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by

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

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ABSTRACT - Life histories of juvenile sockeye and chum salmon 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", would be determined as 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 objective of the North Pacific Anadromous Fish Commission (NPAFC) is to promote the conservation of anadromous stocks in the Convention Area (Article VIII-2). A goal of scientific research for the Committee on Scientific Research and Statistics (CSRS) are, therefore, to establish the conservation methods for each anadromous stocks, which may be defined as local population (deme) or Mendelian population (Fisheries Agency of Japan, 1993). Fisheries Agency of Japan proposes that stock assessment of salmon in the North Pacific Ocean should be recognized as a most important issue of the CSRS (Fisheries Agency of Japan, 1994). It is a matter of course that the establishment of stock assessment method is based on the elucidation of their life history. The aim of the present study is to review life-history strategy and migration pattern of Pacific salmon (*Oncorhynchus* spp.).

The migrations of fishes are generally classed biologically as "alimental" 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 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*), a species which migrates seaward at the 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 would have obtained the ability of homing migration for maximizing reproductive success in fresh water.

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 sockeye tends to have a higher growth rate and to mature at an earlier age than the anadromous individuals (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 stages: i) the occurrence of "residual" offspring among progeny of anadromous stock; and ii) the modification of progeny of such 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), but particularly in northern populations, some individuals 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).

Sockeye salmon are reproduced by an artificial enhancement program in Lake Shikotsu. They were 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 are 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. They would be,

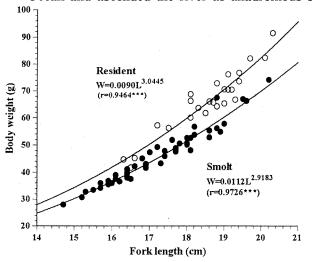


Fig. 1. Relationships between fork length (L) and body weight (W) of resident and smolt sockeye salmon in Lake Shikotsu collected on July 15, 1987

therefore, classified to the residual sockeye salmon. Most of 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 a lacustrinelimnological 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. Based on the allometry between fork length and body weight, Lake Shikotsu sockeye salmon smolts are more slender in body shape than residuals (Fig. 1). Fig. 2 shows a relationship between the population size and smolt rate (number of smolts / population size) of Lake Shikotsu sockeye salmon. Smolts occurring in 1984-1986 (145 \pm 4 mm) were significantly smaller (P < 0.001) in fork length and higher (P < 0.001) in smolt rate than those in other years (183 \pm 15 mm). 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 have two tactics of residence and migration. Namely, Lake Shikotsu sockeye salmon usually remain in the lake as a residual type if they can sufficiently obtain their resources such as food and habitat, whereas a part of the population migrate seaward as smolts after one or two years in the lake when they do not have enough those resources satisfying their energy metabolism.

Migration pattern of juvenile chum salmon

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 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

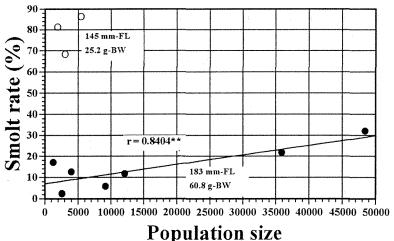


Fig. 2. Relationship between population size (P) and smolt rate (S) of lacustrine sockeye salmon in Lake Shikotsu: S=0.0000045P+0.0699 (r=0.8404**). The population size shows total numbers of smolt and adult, and the smolt rate represents the number of smolt per population size. Data are obtatined from Kaeriyama (1991).

juveniles migrate downstream immediately after the emergence. Especially, most of enhanced juveniles migrate seaward at fry stage (FL < 50 mm) less than 10 days after the 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 between wild population (54 \pm 7 mm) staying during long period in the Bibi River at low density and enhanced juveniles (40 \pm 6 mm) migrating seaward immediately after the release at high density in the Tokachi River (Fig. 3).

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 reveals data for specific growth

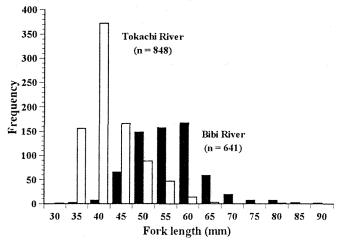


Fig. 3. Frequency distribution of fork length of juvenile chum salmon from Tokachi (enhanced) and Bibi (wild) rivers.

rate of marked juvenile chum salmon as a function of days after release and distance from the

released river (Fig. 4). These results indicate that larger juveniles which have higher growth rate migrate more rapidly and farther away from released rivers than others with an increase in a population density.

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 would be generally observed for species of the genus *Oncorhynchus*.

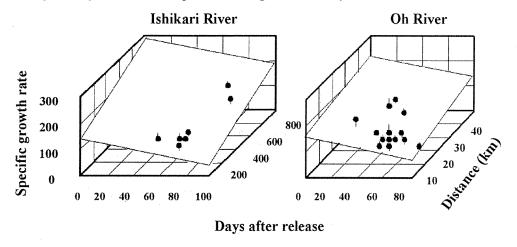


Fig. 4. Multiple regression analysis in specific growth rate (G) of marked juveniles on days after release (t) and distance from release river (k: km) in chum salmon population released from the Oh and Ishikari rivers (modified from Kaeriyama, 1986). Oh River: G=-1.450t+1.853k+163, Ishikari River: G=-1.010t+0.147k+140.

Migration model of the genus Oncorhynchus

Based on the above consideration. migration pattern of the Oncorhynchus conforms to the "ideal free distribution model", modified from Fretwell and Lucas (1970). The growth rate (G) as a profitability of the resource acquisition can be represented by function of population density (D) and habitat area (H). Given in Fig. 5, the X-axis is "density" of a population, the Y-axis is "growth rate" of individual, and "H" is a "habitat area". The habitat area enlarges from "H1" to "H3" (from a river, through coastal waters, to the ocean). For instance, juveniles stay on "H1" and keep high growth rate (more

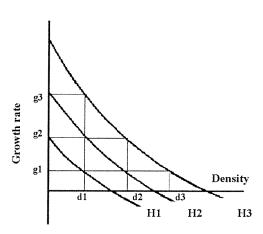


Fig. 5. Migration model of the genus Oncorhynchus.

than "g1") at "low density". With an increase in population density, their growth rate may decrease. When the density exceeds "d1" and the growth rate falls less than "g1", juveniles migrate to wider habitats such as "H2" and "H3". Even if the density is low, fish which need higher energy metabolism or more resources ("g3") can migrate to wider habitats ("H2" or "H3").

In conclusion, expanding the habitat area, species of Oncorhynchus are able to get more

resources. By contrast, they are received many risks such as osmoregulation, energetic demands of swimming, exposure to predators, mobilization to non-adaptable habitat by water current with the migration. Therefore, benefits of their migration may be determined as a trade-off between the profitability of resource acquisition and risks with migration. The life history strategy and migration pattern of the genus *Oncorhynchus* would reflect an evolution of anadromous fish which have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in the freshwater.

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