



Title	. LIFE HISTORY STRATEGY AND MIGRATION PATTERN OF JUVENILE SOCKEYE AND CHUM SALMON
Author(s)	KAERIYAMA, Masahide
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or IV fish, and are significantly elevated in fully-smoltified fish at the peak migration period. Nipping behavior is reduced concurrently. Thyroid hormones, together with growth hormone and cortisol, play an important role in smolting and various behavioral changes which for downstream migration (Iwata, 1995). Godin et al. (1974) observed a reduction in aggressive behavior in yearling Atlantic salmon following intraperitoneal injection of thyroxine. However, this experiment was conducted during July and August and not during the parr-smolt transformation period. The negative relationship between plasma thyroxine levels and nipping behavior observed during this experiment suggests that T_4 may play a role in reducing aggressive behavior during smolting. Loss of aggressive behavior is a necessary component in the transformation of salmon from territorial stream fish to shoaling lake or oceanic fish. Reduction of aggression may induce other behavioral changes which are necessary for the formation of social relationship among individuals in a school.

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VII. LIFE HISTORY STRATEGY AND MIGRATION PATTERN OF JUVENILE SOCKEYE AND CHUM SALMON

Masahide KAERIYAMA

Research Division, National Salmon Hatchery, Nakanoshima,
Toyohira-ku, Sapporo 062, Japan

Abstract

Life histories of juvenile sockeye and chum salmon show a conditional strategy which has two tactics of residence and migration. They usually remain in lake and river if they can obtain sufficient resources such as food and habitat, whereas salmon migrate seaward when they do not have enough of those resources to satisfy their energy metabolism. Their migration pattern, controlled by effects of "prior residence" and "precedent migration", is determined as a trade-off between the profitability of resource acquisition and risks such as osmoregulation, energetic demands of swimming, exposure to predators, and movement to a non-adaptable habitat by water current.

Introduction

The migrations of fishes are generally classed biologically as “alimetal” for food procurement, “climatic” for reaching a region of better climate, “gametic” for reproduction (Harden-Jones, 1968), and oceanographically as “mobilization” by water current (McKeown, 1984). For diadromous fishes, alimetal and gametic migrations influence their adaptation and differentiation through intraspecific competition.

McDowall (1987) estimated the total number of fish species as about 20,000 and considered that about 162 (0.8%) of these are diadromous. Of these species, 87 (54%) are anadromous, 41 (25%) catadromous, and 34 (21%) amphidromous. Baker (1978) showed that anadromy is greatest in polar-temperate environments, and that catadromy is greatest in the tropics. In 6 species of Pacific salmon (genus *Oncorhynchus*), species which migrate seaward at an earlier developmental stage can have more abundance and a wider area of ocean distribution (Kaeriyama, 1985). Anadromous species have evolved when food resources in the sea exceed those in fresh water, and catadromous species have evolved when freshwater food resources exceed those in the sea (Gross, 1987). Pacific salmon may have obtained the ability of homing migration for maximizing reproductive success in fresh water.

The purpose of this paper is to review the migration of Pacific salmon by focusing on the life history strategy of sockeye salmon (*O. nerka*), which have a diverse life history pattern, and chum salmon (*O. keta*), which migrate seaward immediately after emergence.

1. Migration and freshwater residence of sockeye salmon

Although sockeye are primarily anadromous, there are distinct populations called “residual” sockeye and kokanee salmon. Residual sockeye are progeny of anadromous parents. A part of them, however, remain in fresh water to mature and reproduce. The residual population tends to have a higher growth rate and to mature at an earlier age than the anadromous population (Ricker, 1938; Simirnov, 1959). The kokanee, on the other hand, have fully adapted to freshwater life. Ricker (1940) considered the evolution of kokanee as occurring in the following two stages: (i) the occurrence of “residual” offspring among the progeny of an anadromous stock; and (ii) the modification of progeny of residuals into typical kokanee. In anadromous sockeye salmon, juveniles typically rear in lakes for one or more years before the seaward migration (lake type), but, particularly in northern populations, some individuals either go to the sea immediately after their emergence (sea type) or inhabit river channels for at least one year (river type) (Wood et al., 1987).

Residual sockeye salmon are produced by an artificial enhancement program in Lake Shikotsu. They were originally transplanted from the residual population in Lake Akan, Hokkaido Island, in 1893 and from an anadromous population in Lake Urumbetsu, Iturup Island, during 1925-1940. Although they have been geographically landlocked in Lake

Shikotsu for more than 15 generations, smolts appear in this lake (Kaeriyama, 1991). Those smolts were released to a river flowing into the Pacific Ocean, and ascended the river as anadromous sockeye salmon after 1-3 years. Most of the smolts, 3 years old (2+), migrated downstream between late June and early July. The age and season of these Lake Shikotsu smolts during the downstream migration corresponded with the seaward migration timing of smolt sockeye salmon in Lake Urumobetsu, although the lacustrine-limnological environment in Lake Shikotsu differs much from that in Lake Urumobetsu. On the other hand, progeny of sockeye salmon derived from Lake Shikotsu and returning as anadromous type had several life history patterns, including precocious, residual, and anadromous types (Kaeriyama *et al.*, 1992; Kaeriyama, 1994).

In Lake Shikotsu, smolts were smaller than residual fish. Based on the allometry between fork length and body weight, Lake Shikotsu sockeye salmon smolts are more slender in body shape than residuals (Fig. 10). Figure 11 shows the relationship between population

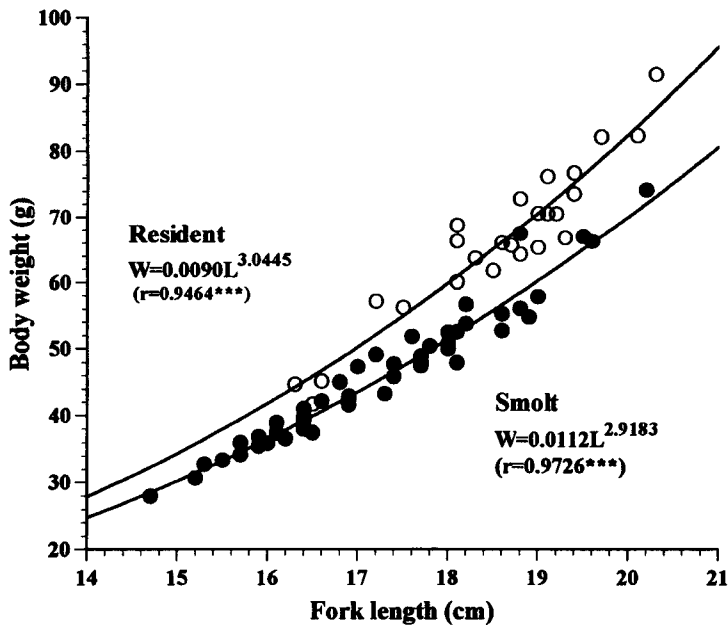


Fig. 10. Relationships between fork length and body weight of residual and smolt sockeye salmon in Lake Shikotsu on July 15, 1987.

size and smolt rate (number of smolts/ population size) for Lake Shikotsu sockeye salmon. In 1984-1986, smolts (145 ± 4 mm) were significantly smaller ($P < 0.001$) in fork length and smolt rates were significantly higher ($P < 0.001$) than those in other years (183 ± 15 mm). A significant positive relationship between population size and smolt rate was observed except for the 1984-1986 populations ($r = 0.8404$, $P < 0.01$). These results indicate (1) that residence

or seaward migration may be affected by both the population density and the resource condition, which reflects their growth, in the lake, and (2) that they may migrate seaward when they do not fully benefit from their resources.

These results also suggest that the life history of sockeye salmon may be a conditional strategy that has two tactics of residence and migration. Namely, Lake Shikotsu sockeye salmon usually remain in the lake as a residual type if they can obtain sufficient resources such as food and habitat, whereas a part of the population migrates seaward as smolts after one or two years in the lake when they do not have enough resources to satisfy their energy metabolism.

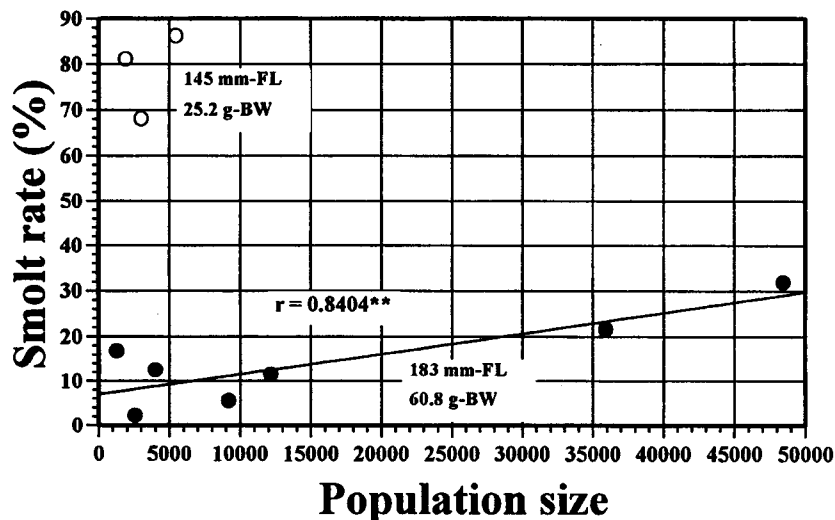


Fig. 11. Relationship between population size (P) and smolt rate (S) of lacustrine sockeye salmon in Lake Shikotsu: $S = 0.0000045P + 0.0699$ ($r = 8404^{**}$). The population size shows total numbers of smolt and adult, and the smolt rate represents the number of smolt per population size in a population. Fork lengths of smolt population are 183 + 15 mm in 1978-1983 and 987-1988 (solid circles), and 145 + 4 mm in 1984-1986 (open circles). Data are obtained from Kaeriyama (1991).

2. Migration pattern of juvenile chum salmon

For juvenile chum salmon, the migration pattern is controlled by effects of “prior residence” in spawning areas and “precedent migration” in rivers and sea (Kaeriyama, 1986). Juvenile chum salmon migrate from early spring to early summer in Japan. Only a few fry emerging initially from spawning redds in early spring remain in rivers for several months with low specific growth rate (Kaeriyama, 1996). Numerous juveniles migrate downstream immediately after emergence. Especially, most enhanced juveniles migrate seaward at the fry stage (FL < 50 mm) less than 10 days after release because of high population density (Kaeriyama and Sato, 1979; Mayama et al., 1982). There is a significant

difference ($P < 0.01$) in fork length during seaward migration between a wild population (54 ± 7 mm) staying for a long period in the Bibi River at low density and enhanced juveniles (40 ± 6 mm) migrating seaward immediately after the release at high density in the Tokachi River (Fig. 12).

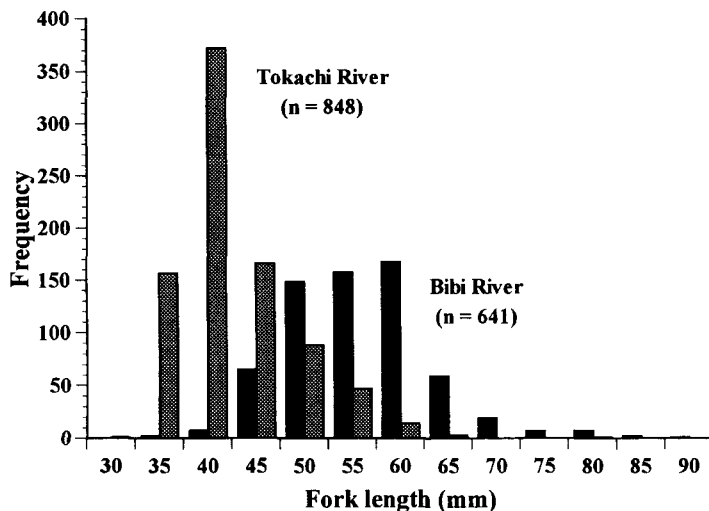


Fig. 12. Frequency distribution of fork length of juvenile chum salmon from Tokachi (enhanced) and Bibi (wild) rivers.

Because chum salmon spawn in areas of upwelling groundwater, there may be little change in water temperature and few prey around the spawning area. Prior individuals, therefore, have a low growth rate (Specific Growth Rate; $SGR < 0.006$). On the other hand, numerous juveniles migrating downstream stay temporarily at the estuary, where there is much food and a rise in water temperature during the spring. They rapidly grow in the estuary ($SGR > 0.01$). Growth inversion occurs between a few prior-resident and numerous migrating juveniles (Kaeriyama, 1986).

Juvenile chum salmon remain in the coastal sea for a time and migrate offshore at post-fingerling stage. This offshore migration is usually preceded by larger individuals, which have higher growth rate, than by others in a population (Kaeriyama, 1986). For instance, larger marked juveniles released into the Kitakami River in the spring of 1983 began to migrate offshore and to eat pelagic organisms earlier than others. Juveniles caught offshore preyed on pelagic organisms such as *Themisto japonica* and *Euphausia pacifica*. They showed much better growth than those from neritic or inshore waters, which fed on coastal zooplankton and terrestrial insects, respectively. On the other hand, a significant multiple regression plane indicates that the specific growth rate of marked juvenile chum salmon is a

function of days after release and distance from the released river (Fig. 13). These results suggest that larger juveniles which have higher growth rate migrate more rapidly and farther away from release rivers than those with higher population densities.

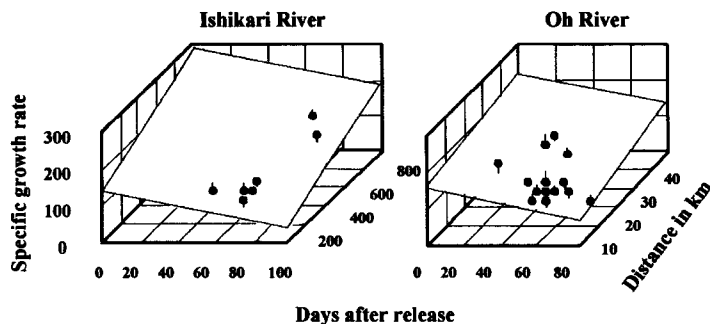


Fig. 13. Multiple regression analysis of specific growth rate (G) of marked juveniles on days after release (t) and distance from release river (k) in chum salmon population released from the Oh and Ishikari rivers (Modified from Kaeriyama, 1986). Oh River: $G = -1.450t + 1.853k + 163$, Ishikari River: $G = -1.010t + 0.147k + 140$.

In summary, the life history strategy of chum salmon may correspond to the conditional strategy of sockeye salmon. The prior-resident individuals may result from a phenotype of resident tactics in the conditional strategy. Their migration pattern indicates the precedent migration of larger juveniles. Because this life history strategy is also known for masu salmon (*O. masou*) (Mayama, 1992), the conditional strategy and the precedent migration pattern may apply to all species of the genus *Oncorhynchus*.

3. Conclusion

Expanding the habitat area, species of *Oncorhynchus* are able to get more resources. In contrast, by migrating they incur many risks such as osmoregulatory demands, energetic demands of swimming, exposure to predators, movement to non-adaptable habitat by water current. Therefore, the benefits of their migration may be a trade-off between the profitability of resource acquisition and risks associated with migration.

The life history strategy and migration pattern of the genus *Oncorhynchus* evidently reflect an evolution of anadromous fish that have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in fresh water.

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