Life History Strategy and Migration Pattern of Juvenile Sockeye (*Oncorhynchus nerka*) and Chum Salmon (*O. keta*) in Japan: a Review

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Kaeriyama, M., and H. Ueda. 1998. Life history strategy and migration pattern of juvenile sockeye (*Oncorhynchus nerka*) and chum salmon (*O. keta*) in Japan: a review. N. Pac. Anadr. Fish Comm. Bull. No. 1: 163-171

Life histories of sockeye (*Oncorhynchus nerka*) and chum salmon (*O. keta*) show a conditional strategy which have two tactics of residence and migration. They remain in lakes and rivers if they can obtain sufficient resources such as food and habitat, or migrate seaward when they do not have enough resources to satisfy their energy metabolism. Their migration pattern, controlled by effects of "prior residence" and "precedent migration", may be influenced by 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. The life history strategy and migration pattern of the genus *Oncorhynchus* reflect an evolution of anadromous fish by which they have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in freshwater.

INTRODUCTION

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 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 and catadromy are the most in polar-temperate and tropical environments, respectively. 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 (*Oncorhynchus spp.*) 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 Japanese Pacific salmon by focusing on variation in the life history strategy of sockeye salmon (*O. nerka*), which have a diverse pattern of the life history, and chum salmon (*O. keta*), which migrate seaward immediately after emergence, but may reside for a short period of time in freshwater.

OCEAN DISTRIBUTION AND BIOMASS OF PACIFIC SALMON

Of the six species of Pacific salmon, masu salmon (*O. masou*) have the most limited distribution and the least abundance. They occur only in areas of the Far East. Coho (*O. kisutch*), chinook (*O. tshawytscha*), and sockeye salmon have the relatively wide distribution in the North Pacific Ocean. Chum and pink salmon (*O. gorbuscha*) have the widest distribution in the North Pacific Ocean. Pink salmon also have the most abundant among Pacific salmon. In general, the more abundant species of Pacific salmon have the wider ocean distribution in the North Pacific Ocean (Fig. 1).

The six species of Pacific salmon vary widely in

Fig. 1 Relationship between the ocean distribution index and the biomass in Pacific salmon. The ocean distribution index indicates matrix numbers of 2° X 5° area where salmon were caught until 1985. The biomass shows an average total catch by species in 1952-1975 (Kaeriyama 1985).

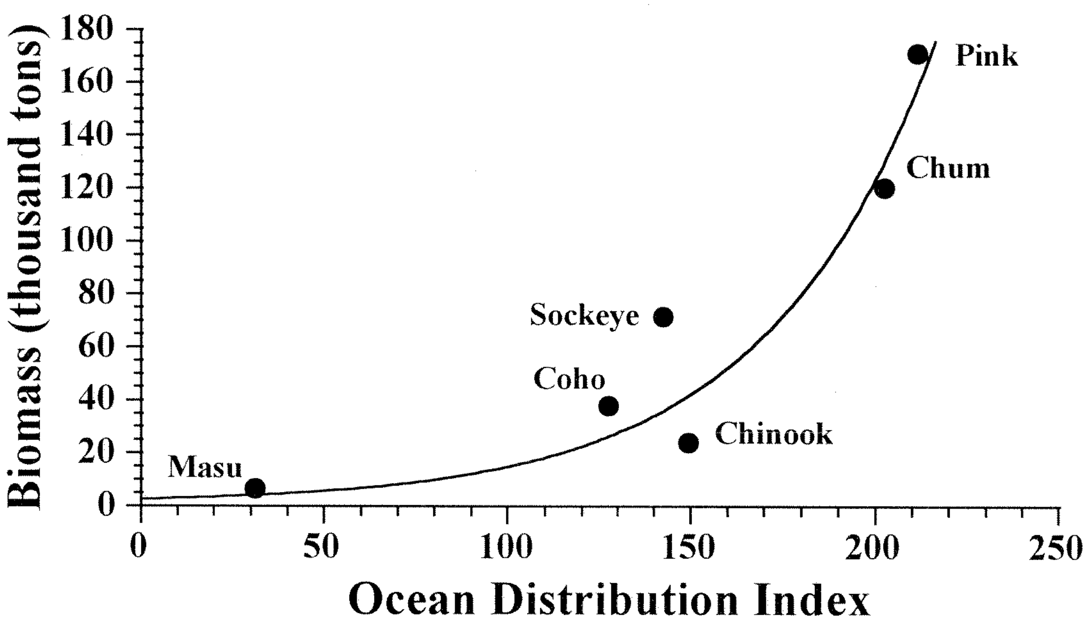
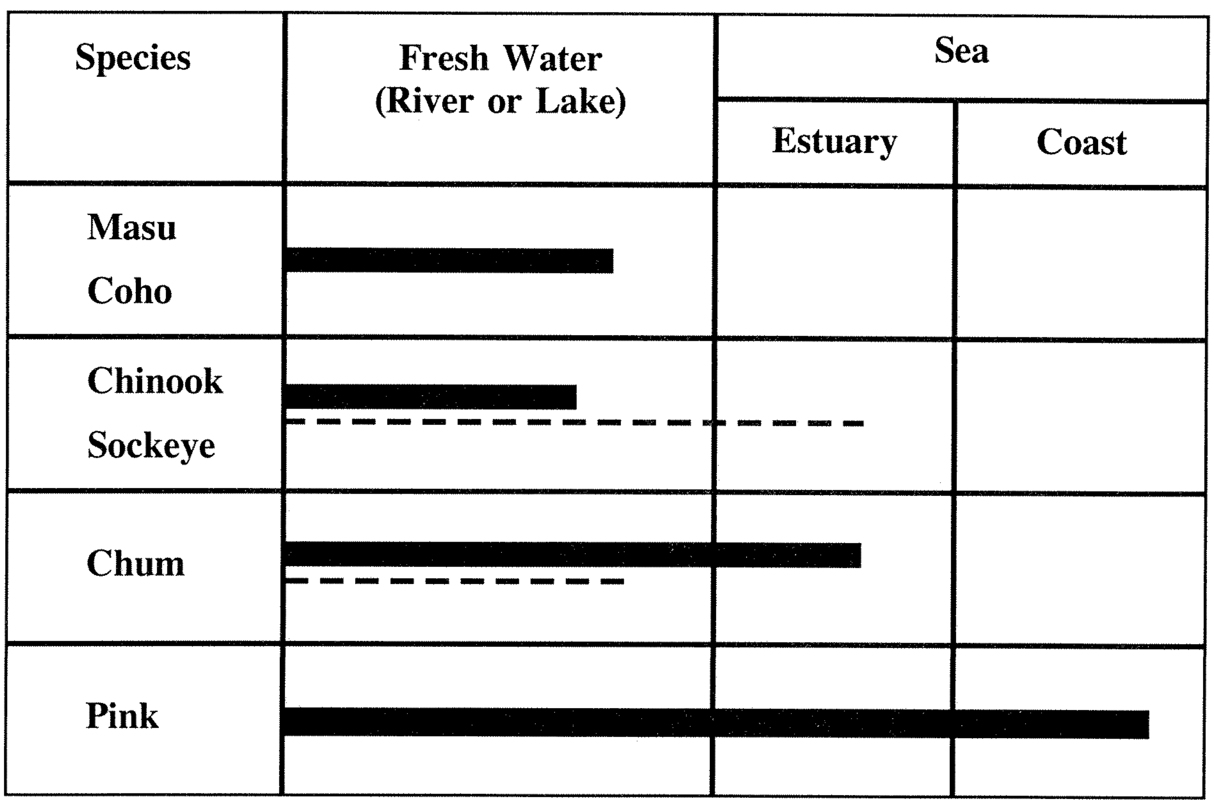


Fig. 2 Area of the downstream migration at the underyearling stage in species of Pacific Salmon.



their freshwater residence and migration pattern (Fig. 2). Masu and coho salmon reside in freshwater for at least one or two years before migrating seaward as smolt. Most individuals of chinook and sockeye salmon rear in freshwater for one or more years before seaward migration. A portion of them, however, enter the sea at the underyearling stage, known as ocean-type or sea-type stocks (Clarke et al. 1989; Wood et al. 1987). Numerous chum salmon fry migrate seaward immediately after emergence. Only a few juveniles reside in the river for up to several months (Kaeriyama 1986). All pink salmon enter the sea as fry immediately after the emergence (Heard 1991).

In Pacific salmon, the species that migrate seaward at an earlier developmental stage and rear in the sea may have greater abundance and a wider area of ocean distribution than the species that rear extensively in freshwater (Kaeriyama 1985).

MIGRATION AND FRESHWATER RESIDENCE OF SOCKEYE SALMON

Sockeye and chinook salmon exhibit the most diverse life histories among Pacific salmon. For instance, adult sockeye salmon have the largest number of common age-groups (Table 1). Although sockeye are primarily anadromous, there are distinct populations of "residual" sockeye and kokanee salmon (Ricker 1940). Residual sockeye are, at least in part, progeny of anadromous parents (Burgner 1991). A part of them, however, juveniles 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 a freshwater existence and presumably diverted from a common anadromous stock in recent geological times (Ricker 1940). However, the process of evolution is not clear (Burgner, 1991). In anadromous sockeye salmon, juvenile 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).

Lacustrine sockeye salmon are fully reproduced by artificial enhancement program within Lake Shikotsu. They were originally transplanted from the residual population in Lake Akan, Hokkaido Island, in 1893 and from the anadromous population in Lake Urumobetsu, Iturup Island, during 1925-1940. They produce smolts regardless of being geographically landlocked over 15 generations in the lake (Kaeriyama 1991). Those smolts ascended the other river, where they were artifically released, as anadromous sockeye salmon after 0-3 years of marine life. Most of the smolts, 3 years old (age-2.0), migrated downstream between late June and early July. The age and timing at seaward migration of Lake Shikotsu smolts corresponded with those of sockeye salmon smolt in Lake Urumobetsu, although the limnological environments of Lake Shikotsu differ much from those of Lake Urumobetsu. On the other hand, progeny of sockeye introduced to Lake Shikotsu led more diverse life history patterns including precocity (precocious male returning the river several months after marine life; 200 mm in mean fork length), lacustrine (250 mm in mean fork length), and anadromy (400 mm, 520 mm, and 590 mm in mean fork lengths of age- .1, .2, and .3) (Kaeriyama et al. 1992; Kaeriyama 1994).

Of the same population (age-2.0) in Lake Shikotsu, smolts captured in outlet of the lake by set nets were smaller than residual fish taken in the center of the lake by gill nets (Fig. 3). Based on the allometry between fork length and body weight (Fig. 4), Lake Shikotsu sockeye salmon smolts are more slender in body shape than residuals. Fig. 5 shows a relationship between the population size and smolt rate (number of smolts / population size) of Lake Shikotsu sockeye salmon. In 1984-1986, smolts (145 $\pm$ 4 mm) were significantly smaller ($P < 0.001$) in fork length and smolt rate was significantly higher ($P < 0.001$) than those in other

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.

Fig. 3 Frequency distribution of body weight of residual and smolt sockeye salmon collected in Lake Shikotsu on July 15, 1987.

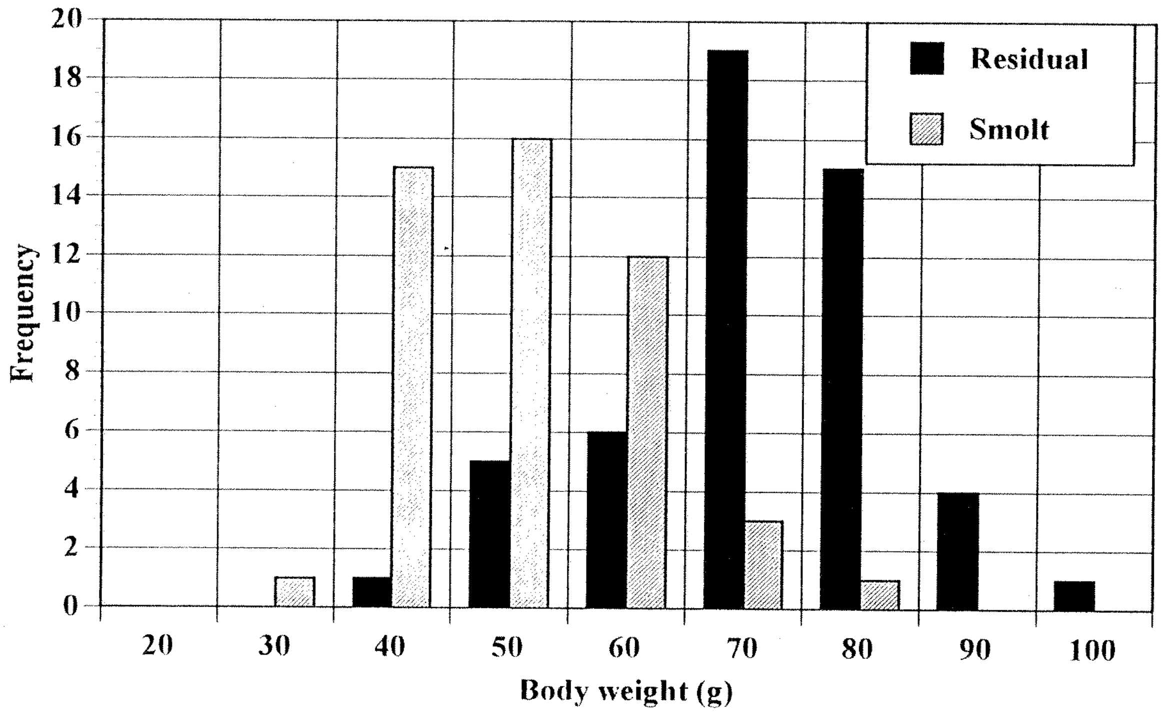


Fig. 4 Relationships between fork length and body weight of residual and smolt sockeye salmon collected in Lake Shikotsu on July 13, 1987.

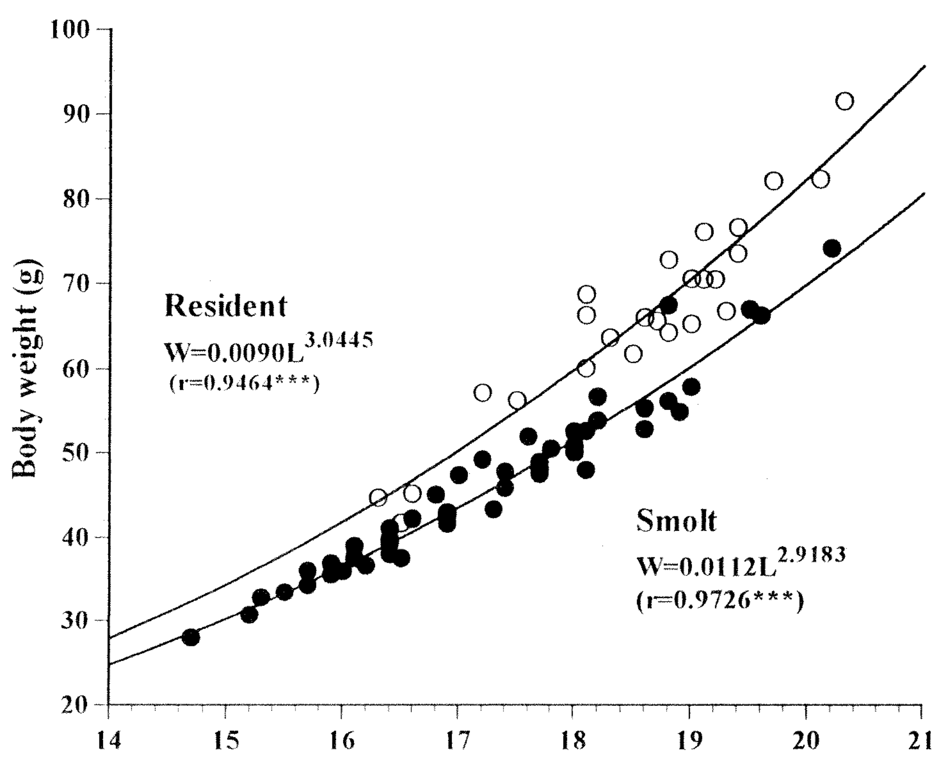
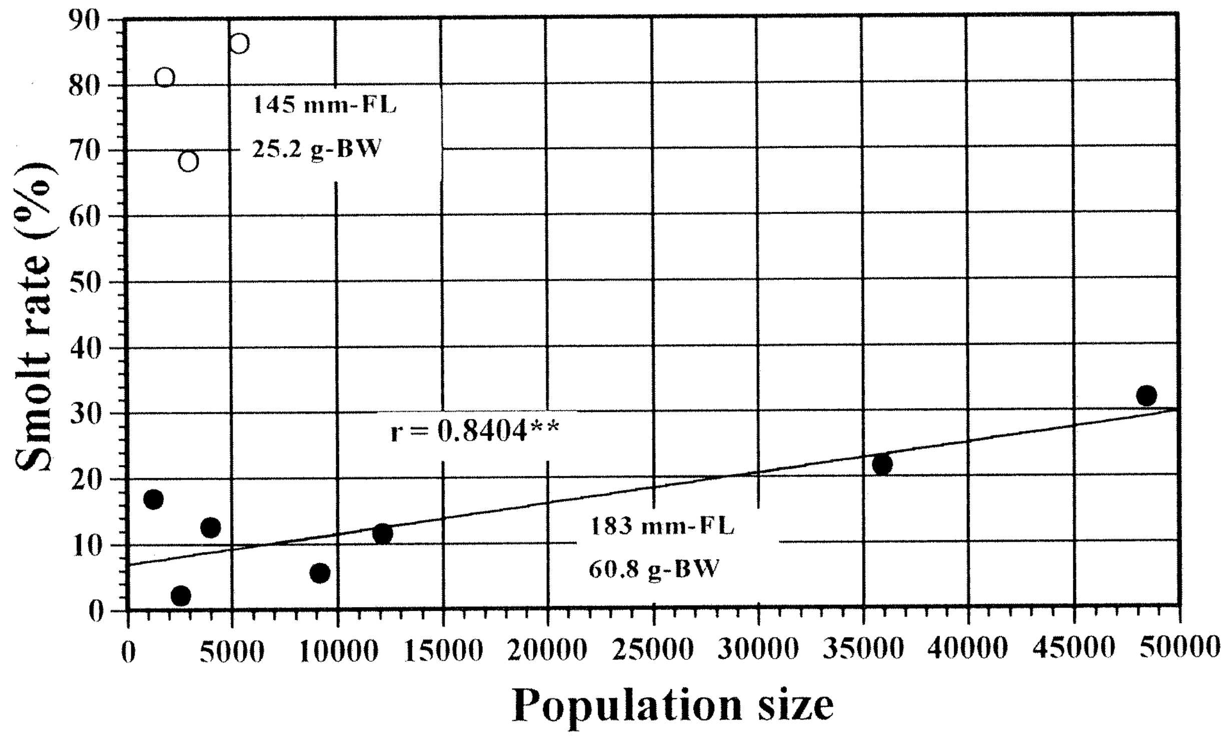


Fig. 5 Relationship between population size (P) and smolt rate (S) of lacustrine sockeye salmon in Lake Shikotsu: S = 0.0000045P + 0.0699 (r = 0.8404). The population size shows total numbers of smolt and adult, and the smolt rate represents the number of smolt per population size in a population. Fork lengths of smolt populstion are 183 ± 15 mm in 1978-1983 and 1987-1988, and 145 ± 4 mm in 1984-1986. Data are obtained from Kaeriyama (1991).**



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 the resources in the lake.

These results also suggest that the life history of sockeye salmon may be a conditional strategy that has two tactics of residence and migration. Lake Shikotsu sockeye salmon 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. These smolts grow to the anadromous type larger than the residual type.

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 to the sea from late winter to early summer in Japan. Kaeriyama (1986) divided the migrating juvenile into three groups: (1) the "river" type, which remain in the river until early summer; (2) the "foraging migration" type, which migrate to the coastal area where they forage until the Oyashiko Current approaches; and (3) the "escape migration" type, which remain in the coastal area until early summer.

The small percentage of fry that emerge from spawning redds in early spring and remain in rivers for several months are characterized by low specific growth rate. These early emerging individuals tend to dominate over numerous late emerging individuals in the river (Kaeriyama 1996). Their migration behaviors has been sometimes observed as the delayed seaward migration (Mason 1974). Most of wild juveniles migrate downstream immediately after the emergence. Most of enhanced juveniles migrate seaward from rivers at the fry stage (fork length < 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 the wild population (54 ± 7 mm) staying during long period in the Bibi River at low density (less than a million juveniles) and enhanced juveniles (40 ± 6 mm) migrating seaward immediately after the release at high density (more than 50 million juveniles) in the Tokachi River (Fig. 6).

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. Early emerging individuals, therefore, have a low growth rate (Specific growth rate; SGR < 0.006). On the other hand, numerous juvenile migrating downstream temporarily stay in the estuary, where increased food abundance and higher temperatures are available for growth. They rapidly grow in the estuary (SGR > 0.01). Namely, growth inversion occurs between a few prior-resident and numerous migrating juveniles (Fig. 7).

Juvenile chum salmon remain in the coastal sea for a time and migrate offshore at post-fingerling stage in Japan. This offshore migration is usually preceded by larger individuals (the "foraging migration" type; 120 mm in mean fork length), which have the higher growth rate and forage more actively on prey than others (the "escape migration" type; 80 mm in mean fork length), which passively escape from unsuitable environmental conditions such as higher temperature (Kaeriyama 1986; Salo 1991). For instance, larger marked juveniles released into the Kitakami River in the spring of 1983 began to migrate offshore and to feed on pelagic organisms earlier than the others. Juveniles caught offshore preyed on pelagic organisms such as *Themisto japonica* and *Euphausia pacifica*. They showed much better growth than those from neritic and inshore waters, which fed on coastal zooplankton and terrestrial insects, respectively (Kaeriyama 1986). 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. 8). These results suggest that larger juveniles which have a higher growth rate migrate more rapidly and farther away from release river. Namely, larger juveniles which have the higher energy metabolism and growth rate migrate more rapidly than others in chum salmon as well as in sockeye salmon.

Fig. 6 Frequency distribution of fork length of juvenile chum salmon from the Tokachi (enhanced) and Bibi (wild) rivers.

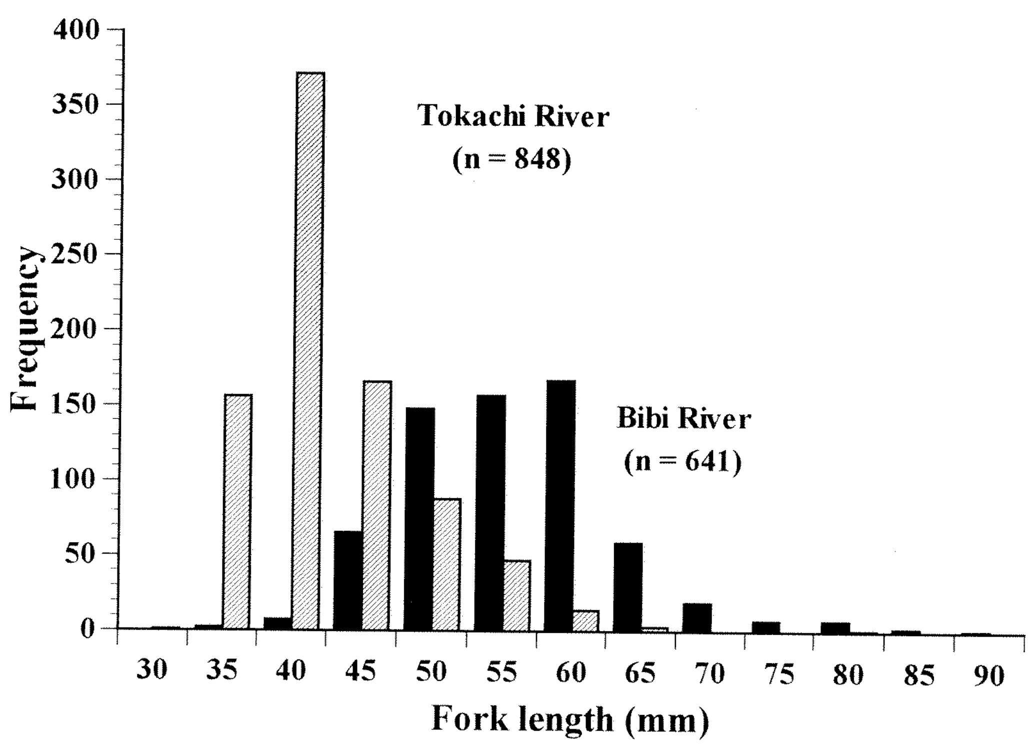


Fig. 7 **A model of growth inversion between a few prior-resident (SGR=0.006) and numerous migrating juveniles chum salmon (SGR=0.010) in the river and at the coastal sea. The SGR shows a specific growth rate.**

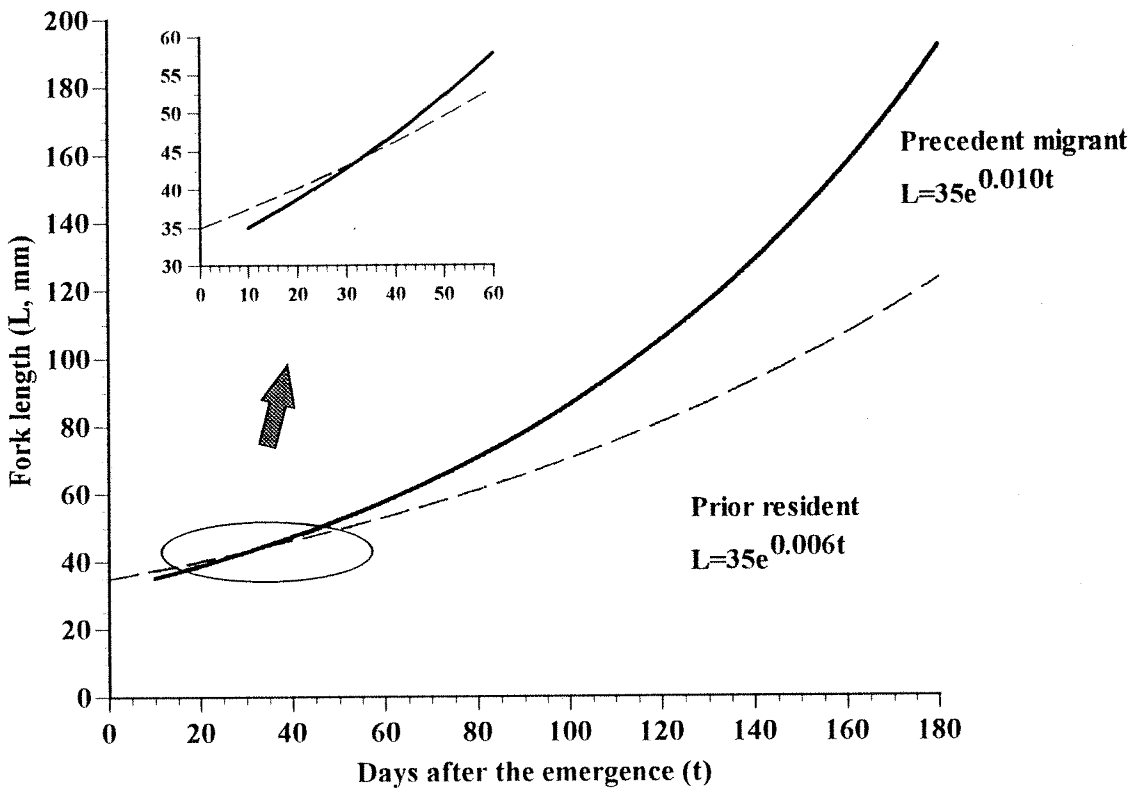
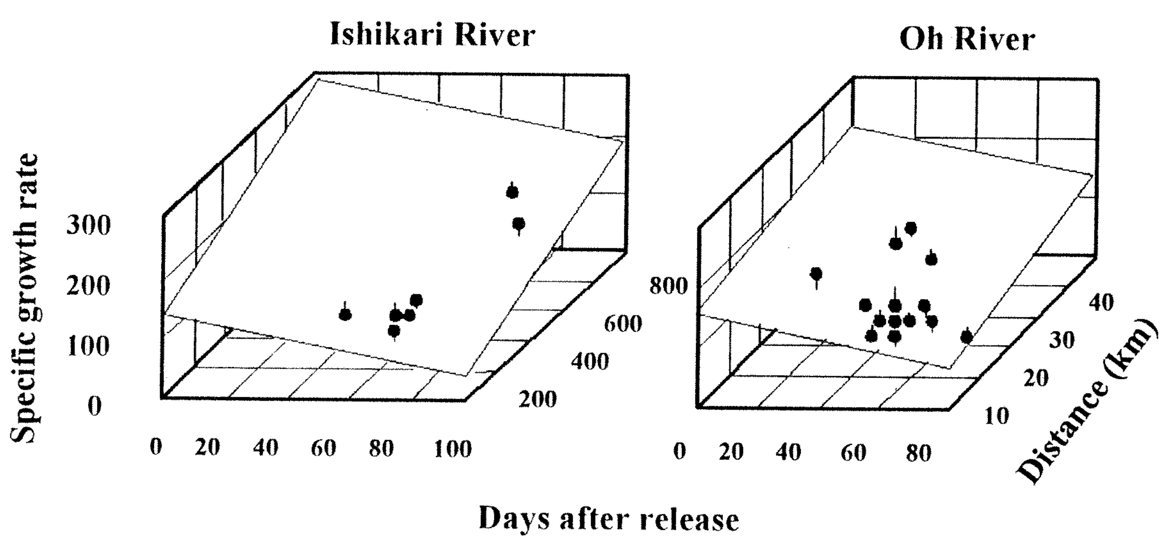


Fig. 8 **Multiple regression analysis in specific growth rate (G) of marked juveniles on days after release (t) and distance from release river (k: km) in chum salmon population released from Oh and Ishikari rivers (Modified from Kaeriyama 1986). Oh River: G = -1.450t + 1.953k + 163, Ishikari River: G = -1.010t + 0.147k + 140.**



CONCLUSIONS

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 large juveniles. This life history strategy is also known for masu salmon, which is supposed the most primitive species in Pacific salmon. Early emerging juveniles reside dominantly in upper rivers to mature and reproduce as parr. Late emerging juveniles migrate downstream, spend one or two years in middle- or lower-rivers, and migrate seaward as smolts (Kubo, 1980; Mayama, 1992). The conditional strategy and the precedent migration pattern, therefore, may apply to all species of Pacific salmon.

Expanding the habitat area, therefore, Pacific salmon 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 through migration. 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 evolution of anadromous fish that have acquired anadromy for obtaining food resources in the sea and homing ability for reproduction in the freshwater.

ACKNOWLEDGEMENTS

We especially thank Katherine W. Myers and Kazuya Nagasawa for useful comments on the manuscript, and Mart R. Gross and Masa-aki Fukuwaka for discussions on the life history evolution.

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