Density-Dependence of Chum Salmon in Coastal Waters of the Japan Sea

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Abstract: To investigate factors regulating abundance of hatchery-reared chum salmon (*Oncorhynchus keta*), we examined survival, distribution, and nutritional condition of juveniles in the coastal waters of the Japan Sea. Over the past 10 years, the number of returning chum adults has fluctuated around 600,000 along the coast of Honshu. Survival during ocean life correlated negatively with the number of released juveniles and sea surface temperatures in coastal waters. To investigate factors affecting nutritional condition of juveniles, we collected chum salmon juveniles off Yamagata, Honshu, in March–May from 1994 to 1996. When density of juveniles increased the weight of their stomach contents decreased, indicating a negative effect of chum abundance on prey organisms. Results indicate that a restricted nursery area intensifies intraspecific competition of chum salmon juveniles for food resources. The coastal carrying capacity may regulate abundance of chum salmon along the Japan Sea coast of Honshu, Japan.

INTRODUCTION

Anadromous Pacific salmon (*Oncorhynchus* spp.) migrate between freshwater habitats and the ocean. Smolts are vulnerable to high mortality soon after they enter the sea (Pearcy 1992). In some salmon stocks, year-class strength is determined in early ocean life (Hartt 1980; Pearcy 1992). Hatchery-reared chum salmon (*O. keta*) reach the sea within several days after release in a river (Mayama et al. 1982; Kaeriyama 1986). During early sea life, chum salmon suffer high mortality (Bax 1983), and distribution is limited to coastal waters (Fukuwaka and Suzuki 1998a; see review by Salo 1991). Biotic and abiotic environments in coastal waters may be influenced by drainage from the land, tidal action, or human activity, and may change temporally and spatially.

The survival of hatchery-reared Pacific salmon is often depressed in southern regions of a species' distribution (Mahnken et al. 1998). In Japan, most chum salmon populations are sustained by hatcheries. In the last 20 years, an inverse density-dependence has been observed between the number of juvenile chum salmon released and the number of adults returning (McNeil 1991). However, on the Japan Sea coast (western coast of Honshu), ocean survival is lower than on the Pacific side (eastern coast) of Japan, which is a serious problem for Japan's salmon enhancement program.

For ocean management of hatchery-reared salmon, factors depressing their survival need understanding. Thus, the objectives of this study are: 1) to test for density-dependence in ocean survival, 2) to identify environmental factors affecting ocean survival, and 3) to hypothesize the regulatory mechanisms of hatchery-reared adult chum salmon along the Japan Sea coast.

MATERIALS AND METHODS

Study Area

The coastal waters of the Japan Sea off Honshu, Japan, are near the southern limit of chum salmon distribution in the western North Pacific (Salo 1991). On this coast, the geographical range of industrial hatchery production of chum salmon extends from the Aomori Prefecture to the Toyama Prefecture (Fig. 1). The northern areas of the coast are characterized by open sand beaches and narrow estuaries at river mouths (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985). The coastal waters of the Japan Sea are strongly affected by the Tsushima Current. Currents generated by tides are relatively small. The Tsushima Current is

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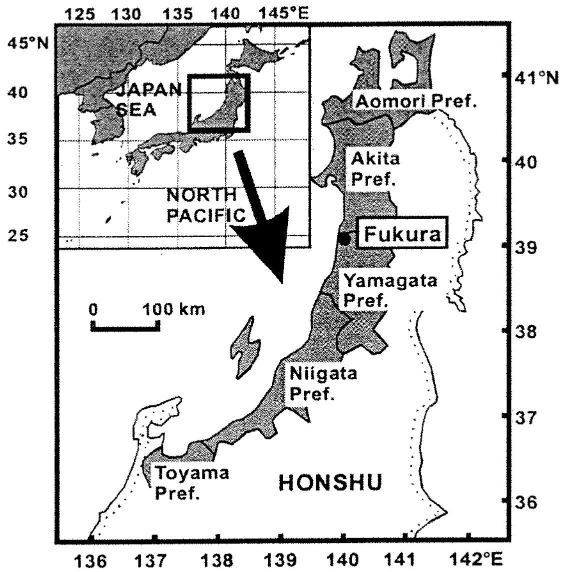
Fig. 1. Map of study site. Solid shaded area indicates prefectures along the Japan Sea coast of Honshu, Japan, where chum salmon juveniles are produced in hatcheries.



characterized by a high temperature (minimum 8°C at 100 m depth) and high salinity (> 34.1 psu) water mass flowing northward along the continental shelf (Kawabe 1982). River discharges increase in the spring due to snow melt; these discharges result in freshwater plumes in nearshore regions (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985) and these plumes are the chief habitat of juvenile chum salmon (Fukuwaka and Suzuki 1998a).

Abundance and Survival

The number of released chum salmon juveniles, the number of adults caught in rivers, and the number of adults caught in coastal waters were provided by the National Salmon Resources Center (NSRC 1998a, b, 1999a, b) (formerly the Hokkaido Salmon Hatchery: HSH 1993–1997) and the Fisheries Agency of Japan (FAJ) (Honshu Keison Zousyoku Shinkoukai 1991) in 1970–1998. The age composition of adults caught in rivers was provided by NSRC and FAJ (HSH 1972–1995, NSRC 1999a). The number of returning adults was equivalent to the sum of the numbers of adults caught in rivers and in coastal waters. The number of adults in each year-class was determined by the age composition. For 1992–1998 year-classes, we cannot calculate numbers of adults completely, because age at maturity of chum salmon ranges from 2–6 years.

To evaluate effects of numbers of released juveniles and coastal environmental variables on ocean survival, we used step-wise multiple regression ($p \leq 0.05$ to add and $p \geq 0.10$ to remove; Sokal and Rohlf 1995). The significance of the regression coefficient was tested using the t-test. The survival rate through the entire ocean life was calculated using the equation: $S_i = A_i / J_i$, where S_i is the survival rate of the i-th year-class, A_i is the number of returning adults in the i-th year-class, and J_i is the number of released juveniles in the i-th year-class. The survival rate and the number of released juveniles used in the analysis were log-transformed.

As coastal environmental variables, we used sea surface temperature (SST) and salinity within 50 km off the Niigata Prefecture and Yamagata Prefecture in early May, because the spatial distribution of chum salmon juveniles was restricted within coastal waters (Fukuwaka and Suzuki 1998a). In early May, SST reached near the upper limit of distribution of juvenile chum salmon and river plumes extended to offshore (Fukuwaka and Suzuki 1998a). SST and salinity data were provided by the Niigata Prefectural Fisheries Experimental Station (1970–1983, 1970–1997) and the Yamagata Prefectural Fisheries Experimental Station (1985, 1993).

Nutritional Condition of Juveniles

We set a line transect from the mouth of the Gakko River to the southern edge of Tobishima Island off Fukura, Yamagata Prefecture, Japan (Fukuwaka and Suzuki 1998a). The shoreline of the southern area of the river mouth is an open sandy beach and the northern area is a rocky shore. We placed five sampling stations along the line transect at 2, 5, 10, 15, and 20 km from shore. At these stations, water depth was 10 to 200 m.

At all sampling stations from March to May in 1994 to 1996, we collected chum salmon juveniles with surface trawls, zooplankton with a modified NORPAC net, and we simultaneously measured water temperature and salinity using a CTD (Fukuwaka and Suzuki 1998a; Suzuki and Fukuwaka 1998). Surface trawls were towed at ca 4 $km \cdot h^{-1}$ by 2 vessels trawling parallel to the shoreline in one set of 30 minutes, or three sets of 15 minutes at each station. The net was 8 m wide and 4 m deep at the mouth and equipped with 25 to 34 mm stretched mesh in the body and 7.5 mm mesh in the cod end. Catch per unit effort (CPUE) was calculated as number of collected juveniles per 30 minutes net trawl. Collected juveniles were fixed in 10% buffered formalin. Fork length of juveniles was measured to the nearest 0.01 mm and body weight was measured to the nearest 0.001 g. Stomach content weight of juveniles was measured to the nearest 0.001 g for 30 specimens at each station (Suzuki and Fukuwaka 1998).

The condition factor was used to evaluate fish condition: $CF = BW / FL^3 \cdot 10^6$, where CF is the condition factor, BW is the body weight of juveniles, and FL is the fork length. Relative stomach content weight was used as an index of stomach fullness: RSC = SCW / BW · 10^2, where RSC is the relative stomach content weight, SCW is the stomach content weight, and BW is the body weight.

To estimate prey abundance, a modified NORPAC net with a flow meter was towed vertically from the bottom or, at deeper stations, 20 m depth to the surface. Collected zooplankton was fixed in 10% buffered formalin and the number of individuals in each taxon counted (Suzuki and Fukuwaka 1998). Zooplankton taxa were divided into two size groups: smaller taxa, such as *Evadne nordmanni*, *Podon leuckarti*, euphausiid calyptopis larvae, or *Oikopleura* sp.; and large taxa, such as euphausiid furcilia larvae, polychaetes, *Calanus sinicus*, or *Neocalanus plumchrus* copepodid V stage.

The relationship between environmental factors and nutritional conditions was analyzed by linear regression. The correlation coefficient of the relationship was tested using the *t*-test. Because environmental factors were correlated with each other, we used path analysis to evaluate the strength of effect of environmental factors on nutritional condition of juveniles (Sokal and Rolf 1995). The path coefficient was tested using the *t*-test.

RESULTS

Juvenile-Adult Relationship

Numbers of chum salmon released as juveniles along the Japan Sea coast of Honshu increased from 1970 to 1980, but gradually decreased thereafter (Fig. 2A). The mean number of juveniles released (1970–1998) was 203 million (SD ± 74.8 million). The mean number of returning adults was 510,000 (SD ± 190,000) in this period. The number of returning adults fluctuated around 600,000 in recent years (1989–1999) (Fig. 2B). Mean year-class survival at sea was 0.318% (SD ± 0.145%). Year-class survival declined from 1970 to 1982, but increased thereafter (Fig. 2C).

Ocean survival was correlated negatively with number of released juveniles and coastal SST in early May (Table 1). This indicates that ocean survival is density-dependent, and related to water temperature.

Nutritional Condition of Juveniles

The condition factor and the relative stomach content weight (RSC) of chum salmon juveniles were correlated positively with SST and negatively with surface salinity in coastal waters off Fukura, Yamagata (Figs. 3 and 4). The regression equations for the relationships are condition factor = 0.147 · SST + 4.98 (R^2 = 0.218, p < 0.001; Fig. 3A), condition factor = -0.0618 salinity + 8.37 (R^2 = 0.141, p < 0.001; Fig. 3B), RSC = 0.634 SST – 4.96 (R^2 = 0.346, p < 0.001; Fig. 4A), and RSC = -0.235 salinity + 8.71 (R^2 = 0.174, p < 0.001; Fig. 4B). SST was 8.6–14.2°C and salinity was 18.5–34.0 psu in March to May in 1994–1996.

Fig. 2. Annual changes in numbers of released juveniles (A), returning adults (B), and ocean survival rate of year-class (C) for hatchery-reared chum salmon in 1970–1998 along the Japan Sea coast of Honshu, Japan.

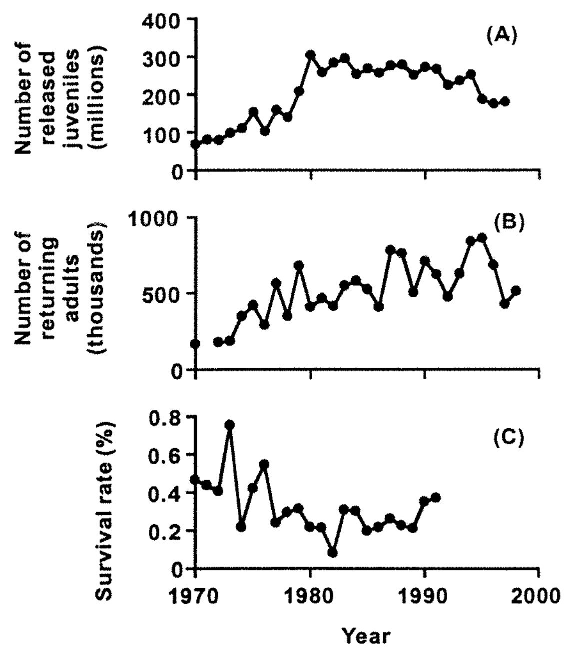
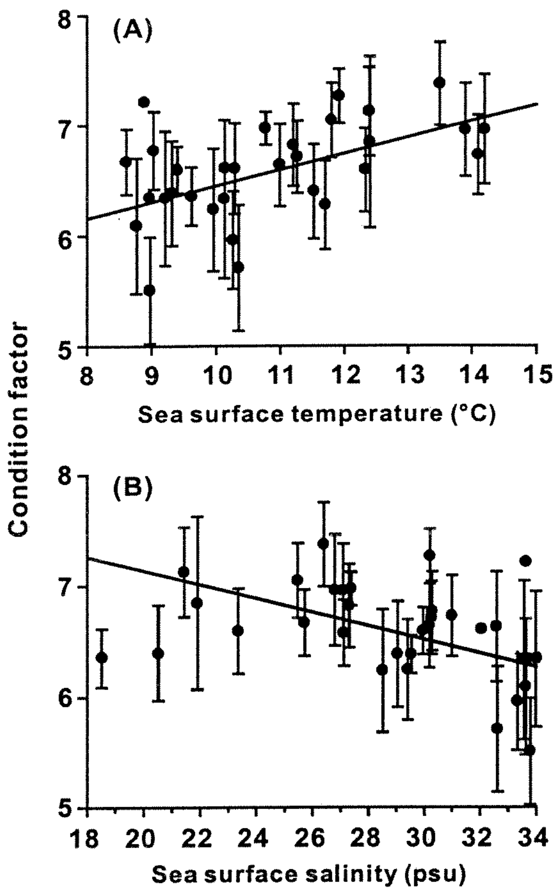


Table 1. Stepwise multiple regression analysis between ocean survival and number of released juveniles, coastal sea surface temperature in early May of the year of release, and coastal surface salinity in the same period, for 1970–1991 year-classes of chum salmon along the Japan Sea coast of Honshu. The degrees of freedom in the significance test are 19.

Variable	Standard partial regression coefficient	Partial regression coefficient	*t*	*p*
Intercept		-1.39	-3.64	0.0017
Number of released juveniles	-0.474	$-1.14 \cdot 10^{-9}$	-2.76	0.0125
Sea surface temperature	-0.393	-0.0719	-2.29	0.034
Surface salinity	Not added			

Fig. 3. Regressions of condition factor of chum salmon juveniles on sea surface temperature (A), and on sea surface salinity (B) in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equations: condition factor = 0.147 · SST + 4.98, R^2 = 0.218, $p < 0.001$, n = 465; condition factor = -0.0618 · salinity + 8.37, R^2 = 0.141, $p < 0.001$, n = 465.



The relative stomach content weight (RSC) was negatively correlated with CPUE (Fig. 5). The regression equation is RSC = -0.0251 · CPUE + 2.96 (R^2 = 0.174, $p < 0.001$). This indicates that intraspecific competition for food occurs in chum salmon juveniles. In the path diagram, the correlation between density of juveniles (CPUE) and stomach content weight was not significant (Fig. 6). CPUE of juveniles was negatively correlated to prey abundance, which affected stomach content weight significantly, and therefore CPUE affected stomach content weight indirectly. SST and salinity affected biotic factors such as prey abundance or CPUE of juveniles, and stomach content weight of juveniles.

DISCUSSION

We found that survival of chum salmon correlated with coastal sea surface temperature and number of juveniles released from hatcheries along the Japan Sea coast of Honshu. The survival rate of hatchery-reared fish may be affected by biotic and abiotic environmental factors in freshwater, coastal, and oceanic habitats. The spatial extension of estuaries, coastal water temperatures, and coastal salinity also affected the marine survival of hatchery-reared Pacific salmon (Blackbourn 1990; Coronado and Hilborn 1998; Mahnken et al. 1998; Willette et al. 1999). Long-term or decadal-scale climate changes also affect the production of salmonids in the North Pacific (e.g. Beamish et al. 1999). Density-dependence is often a cause to depress the survival rate in hatchery-reared salmon stocks, such as the North American stocks of coho salmon and of the Prince William Sound stocks of pink salmon (e.g. Coronado and Hilborn 1998; Willette et al. 1999). Coastal environmental factors at release or numbers of released juveniles may be a key to the success of enhancement programs for Pacific salmon.

Fig. 4. Regression of relative stomach content weight of chum salmon juveniles on sea surface temperature (A), and sea surface salinity (B) in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equations: RSC = 0.634 · SST – 4.96, R^2 = 0.346, $p < 0.001$, n = 465; RSC = -0.235 · salinity + 8.71, R^2 = 0.174, $p < 0.001$, n = 465.

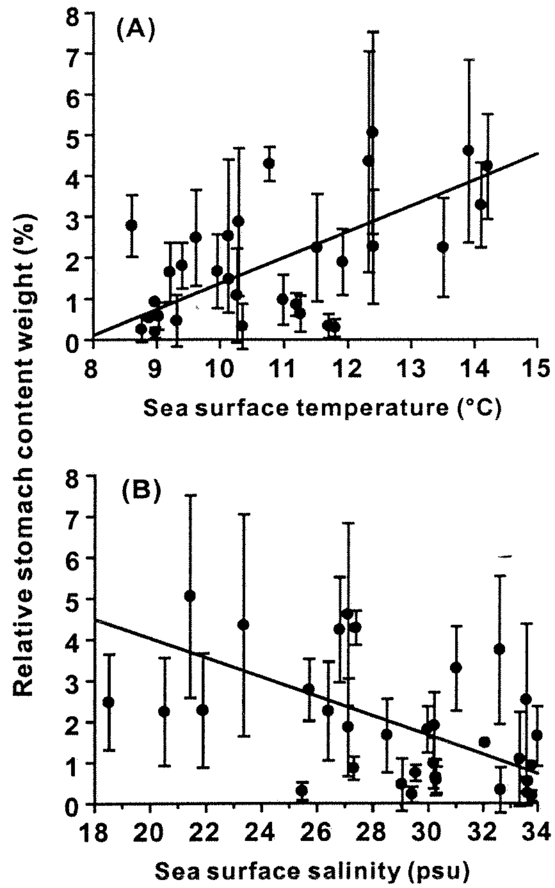


Fig. 5. Regression of relative stomach content weight on CPUE of chum salmon juveniles in the coastal water off Fukura, Japan Sea, 1994–1996. Vertical bars, standard deviation. Regression equation: RSC = -0.0251 · CPUE + 2.96, $R^2 = 0.174$, $p < 0.001$, $n = 465$.

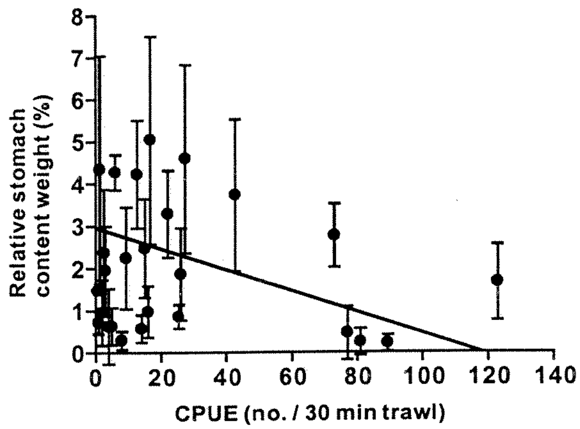
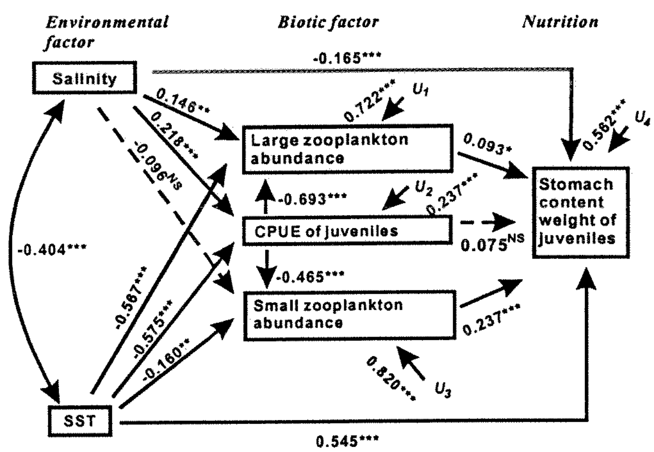


Fig. 6. Path diagram illustrating the relationships among environmental factors, biotic factors, and nutritional condition of chum salmon juveniles in the coastal water off Fukura, Japan Sea, 1994–1996. *U* is a residual variable. Arrows indicate the effect of one variable on another; dashed arrows not statistically significant ($p > 0.05$). Path coefficients are printed near the arrows. ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; NS, $p > 0.05$.



Survival of chum salmon correlated negatively with coastal sea surface temperature. Mortality of chum fry and small fingerlings in the early sea life accounted for over 90% of the whole sea mortality in our study area (Fukuwaka and Suzuki 1998b). Year-class strength of hatchery-release chum salmon is determined by early sea mortality, which may be affected by coastal environment or predation by piscivorous fish or sea birds (Bax 1983). However, Nagasawa (1998) could not find any evidence that predation by fish in early sea life has much impact on abundance of Japanese chum salmon stocks. Early sea survival of salmonids was affected by coastal environment such as SST or salinity, as well as prey abundance, primary production, or number of released juveniles (Blackbourn 1990; Coronado and Hilborn 1998; Willette et al. 1999).

The temporal and spatial distribution of environments suitable for survival of chum salmon juveniles may be narrow in coastal waters of the Japan Sea. Sea surface temperature in our study area reached near the upper limit for chum salmon juveniles in May. Coastal water temperature at release time strongly affects the survival of Japanese hatchery-reared chum salmon (Mayama 1985). Spatial distribution of chum salmon juveniles was restricted within a river plume in coastal waters (Fukuwaka and Suzuki 1998a).

Intraspecific competition for food within a limited distribution may cause density-dependent early sea mortality of chum salmon juveniles released from hatcheries. The analysis of nutritional condition indicates that the food consumption by chum salmon juveniles correlates negatively with their density through reduction in abundance of prey organisms (Fig. 6). Aggregated distribution of juveniles might exacerbate intraspecific competition (unpublished data). Early sea survival of slower growing chum salmon was lower than that of faster growing fish in the Nanaimo River, British Columbia (Healey 1982). Food competition may cause reduction of somatic growth in early sea life of chum salmon. Early sea distributions of Pacific salmon are restricted in estuaries or coastal waters (Pearcy 1992). Intraspecific competition may strongly affect early sea survival and growth not only of hatchery-reared chum salmon but also of other salmonid species, such as chinook salmon (*O. tshawytscha*) (Wissmar and Simenstad 1988; Simenstad 1997).

CONCLUSIONS

Density-dependent sea survival occurred in juvenile hatchery-reared chum salmon along the Japan Sea coast of Honshu, Japan. Survival is negatively correlated with high coastal SST during early sea life. The food consumption by juveniles correlated negatively with density through reduction in abundance of prey organisms. These results indicate that intraspecific competition for food within a narrow nursery area limited by environmental factors strongly affects early sea survival for hatchery-reared chum salmon. The coastal carrying capacity may regulate abundance of chum salmon along the Japan Sea coast of Honshu, Japan.

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