

Effects of Population Density and Habitat Environment on Life History Strategy and Migration of Juvenile Sockeye (*Oncorhynchus nerka*) and Chum Salmon (*O. keta*)

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Abstract. — Life histories of juvenile sockeye (*Oncorhynchus nerka*) and chum salmon (*O. keta*) show a conditional strategy which have two tactics of residence and migration. They usually remain in lake and river if they can sufficiently obtain their resources such as food and habitat, whereas salmon migrate seaward when they do not have enough those resources satisfying their energy metabolism. Their migration pattern, controlled by effects of “prior residence” and “precedent migration”, may involve a trade-off between the profitability of resource acquisition and risks such as osmoregulation, energetic demands of swimming, exposure to predators, and mobilization to non-adaptable habitat by water current.

Introduction

The migrations of fishes are generally classed biologically as “alimentary” 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, alimental 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 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. 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 would 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 pattern of life history, and chum salmon (*O. keta*), which migrate seaward immediately after the emergence.

Ocean Distribution and Biomass of Pacific Salmon

Figure 1 shows the known ocean distribution by a species in Pacific salmon. Masu salmon (*O. masu*) has a limited distribution around coastal seas of the Far East. On the other hand, pink salmon (*O. gorbuscha*) has the widest distribution to the North Pacific Ocean in the 6 species. The relationship between the ocean distribution and the biomass of them indicates that a species which ranges a wider area can have more abundance in the North Pacific Ocean (Fig. 2).

Figure 3 demonstrates distribution areas of underyearling Pacific salmon at the downstream migration. Masu and coho (*O. kisutch*) salmon spend in the river for at least one or two years before migrating seaward as smolt. Most individuals of chinook (*O. tshawytscha*) and sockeye salmon usually rear in the freshwater for one or more years before seaward migration. A part of them, however, enter the sea at the underyearling stage such as ocean-type or sea-type stocks (Wood et al., 1987; Clarke et al., 1989). Numerous fry chum salmon migrate seaward immediately after the emergence. Only a few juvenile spend in the river for several months (Kaeriyama, 1986). All of pink salmon enter to the sea as fry

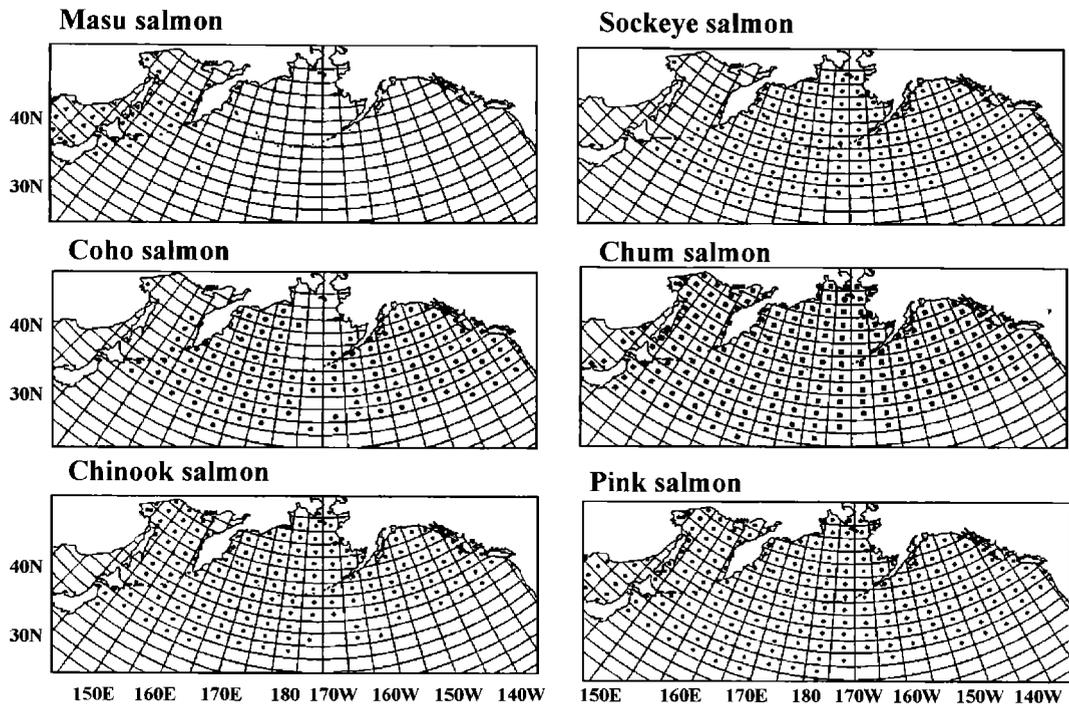


Fig. 1. Known ocean distribution of 6 species in the genus *Oncorhynchus* (Kaeriyama, 1985).

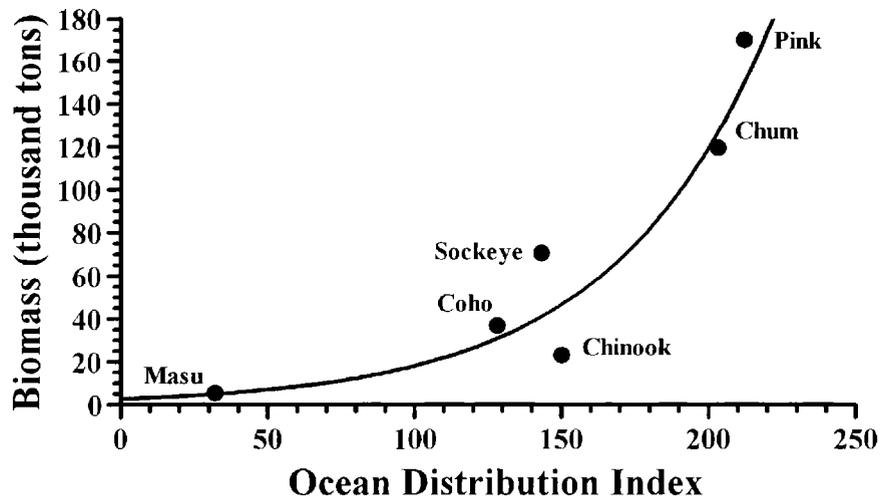


Fig. 2. Relationship between the ocean distribution index and the biomass in Pacific salmon. The ocean distribution index indicates matrix numbers of $2^{\circ} \times 5^{\circ}$ area where salmon were caught until 1985. The biomass shows average catch by species in 1952-1975 (Kaeriyama, 1985).

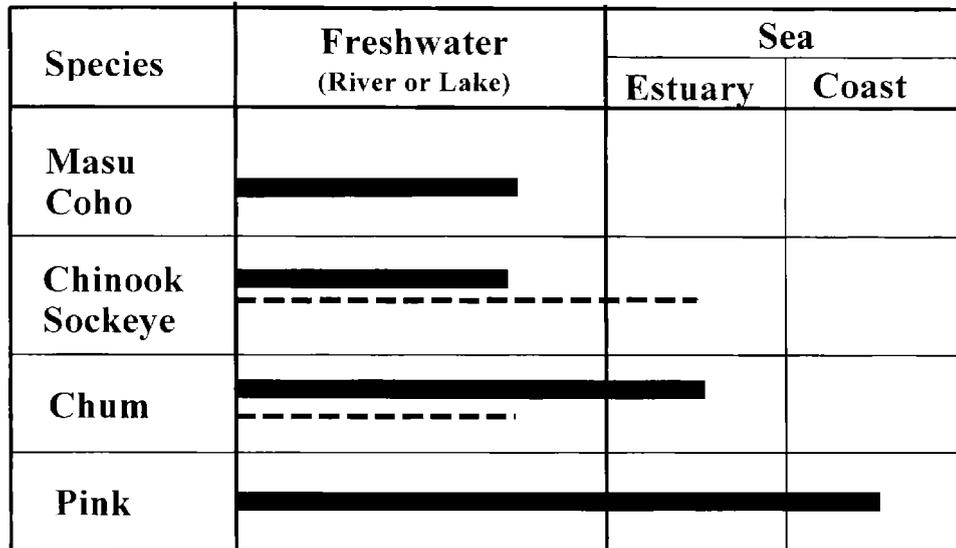


Fig. 3. Distribution areas of underyearling Pacific salmon at the downstream migration.

immediately after the emergence (Heard, 1991).

In six species of Pacific salmon (genus *Oncorhynchus*), namely, a species that migrates seaward at an earlier developmental stage may have greater abundance and a wider area of ocean distribution than later migrants (Kaeriyama, 1985).

Migration and Freshwater Residence of Sockeye Salmon

Sockeye and chinook salmon exhibit the most diverse life histories in Pacific salmon. For instance, adult sockeye salmon have the most number of common age-groups in Pacific salmon (Table 1). 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 the following two steps: (i) the occurrence of “residual” offspring among the progeny of an anadromous stock; and (ii) the modification of the progeny of residuals into the typical kokanee. In anadromous sockeye salmon, juveniles typically rear in lakes for one or more years before the seaward migration (lake type). Some individuals in northern populations go to the sea immediately after their emergence (sea type) or inhabit river channels for at

Table 1. The most common age-groups of genus *Oncorhynchus* by species based on Major et al. (1978), Healey (1986), Burgner (1991), Salo (1991), Healey (1991), and Sandercock (1991).

Species	Age-groups	Numbers
Pink Salmon	0.1*	(1)
Chum salmon	0.1*, 0.2*, 0.3*, 0.4*, 0.5*	(5)
Sockeye salmon	0.2, 0.3, 0.4, 0.5, 1.0*, 1.1*, 1.2*, 1.3*, 1.4, 2.1*, 2.2*, 2.3, 2.4, 3.1, 3.2, 3.3, 3.4, 4.1, 4.2, 4.3	(20)
Chinook salmon	0.1, 0.2, 0.3, 0.4, 0.5, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 2.1, 2.2, 2.3, 2.4, 2.5	(16)
Coho salmon	1.0, 1.1, 2.1, 3.1, 4.1	(5)
Masu salmon	1.1*, 2.1*	(2)

* Common age-groups in Japan.

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 Urumobetsu, 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 the Lake Shikotsu and returning as anadromous type had several life history patterns such as precocious, residual, and anadromous type (Kaeriyama et al., 1992; Kaeriyama, 1994).

In Lake Shikotsu, smolts were smaller than residual fish (Fig. 4). Based on the allometry between fork length and body weight (Fig. 5) and the condition factor (Fig. 6), Lake Shikotsu sockeye salmon smolts are more slender in body shape than residuals. Figure 7 shows a relationship between population 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 rate 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 that (1) their residence or seaward migration may be affected by both the population density and the resource condition, which reflects their growth, in the lake, and that (2) 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 which 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

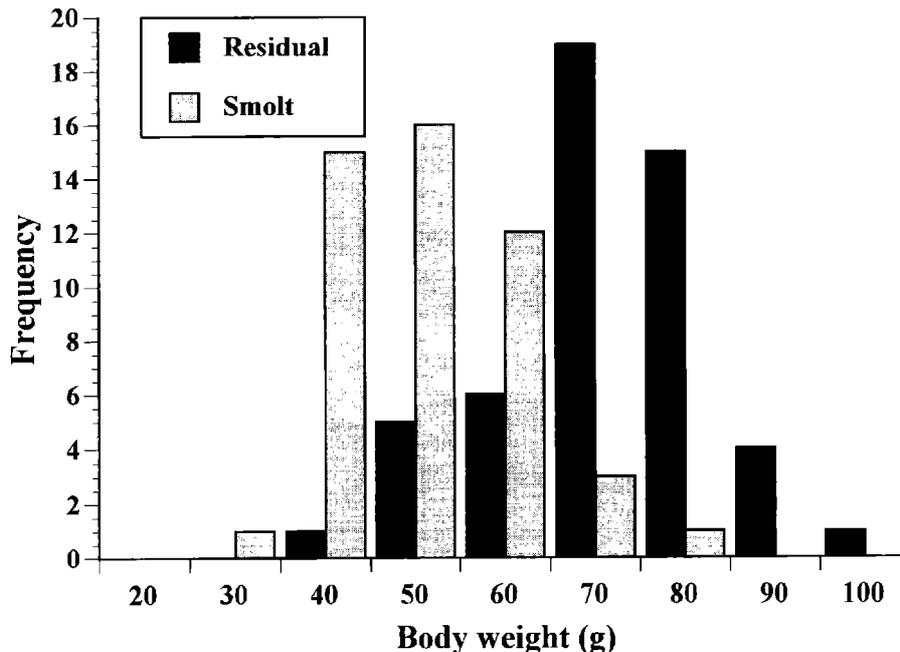


Fig. 4. Frequency distributions of body weight of residual and smolt sockeye salmon (age 2+) collected in Lake Shikotsu on July 15, 1987.

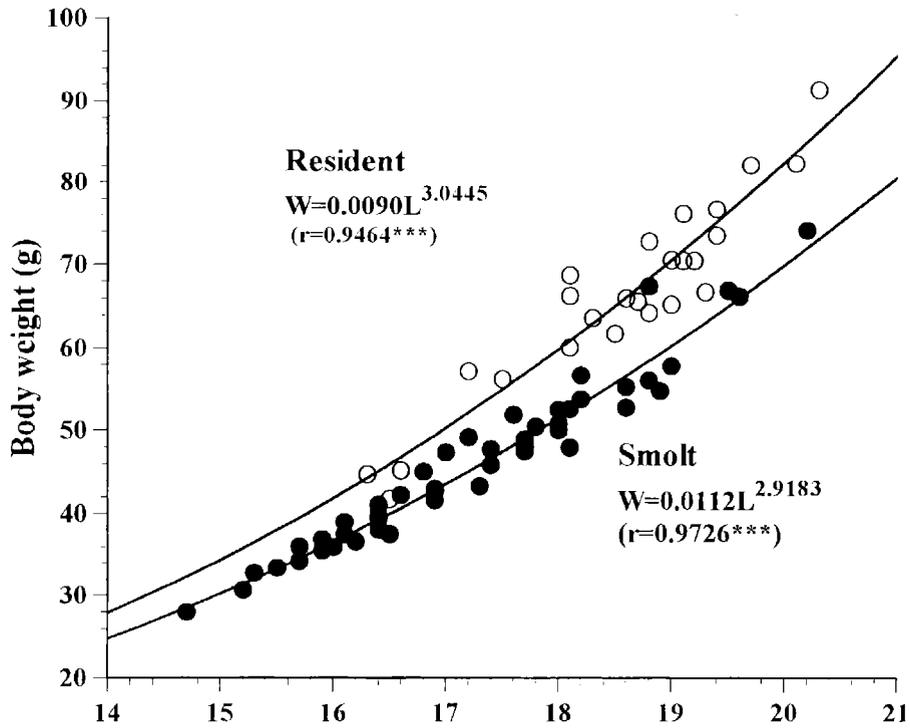


Fig. 5. Relationships between fork length and body weight of residual and smolt sockeye salmon (age 2+) collected in Lake Shikotsu on July 15, 1987.

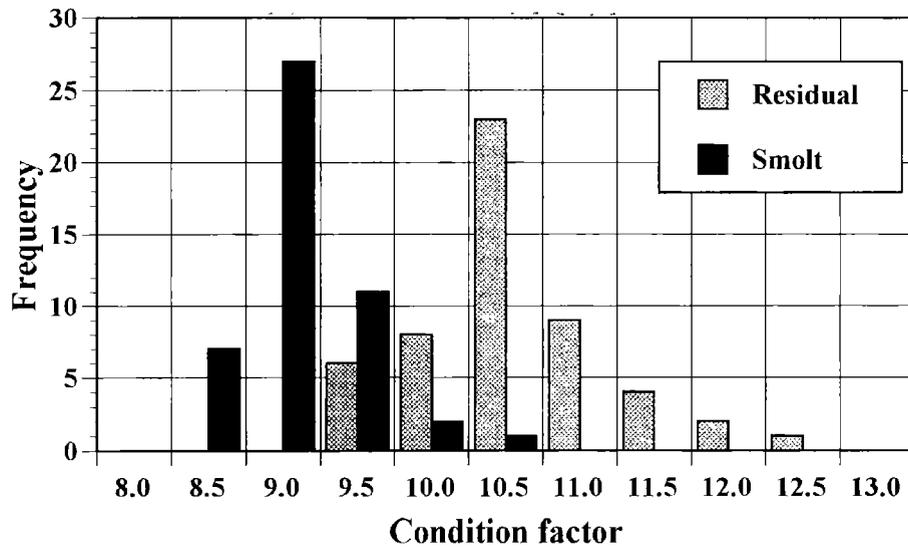


Fig. 6. Frequency distributions of condition factors of residual and smolt sockeye salmon (age 2+) collected in Lake Shikotsu on July 15, 1987.

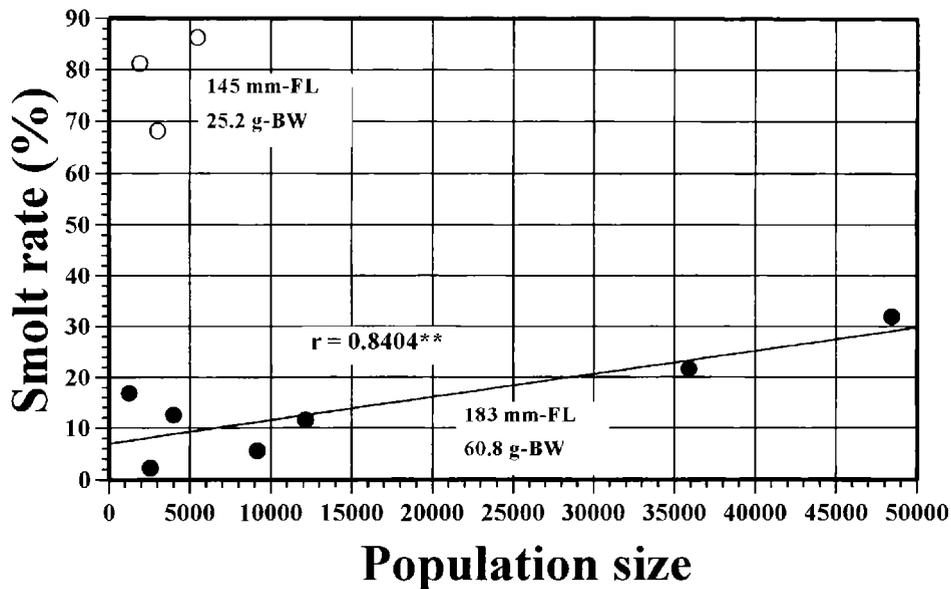


Fig. 7. Relationship between population size (P) and smolt rate (S) of lacustrine sockeye salmon in Lake Shikotsu: $S = 0.000045P + 0.0699$ ($r = 0.8404$, $P < 0.01$). The population size shows total numbers of smolt and adult, and the smolt rate represents the number of smolt per population size in a population. Fork lengths of smolt population are 183 ± 15 mm in 1978-1983 and 1987-1988 (closed circles), and 145 ± 4 mm in 1984-1986 (open circles). Data are obtained from Kaeriyama (1991).

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.

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 at sea (Kaeriyama, 1986). Juvenile chum salmon migrate from late winter 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 (Fig. 8). These prior individuals tend to dominate over numerous posterior individuals in the river (Kaeriyama, 1996). Numerous juveniles migrate downstream immediately after the 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 ($P < 10^{-9}$) in fork length during the seaward migration between wild population (54 ± 7 mm) staying during long period in the Bibi River at low density and enhanced juveniles (40 ± 6 mm) migrat-

ing seaward immediately after the release at high density in the Tokachi River (Fig. 9).

Because the chum salmon spawn in areas of upwelling groundwater, there may be little changes of the water temperature and a few prey around the spawning area. Prior individuals, therefore, have a low specific growth rate ($SGR < 0.006$). On the other hand, numerous juvenile migrating downstream temporarily stay at the estuary, where has much food and a rise in water temperature in the spring. They rapidly grow in the estuary ($SGR > 0.01$). Namely, growth inversion occurs between a few prior-resident and numerous migrating juveniles (Fig. 10).

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 specific 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

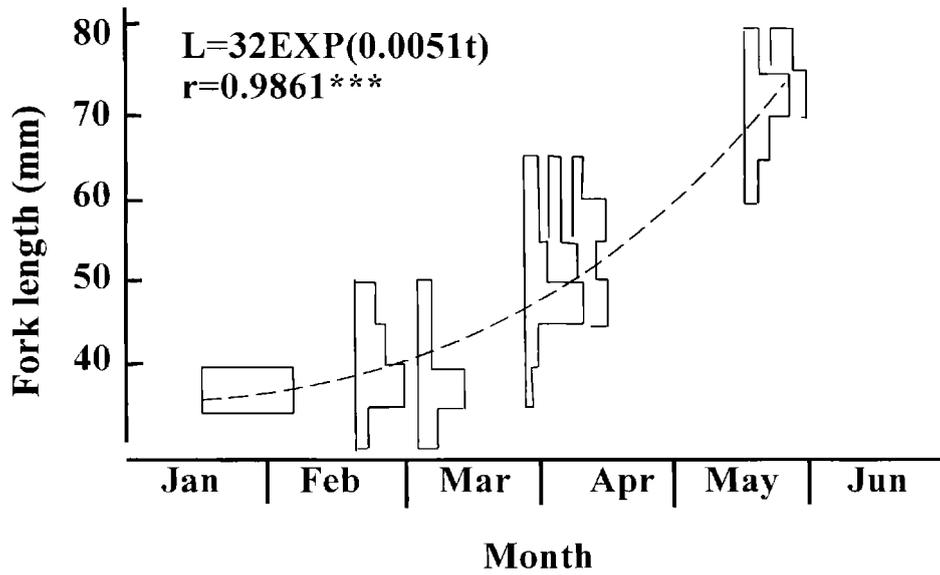


Fig. 8. A growth curve of wild juvenile chum salmon captured and marked around the spawning area in the Kitakami River during the period of January to June in 1980. $L = 32e^{0.0051t}$ ($r = 0.9861$, $P < 0.001$). Data are obtained from Kaeriyama (1986).

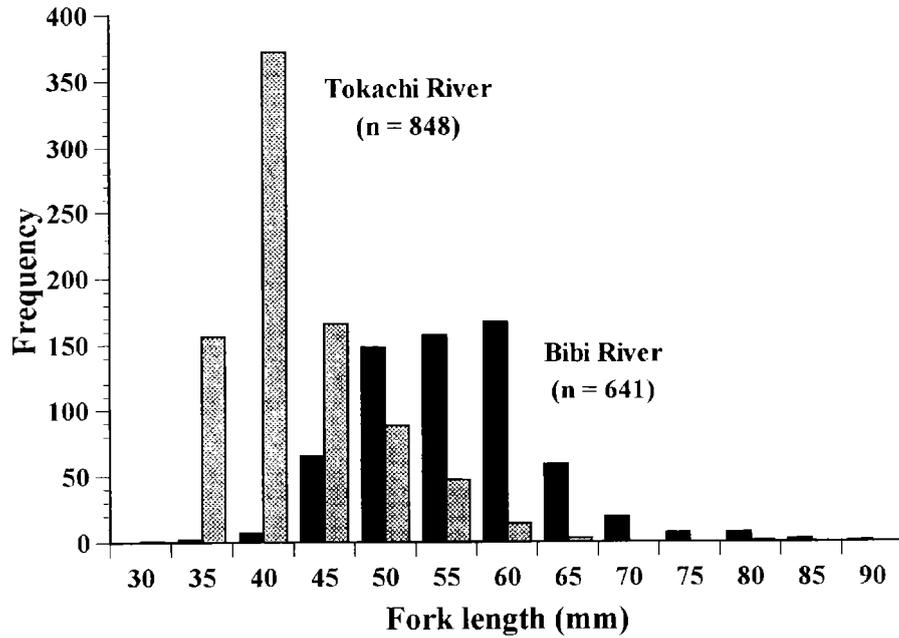


Fig. 9. Frequency distribution of fork length of juvenile chum salmon from Tokachi (enhanced) and Bibi (wild) rivers.

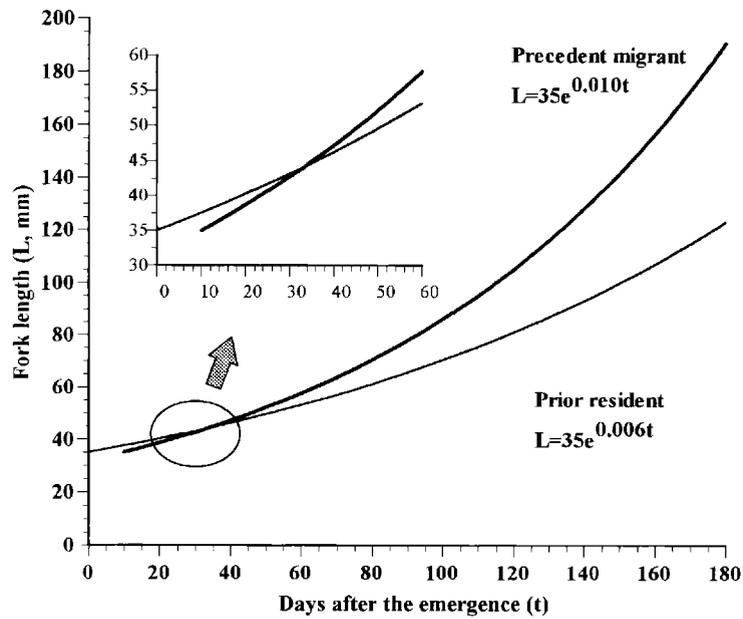


Fig. 10. A model of growth inversion between a few prior-resident (SGR = 0.006) and numerous migrating juveniles chum salmon (SGR=0.010) in the river and at the coastal sea. The SGR shows a specific growth rate.

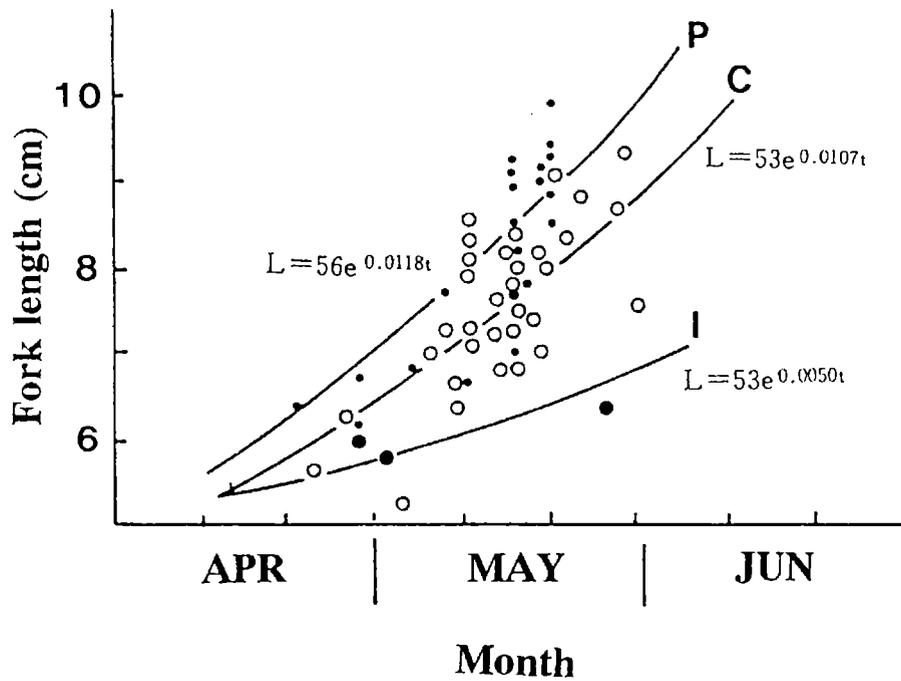


Fig. 11. Growth curves of marked juvenile chum salmon released from the Kitakami River (Kaeriyama, 1986). P (●), offshore migration type (food, pelagic organisms); C (○), neritic residence type (food, coastal zooplankton); I (●), shore residence type (food, terrestrial insects).

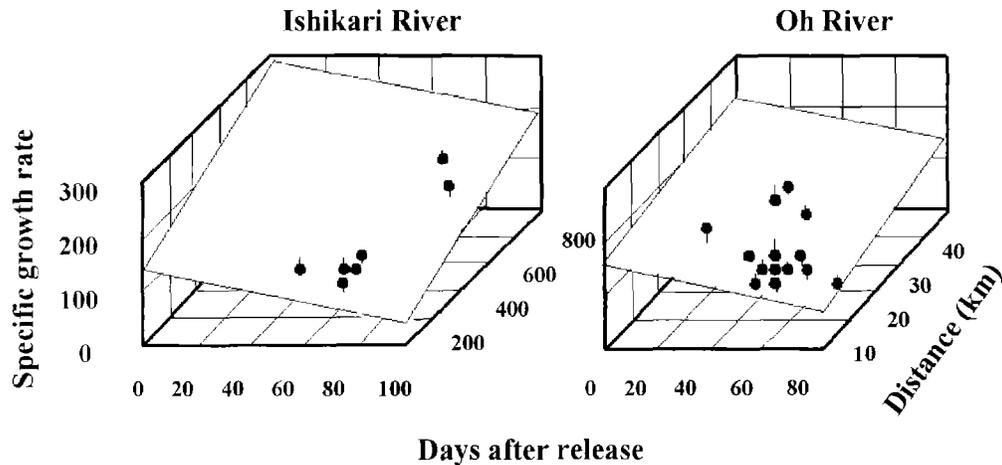


Fig. 12. Multiple regression analysis in specific growth rate (G) of marked juveniles on days after release (t) and distance from release river (k , km) in chum salmon population released from the Oh and Ishikari rivers (Modified from Kaeriyama 1986). Oh River, $G = -1.450t + 1.853k + 163$; Ishikari River, $G = -1.010t + 0.147k + 140$.

insects, respectively (Fig. 11). 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. 12). These results suggest that larger juveniles which higher growth rate migrate more rapidly and farther away from release rivers than those with higher population densities.

In summary, the life history strategy of chum salmon may correspond with 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 juvenile. 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 Pacific salmon.

Conclusion

Expanding the habitat area, therefore, species of *Oncorhynchus* are able to get more resources. In contrast, they incur many risks such as osmoregulation, energetic demands of swimming, exposure to predators, mobilization to non-adaptable habitat by water current with the expansion of distribution area. Therefore, the benefits of their migration may involve 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 evolu-

tion of anadromous fish that have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in the freshwater.

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ベニザケとサケ幼稚魚の生活史戦略と回遊に及ぼす個体群密度と生息環境の影響

帰山雅秀

ベニザケ (*Oncorhynchus nerka*) とサケ (*O. keta*) 幼稚魚の生活史は、残留と移動の2つの戦術からなる条件戦略を示す。幼稚魚は、餌料や生息場などの資源が得られる

ときは残留するが、彼らのエネルギー代謝を満たすだけの十分な資源が得られない場合は降海する。彼らの回遊パターンは、「先住効果」と「先行移動」により制御されており、浸透圧調節能、遊泳エネルギー要求量、被食、および海流による不適な環境への移送などのリスクと資源獲得の好適度とのトレード・オフにより決定されるのだろう。