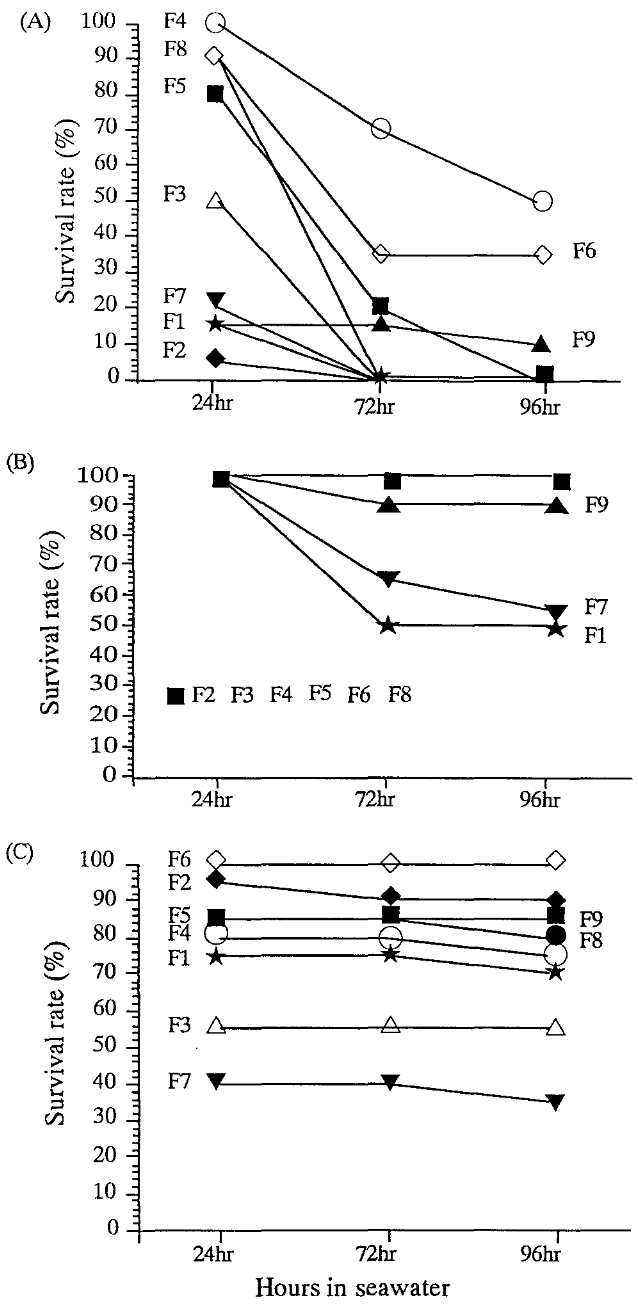

Fig. 2. Changes in survival rate of chum salmon fry at various temperatures after direct transfer from freshwater to seawater. Changes in seawater adaptability of the same families of fry at 3 temperature (A, 3 ℃; B, 7 ℃; C, 12 ℃). Examined samples were taken 20 fish from each family.

Table 2. Analysis of variance table constructed based on juvenile survival experiment at three temperatures for chum salmon fry transferred from freshwater to seawater (32‰) 45 days after hatching

Source of ANOVA	df	Transfer time: 24 hr MS	24 hr F	24 hr P	72 hr MS	72 hr F	72 hr P	96 hr MS	96 hr F	96 hr P
Males	5	2.718	31.852	0.0001	1.716	18.617	0.0001	1.338	16.099	0.0001
Females/Males	12	0.540	6.332	0.0001	1.884	20.440	0.0001	1.447	17.438	0.0001
Transfer time	2	15.434	180.963	0.0001	46.117	500.385	0.0001	55.382	666.454	0.0001
Males×transfer temperature	7	2.029	23.781	0.0001	0.697	7.563	0.0001	0.276	3.324	0.0017
Females×transfer temperature	18	0.623	7.304	0.0001	0.668	7.250	0.0001	0.714	8.587	0.0001
Error	855	0.085			0.092			0.083		
Total	899									

Table 3. Heritabilities estimates from sires and dams for seawater tolerance at three temperatures of chum salmon fry in 1998

Temperature	3 ℃			7 ℃			12 ℃		
Heritability	h^2_S	h^2_D	h^2_{SD}	h^2_S	h^2_D	h^2_{SD}	h^2_S	h^2_D	h^2_{SD}
	0.34(0.37)	0.79(0.35)	0.57(0.27)	0.40(0.34)	–	0.86(0.51)	0.32(0.25)	0.73(0.45)	0.32(0.29)

Standard errors are given in parentheses; – = undetermined

Table 4. Correlations for seawater adaptability between body weight of fry, body weight of dam, egg size, egg weight and temperatures of chum salmon fry after direct transfer from freshwater to seawater on March 9, 1998

Trait	Tem.	3 ℃			7 ℃			12 ℃		
	Hour	24 hr	72 hr	96 hr	24 hr	72 hr	96 hr	24 hr	72 hr	96 hr
BW(fry)		0.09	-0.33	-0.38	-	0.20	0.13	0.23	0.20	0.27
BW(dam)		0.06	0.24	0.36	-	0.07	0.05	0.25	0.25	0.22
Egg size		0.08	0.30	0.38	-	0.16	0.08	0.30	0.31	0.29
Egg weight		0.14	0.33	0.40	-	0.23	0.14	0.14	0.11	0.17

Tem. = temperature; - = undetermined

were low among survival-related traits of chum salmon.

Discussion

For most species of salmon, the 24 hr challenge period is best for detecting differences in short term seawater adaptation since plasma sodium is then at or near the maximum level (Clarke and Blackburn, 1977; Davis and Shand, 1978; Virtanen and Oikari, 1984; Hogstrand and Haux, 1985; Blackburn and Clarke, 1987). According to Iwata et al. (1982), the optimal period for determining seawater tolerance was shorter for chum salmon than the other salmonids. The estimation of plasma sodium levels, however, may not be a convenient method for determining seawater adaptability of fish with too small size to provide enough blood sample. As in our experiments the survival was related to their seawater adaptability, when they were disposed to different temperatures in seawater, duration of survival differed. The interval after transfer from freshwater to seawater had no significant influence on seawater adaptability of chum salmon fry in our experiment with 24, 72 and 96 hr intervals among analyses in each temperature. Thus, it is difficult to decide the best test duration for a seawater tolerance test. In this study, we analyzed seawater tolerance for suitable survival after transfer to seawater of chum salmon fry.

It has been accepted that salmonids exhibit a sharp increase in seawater tolerance as fish grow, and that at a given age, the larger fish are more resistant than smaller one (Ewing et al., 1980; Wanger et al., 1969). However, when the seawater adaptability of chum salmon fry was examined by following the changes in the plasma Na^+ levels, smaller fry or fry with shorter time in freshwater adapted to seawater more efficiently than the larger fish (Iwata et al., 1982). Iwata et al. (1982) also reported the osmoregulatory ability of fry in seawater gradually decreased with an increase in body weight or in time spent in freshwater.

The effect of size on the development of seawater adaptability has been recognized for anadromous salmonid species such as sockeye salmon (*O. nerka*), masu salmon, steelhead trout (*O. mykiss*) and Atlantic salmon; they are unable to resist seawater as under-yearlings, but are able to adapt to seawater at a later stage after smolting (see Johnsson and Clarke, 1988; Foote et al., 1992).

In the present study, body weight was not significantly related survival in the seawater of chum salmon fry at 45 days after hatching. Since the effect of size on survival for brook trout, *Salvelinus fontinalis*, in the seawater was reported to decrease with increasing size (McCormick and Naiman, 1984), logarithmic transformations were used to examine the relationship between seawater hazard rate and fork length by least squares regression. Taylor (1990), however, suggested that the larger size in egg and fry for coho salmon may represent an adaptation. However, the weak relationship between survival in saltwater and fry size at ponding for coho salmon from Robertson Creek suggested that maternal effects (i.e., fry size) may not fully account for survival differences observed between interior and coastal populations (Murray et al., 1993). Dempson (1993) were suggested that Arctic char of a size consistent with those normally migrating to ocean would be expected to be able to tolerate seawater, and the fate of smaller individuals was uncertain. At 30‰, seawater tolerance was size-dependent in Fraser River char stock, as has been reported in other studies with Arctic char (Arnesen et al., 1992; Staurnes et al., 1992).

In this study, the heritabilities of survival in seawater in chum salmon were estimated to be 0.32~0.34 for sires at 45 days after hatching in 1998. Similar results were obtained by Murray et al. (1993) who estimated heritabilities of 0.1~0.3 for survival in seawater of coho salmon from Robertson Creek. These heritabilities were higher than those normally observed for a trait highly correlated with fitness (Kanis et al., 1976; Gall and Gross, 1978; Robinson and Luempert, 1984). The present results also show that the seawater adaptability of fry chum salmon was influenced by maternal effects. The relatively high additive genetic variation observed for survival suggests that fry from some families were more suited to survival in seawater than those from other families. Murray et al. (1993) suggested that the high heritabilities for survival may result in the exploitation of two different environments. Murray et al. (1993) suggested that differences in growth and survival in saline environments between coastal- and interio-spawning coho salmon probably reflect genetic differences. Mortalities shortly after ponding have been attributed to maternal effects on survival, size, and growth rate (Withler et al., 1987; Rye et al., 1990) and certain bacterial diseases (T.P. T. Evelyn, Personal Communication, Pacific Biological Station, Nanaimo, B.C.). However, Otto (1971) acknowledged the need for assessing the assumption that there were no genetic differences between resident and migratory fry. We observed differences in survival with respect to seawater among families within a population of chum salmon. Assessing differences among families within population and between populations minimizes problems associated with inferences about a species' response to its environment from single population (Birth, 1987; Taylor, 1990).

Low temperature has been cited as a factor influencing survival of Norwegian char at sea (Wandsvuk and Jobling, 1982). The results of the seawater tolerance tests conducted on small chum salmon in this study suggest that temperature could be an important factor influencing seawater tolerance when water temperatures falls below 3 ℃. At higher temperatures, however, survival was often independent of water temperature. Finstad et al. (1989) reported that the hypoosmoregulatory capacity of Arctic char in summer was sufficient to withstand exposure to 34‰ seawater at low (1 ℃) temperatures. However, this was not the case during the fall or winter. They concluded that there were seasonal changes in the seawater tolerance of Arctic char related to variations in the hypoosmoregulatory capacity induced by photoperiod changes. A similar influence of photoperiod on salinity tolerance has been reported by Arnesen et al. (1992). In this study, poor survival families may also have a genetic basis, with differences observed among males and females ($P<0.005$).

This study demonstrates that temperature dependent variation occurs in the seawater adaptability of chum salmon fry. These temperature effect was more obvious at 3 ℃ than at 7 and 12 ℃. We suppose that the negative effect of low temperature on seawater adaptability in the present study is typical for all chum salmon populations. At the beginning of their downstream migration in low temperature, chum salmon fry probably have poor seawater adaptability. This tests revealed that the optimal temperature for seawater adaptation of chum fry is closer to 7 ℃ than to 3 or 12 ℃. We expect that this optimal temperature would result in higher survival.

To our knowledge, such temperature-dependent, size-independent, and genetic difference for seawater tolerance in the same development has not been reported for chum salmon fry. In earlier studies, Natochin and Bocharov (1962) and Bocharov (19 64) found that both pink and chum salmon fry following prolonged rearing in freshwater (2~7 months after downstream migration) maintained their capability for seawater adaptation. Houston (1961) reported that larger chum fry (1.6 g) exhibited better ion regulation than smaller fry (0.9 g). In contrast, Iwata et al. (1982) found that small chum fry adapted better than large fry. Nakano et al. (1985) and Smirnov and Klyashtorin (1989) demonstrated that in chum salmon, tolerance of seawater does not change with size, whereas tolerance of freshwater after being acclimatized to seawater decreases with size.

In the present study, fry survival in seawater was more influenced by temperature than size of fry in chum salmon. To increase survival after transfer to seawater, we suggest that the releasing timing of chum salmon fry has an important effect on survival in the ocean in relation to the sea condition for seawater temperature. And genetic difference in the same development stage is also important for survival in seawater of chum salmon for seawater tolerance.

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