Partial Migration in Salmonids: Focusing on Asian Endemic Masu Salmon (*Oncorhynchus masou*) and White-Spotted Charr (*Salvelinus leucomaenis*)

Genki Sahashi and Kentaro Morita

Abstract Partial migration is perhaps one of the most striking features of life-history polymorphism, in which a population displays both migratory and resident behavior. Not surprisingly, both plasticity and genetics are involved in the life-history divergence between residents and migrants. The most plausible mechanism for the persistence and evolution of partial migration is a status-dependent conditional strategy, in which the adoption of alternative migratory tactics is influenced by the status (e.g., body size, condition) of individuals to maximize fitness. To uncover the factors affecting life-history divergence, approaches comparing traits (e.g., growth rate) between residents and migrants are common, but care must be taken in interpreting cause and effect as the onset of life-history divergence precedes the actual timing of outmigration. Individuals planning to migrate will change their behavior and growth rate for a period of 6 months or more to pre-adapt to life at sea, which is very different from life in a river. Early studies of partial migration often dichotomously divided the life histories of residents and migrants, but recent studies have shown there is remarkable diversity within migrants. It is important but challenging to study diverse migration life-history strategies. In this review, we focus on Asian endemic masu salmon and white-spotted charr, which to date have received little attention in studies of partial migration, to seek a comprehensive understanding of the partial migration phenomenon in these salmonids.

Keywords Alternative tactics · Anadromous fish · Conditional strategy · Fitness · Maturation · Threshold trait

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1 What Is Partial Migration?

Partial migration, in which a portion of the population migrates while the rest of the population remains as residents, is a common form of migration (Chapman et al. 2011; Pulido 2011). Partial migration is especially common in fishes (Chapman et al. 2012) and is particularly well studied in salmonids (Jonsson and Jonsson 1993; Dodson et al. 2013; Quinn 2021).

All salmonids breed in freshwater (Thorpe 1998). In populations in which partial migration is observed, there are two broadly different types of life histories can be distinguished—residency versus migration—with further life-history differences possible within each type: residents, which live in the freshwater river where they were born until they reproduce, and migrants, which descend to the sea (or a productive habitat such as a lake or the main stream of a large river) to feed prior to reproduction (Fig. 1; Box 1).

Although migrating to the sea provides increased access to food and space for salmonids, allowing them to grow bigger than their resident counterparts, it also brings a higher risk of mortality. By contrast, if they remain in the river, the risk of mortality is low, but the food quality is also lower than in the ocean, and they cannot grow as large. In other words, migration is high-risk and high-reward, whereas residency is low-risk and low-reward. In general, an individual is both physiologically and ecologically constrained from adopting both life histories and must become either a resident or a migrant, which represent alternative life-history tactics (Thorpe 1987) (but recent studies have clarified that migration patterns cannot simply be divided into two groups, but are complex and diverse; see Sect. 6).

Regardless of whether they are residents or migrants, males form a size-dependent competitive hierarchy during reproduction, with larger individuals being dominants and inferior individuals being subordinates or sneakers that steal spawning pairs at the moment of spawning (Koseki and Maekawa 2000; Maekawa et al. 2001; Watanabe et al. 2008; Sato et al. 2016). When resident and migrant males occur together, the migrant males often become dominants and the resident males become sneakers (Fleming 1996, 1998), but the life-history type does not necessarily correspond to the breeding tactics.

The partial migration of salmonids has long been a topic of interest in Japan, as it has in Europe and North America (Morita 2019). In Japan, masu salmon (*Oncorhynchus masou*) and white-spotted charr (*Salvelinus leucomaenis*) are representative species that exhibit partial migration. However, most of the older literature on these two species is written in Japanese, and little is known about them outside of the Japanese-speaking world. In this chapter, we will introduce the Japanese literature and review the partial migration of masu salmon and white-spotted charr.

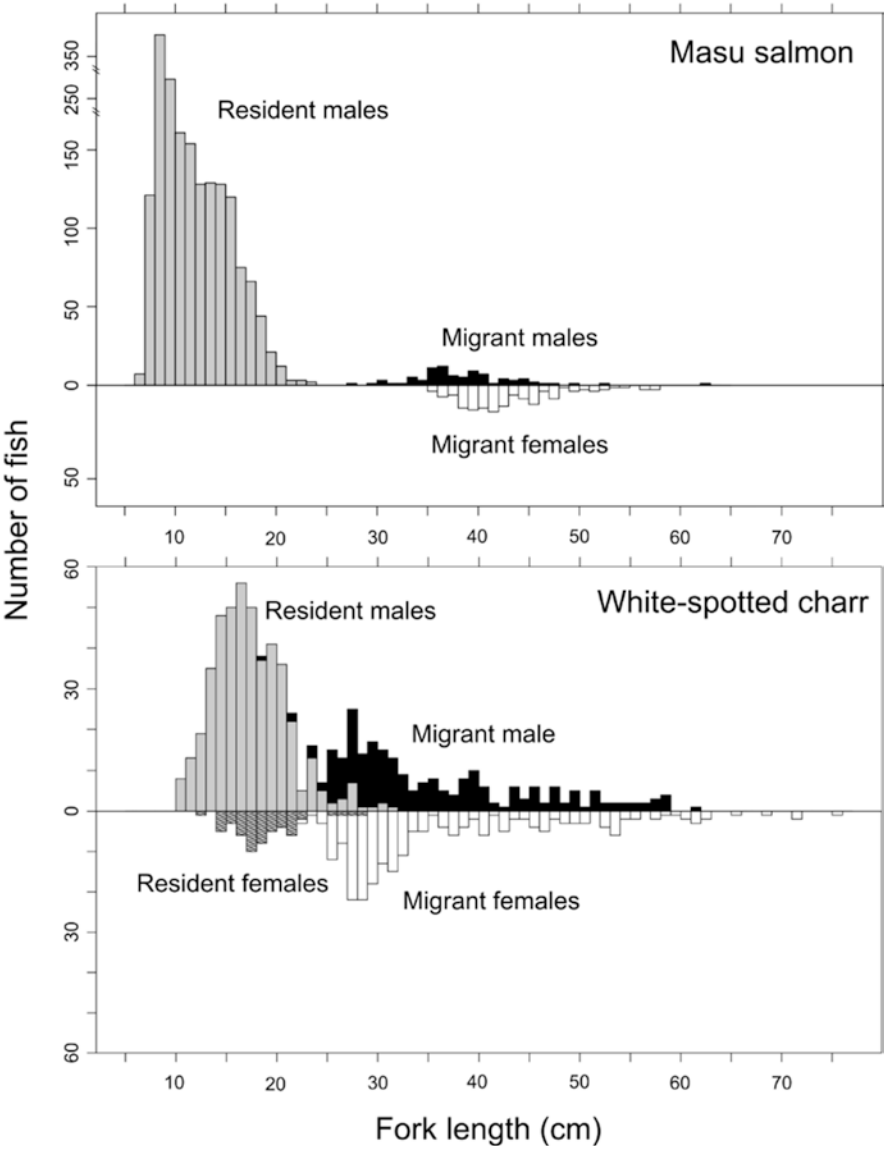


Fig. 1 Body size composition of reproductive individuals of masu salmon and white-spotted charr during the breeding season in Hokkaido, Japan. Resident females are more common in white-spotted charr than in masu salmon. Data sources: Morita (2018) and Morita et al. (2018) for masu salmon, and Morita et al. (2000) and Morita et al. (2013) for white-spotted charr

Box 1. Life Histories of Masu Salmon and White-Spotted Charr

In populations of both species where partial migration is observed (Fig. 2; Table 1), the majority of individuals descend to the sea after spending several years in the river (Kato 1991b; Morita et al. 2009a). The age at smolting is generally age 1+ to 2+ years for masu salmon (Ono 1933a, b; Sugiwaka 1991; Morita et al. 2014), and age 2+ to 4+ years for white-spotted charr (Yamamoto and Morita 2002). Time spent at sea per migration is 1 year for masu salmon (Morita and Sahashi 2018), and 1–8 months for white-spotted charr (Morita 2001). However, the individuals of both species with the fastest growth in early summer (July) become residents. The age at first maturity of residents varies among populations, but the earliest ages are age 0+ years for male and age 1+ years for female masu salmon (Morita et al. 2009b; Morita and Nagasawa 2010; Morita et al. 2014) and age 1+ years for male and age 2+ years for female white-spotted charr (Yamamoto et al. 1999a; Morita and Morita 2007). The residents of both species and migrants of charr are iteroparous (Ono 1933b; Morita 2001; Morita and Morita 2002; Morita et al. 2018). By contrast, migrants of masu salmon are semelparous (Ono 1933a, b). Similar to other semelparous salmonids, migrant female masu salmon guard their spawning beds for 2–8 days after spawning, until their swimming ability declines, and they are swept away (Kato 1991b). By contrast, migrant female charr and resident female masu salmon do not guard their nests after spawning. Most charr migrants that survive spawning return to the sea (Morita 2001; Morita et al. 2013).

There is also a latitudinal cline in the life-history types of mature individuals of both species (Sakai et al. 1992; Yamamoto et al. 1999a; Malyutina et al. 2009). In northern Japan, populations of both species contain both migrants and residents, whereas at the southern limit of distribution in Japan, populations of both species contain only residents; these southern populations showed little migratory behavior and are physically prevented from migrating to the sea by waterfalls, dams, or high-temperature thermal barriers (i.e., they are land-locked) (Kimura 1972, 1989; Yamamoto et al. 1999a). In additions, the pattern of latitudinal clines differs by sex. In northern Japan, all females and most males become migrants, and a portion of males become residents (Sakai et al. 1992; Yamamoto et al. 1999a). On the other hand, near the southern limit, it is almost exclusively females that become migrants (Sakai et al. 1992; Yamamoto et al. 1999a). In landlocked populations, during reproduction, resident males become fighters and large resident male become dominant, whereas small resident males become sneakers (Maekawa et al. 2001). Even in a partially migratory population, if there are no migrant males, the resident male will reproduce as a dominant, paired with a migrant female, instead of becoming a "sneaker" (Watanabe et al. 2008; Sato et al. 2016). As most males diverge into residents and only a few migrant males are found at southerly latitudes, migrant females more often spawn with resident males rather than migrant males (Sato et al. 2016).

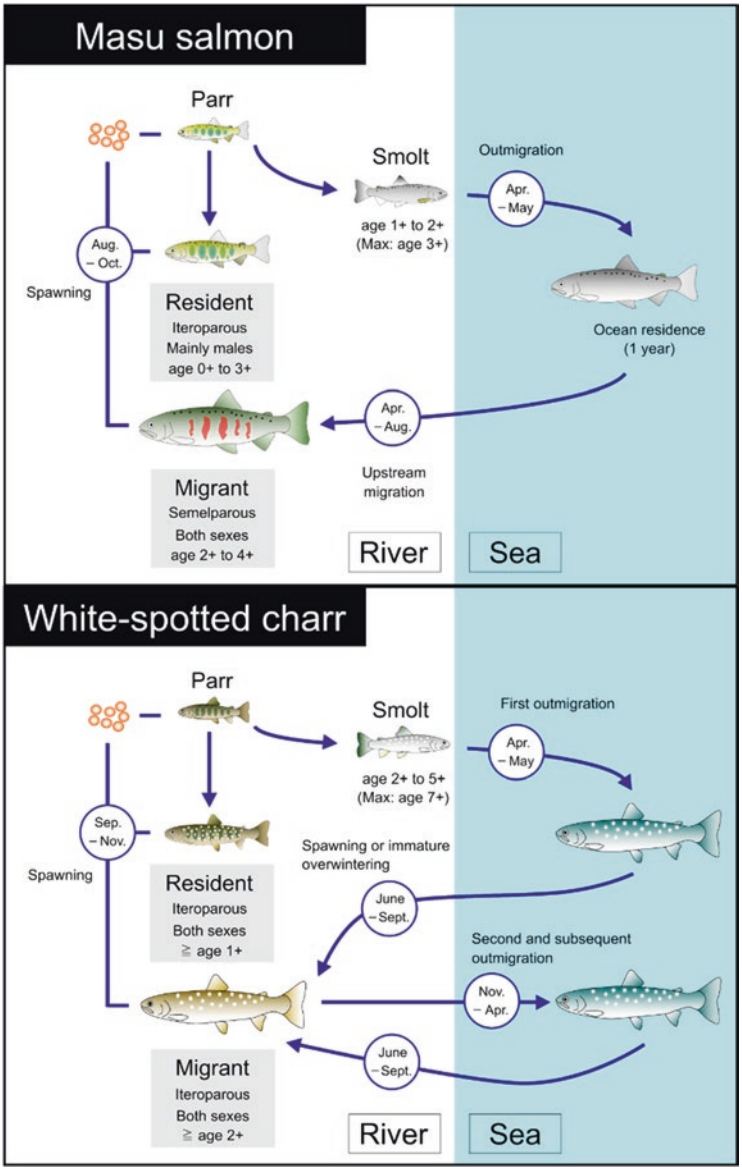


Fig. 2 Life histories of masu salmon and white-spotted charr in populations with partial migration

Table 1 Size at maturity, age at maturity, age at smolting, marine life period, and number of reproduction events of (**a**) masu salmon and (**b**) white-spotted charr

Life history	Size at maturity	Age at maturity	Age at smolting	Marine life period	Number of reproduction	References
(a) Masu salmon						
Migrant (♂♀)	35–65 cm Max: 78 cm	2+ to 4+ years	1+ to 2+ years Max: 3+ years	One year (rarely jack[a] appears)	Semelparous	Hayano et al. (2003); Ivankov et al. (2003); Machidori and Kato (1984); Malyutina et al. (2009); Morita (2018); Morita et al. (2014); Tamate (2015); Tsygir (1988); Tsiger et al. (1994)
Resident (♂)	7–28 cm Max: 36 cm	0+ to 4+ years Max: 6+ years			Iteroparous Max: 3–5 times	Kato (1991a); Morita (2018); Morita et al. (2018); Morita and Nagasawa (2010); Tsunagawa and Shirai (2018)
Resident (♀)[b]	10–28 cm Max: 36 cm	1+ to 4+ years Max: 4+ years			Iteroparous Max: 3 times	Kato (1989); Kiso and Kosaka (1994); Morita (2018); Morita and Nagasawa (2010); Morita et al. (2009b, 2018); Ono (1933a, b); Tsunagawa and Shirai (2018)
(b) White-spotted charr						
Migrant (♂♀)	25–60 cm Max: 108 cm	2+ to 5+ years Max: 17+ years	2+ to 5+ years Max: 7+ years	1–8 months; repeated over several years	Iteroparous 3 times is normal	Morita and Morita (2007); Morita et al. (2009a, 2018); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto and Morita (2002)
Resident (♂)	10–30 cm[c] Max: 58 cm	1+ to 5+ years Max: 17+ years			Iteroparous 3 times is normal	Kimura (1970); Morita (2001); Morita and Morita (2002, 2007); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto et al. (1999a)
Resident (♀)	15–30 cm[c] Max: 71 cm[d]	1+ to 5+ years Max: 17+ years[d]			Iteroparous 3 times is normal	Esin and Sorokin (2012); Morita (2001); Morita and Morita (2002, 2007); Morita et al. (2009a); Savvaitova et al. (2007); Shimoda et al. (2002); Yamamoto et al. (1996, 1999a)

(continued)

Table 1 (continued)

[a] Jacks are anadromous males and return to the river in their first ocean year (i.e., they spend only some months in the sea) (Tsiger et al. 1994)

[b] In Hokkaido, resident female salmon are collected very rarely (Morita and Nagasawa 2010), thus data for the resident female salmon are not covered in the Fig. 1 dataset

[c] Quite rare characteristics, but male charr can mature at age 0+ years and 8.3 cm, and female charr mature at age 1+ years and 9.9 cm (Kato 1992)

[d] A charr captured in the Chitose River was determined to be a female resident, based on trace element analysis of otoliths. Age assessment based on otoliths indicated it was over age 17+ years old, but additional annuli were indistinguishable (Morita and Honda, unpublished data)

2 The Involvement of Both Genetics and Plasticity

Genetics

Crossbreeding experiments conducted with masu salmon nearly a century ago suggested that female residents can produce migrant offspring and that female migrants can produce resident offspring (Soguri 1936). Thus, both migrants and residents belong to the same gene pool. In addition, when female migrant and male resident masu salmon are mated, eggs are fertilized and show normal development, with growth of the offspring tending to be improved when the males are residents as opposed to migrants (Hokkaido Salmon Conservation Society 1936; Hokkaido Salmon Hatchery 1937). However, in most salmonids, the offspring of residents are more likely to become residents, and the offspring of migrants are more likely to become migrants (Nordeng 1983; Ohkuma et al. 2016; but also see Thorpe and Morgan 1980; Yamamoto et al. 2021).

There is a long history of research to identify the genetic differentiation between residents and migrants at the molecular level. However, when residents and migrants are sampled from different locations or time periods, even in the same water system, it reveals differences between local populations and not between life-history types (Hindar et al. 1991; Adams et al. 2016; Fig. 3). For example, in a study of masu salmon, Yu et al. (2010) detected neutral genetic differences (significant Fst) between residents and migrants in the Shari River, eastern Hokkaido, Japan. However, although residents and migrants were collected from the same river system, they were collected from different tributaries, and the migrants were from a tributary where hatchery releases were conducted. Thus, the results may not indicate neutral genetic differences between salmon with different life histories, but differences between salmon from different tributaries (or hatchery versus wild). In many cases, life history is heritable but does not represent a neutral genetic differentiation between different life histories within a population, instead representing a single population belonging to the same gene pool. Note that the interpretation is different when the focus is on adaptive loci rather than neutral markers. If a single locus affects whether fish become migrant or resident, this locus might exhibit high Fst between different life histories within a population.

However, when migrants and residents are reproductively isolated but sympatric, there may be genetic divergence between the two life histories, resulting in distinct populations with overlapping ranges. This was seen with sockeye salmon and kokanee (*O. nerka*) (Wood and Foote 1996) and Atlantic salmon (*Salmo salar*) (Adams et al. 2016). In this case, it is possible to infer to some extent (though not perfectly) from the breeding population size structure whether residents and migrants are genetically distinct populations (Fig. 4).

In recent years, researchers have attempted to identify the genes involved in determining migration tactics in salmonid species. For example, in rainbow trout (*O. mykiss*), multiple genomic regions on several chromosomes have been implicated in life-history divergence (i.e., divergence of alternative migratory tactics) (e.g., Hecht et al. 2013; Rundio et al. 2021). Identification of candidate genes involved in migration is also underway in brown trout (*Salmo trutta*) (Lemopoulos et al. 2018) and sockeye salmon (Veale and Russello 2017). Unfortunately, however, similar studies have not yet been conducted on masu salmon or white-spotted charr, and the genes involved in the life-history divergence of these species are currently unknown.

Plasticity

In addition to genetics, plasticity is also involved in life-history divergence. In masu salmon and white-spotted charr, energy/resource availability, water temperature, river width, and population density are environmental factors that influence the plasticity of tactic expression.

For white-spotted charr, a transplant experiment using a common genetic origin of the fish demonstrated that the narrower the river and the higher the water temperature, the higher the proportion of residents at a given body size (i.e., the lower maturation threshold) (Morita et al. 2009d). Similarly, in masu salmon, higher water temperatures lead to a higher proportion of residents with a lower maturation threshold (Morita and Nagasawa 2010). The lower threshold size in narrower rivers is thought to be due to the relative increase in the number of hiding places for male residents to sneak around during breeding, thus increasing their reproductive success. By contrast, the smaller threshold size in warmer waters is related to the fact that higher temperatures drive plasticity in growth, making these fish more likely to be residents (see Sect. 3 for the relationship between growth and life-history divergence). In the Japanese archipelago, there is a latitudinal cline in water temperature, which is thought to explain the pattern of masu salmon in northern areas being more likely to become migrants and those in southern areas being more likely to become residents (Morita and Nagasawa 2010; Morita et al. 2014).

If female migrants, which have large body size and high fecundity (Morita and Takashima 1998; Morita et al. 2009c; Morita 2018), cannot return from the sea as rivers are blocked by dams, the density of juvenile fish in the river decreases (Morita et al. 2000; Morita and Nagasawa 2010). Such decreases in population density in the river result in better initial growth, which makes residency more likely (Morita et al. 2000; Morita and Nagasawa 2010). Similarly, in other salmonids, density-dependent food availability has been shown to have an effect on life-history divergence via growth conditions (Olsson et al. 2006).

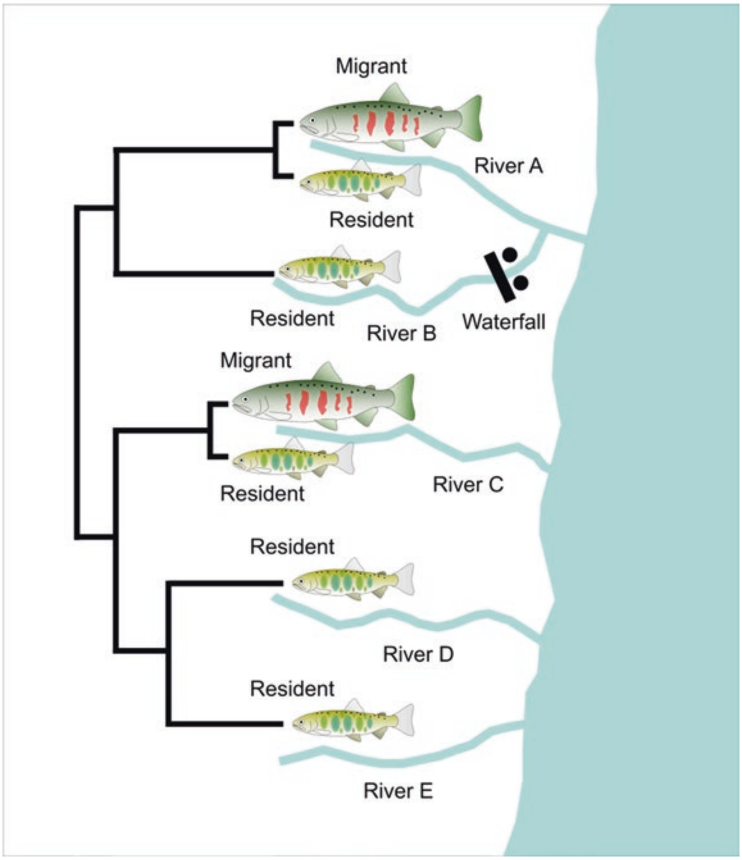


Fig. 3 Conceptual diagram of neutral genetic differentiation between residents and migrants. The length of the black line indicates the neutral genetic difference. Neutral genetic differences are greater between populations than between life-history types (modified from Morita et al. 2009b)

As such, multiple environmental factors are involved in life-history divergence. However, these environmental cues are often not independent of each other, nor are they mutually exclusive. Moreover, although water temperature and food, or a combination of both, affect migration tactics via growth, they do not necessarily have the same growth effects on the phenotypic divergence of migration tactics (Archer et al. 2020).

Genetics and Plasticity Explain Spatial Variation in Partial Migration

Both genetics and plasticity play roles in life-history divergence in masu salmon and white-spotted charr but to what extent do environmentally-induced versus genetically-based differences explain life-history divergence among individuals or populations?

In white-spotted charr, two studies have explored this question, and although the study catchments were in close proximity, conclusions differed. One study

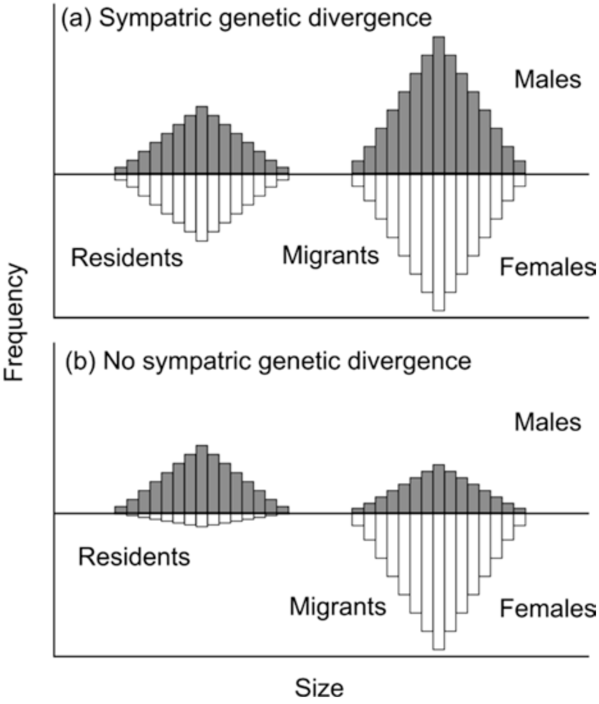


Fig. 4 Genetic relationships and population size structure between residents and migrants. (**a**) Type-assortative mating, with sympatric genetic differentiation between residents and migrants (e.g., sockeye salmon vs kokanee; Wood and Foote 1996); (**b**) no type-assortative mating, and no genetic differentiation between residents and migrants (e.g., masu salmon, white-spotted charr; Fig. 1). In the case of a conditional strategy based on phenotypic plasticity, the sex ratio of the migrants is frequently biased toward females, and that of the residents is biased toward males

suggested that plasticity based on water temperature and river width influences life-history divergence (Morita et al. 2009d). However, the other study suggested that genetic factors based on migration cost affect life-history divergence (Sahashi and Morita 2013). These results may have been influenced by differences between the studies in the range of the physical environmental conditions. For example, water temperatures where Morita et al. (2009d) conducted their study differed by a maximum of 3.4 °C among tributaries, whereas Sahashi and Morita (2013) found a maximum difference of only 0.9 °C among tributaries. By contrast, the migration distance, which is an index of migration cost, was considered to be almost equal among tributaries in Morita et al. (2009d), but differed by up to 82 km in Sahashi and Morita (2013). Although intense research has been conducted in recent years to clarify the relative importance of genetics and plasticity (e.g., Debes et al. 2020), interpretation of the results needs to take into account the research methods and range of physical environments in each study.

3 A Status-Dependent Conditional Strategy to Maximize Individual Fitness

It is important to explore under what conditions an individual migrates to the sea or remains a resident in the river. A number of studies have investigated the relationship between growth status and life-history divergence. The growth status is not limited to body size but also includes body mass index and nutritional status, and these indicators vary among studies (review: Hutchings 2011; Dodson et al. 2013; Sloat et al. 2014; Ferguson et al. 2019).

In principle, in male masu salmon, the fastest-growing individuals do not migrate to the sea but mature and become residents (Kubo 1974; Utoh 1976, 1977; Toda 1992). Female residents are rare and have not been well studied, but as with males, individuals with extremely rapid growth become residents (Morita and Nagasawa 2010). An almost exact pattern of growth and life-history divergence has been observed in white-spotted charr (Yamamoto et al. 1996).

When alternative phenotypes are interpreted using the status-dependent conditional strategy, the fitness of each phenotype is a function of individual status in which: (1) individuals adopt one phenotype to obtain higher fitness at a given status, (2) average fitness is unequal between alternative phenotypes, and (3) fitness of the alternative phenotypes is equal at the switchpoints (i.e., size threshold) (Gross 1996). A threshold for alternative phenotypes has been hypothesized to have additive genetic variation, and the threshold position would move with environmental change under the status-dependent conditional strategy (Gross 1991, Gross and Repka 1998). A number of studies have supported the idea that partial migration is a status-dependent conditional strategy that diverges into migrants or residents depending on growth conditions/status (Lundberg 1988; Jonsson and Jonsson 1993; Chapman et al. 2011; Hatase et al. 2013), however, empirical support for this ultimate mechanism is surprisingly limited. Morita et al. (2014) succeeded in explaining the ultimate mechanism by which rapid growth leads to salmon becoming residents by calculating the expected lifetime reproductive success for the migrant and resident tactics, respectively, as a function of body size at age 0+ years (i.e., early growth conditions) (Fig. 5).

In female masu salmon, the expected lifetime reproductive success of migrants always exceeds that of residents, within the range of realistic body size in the wild; in males, above a certain threshold size, however, the expected lifetime reproductive success of residents is higher than that of migrants (Fig. 5). This explains why in general the proportion of residents is small among females. In other words, this pattern is not driven by small females' physiological inability to mature, but rather by the higher fitness of migrant females compared to resident females. In fact, in landlocked populations, some small females mature at just over 10 cm in size (Table 1a). By contrast, males that are larger than a certain threshold size become residents and have higher reproductive success if they remain small and mature that year instead of migrating to the sea the following year. Therefore, for individuals whose body size is below a certain threshold, migrating to the sea is the best choice when growth status is poor.

The relationship between growth status and expected lifetime reproductive success can vary depending on conditions (Fig. 6). For example, as migration costs increase, the expected lifetime reproductive success of migrants will decrease (Fig. 6b). In this case, the threshold at which the expected lifetime reproductive success of the alternative phenotypes is equal would shift to the left, and it would be adaptive for fish to mature at a smaller size and become residents. In fact, Sahashi and Morita (2013) examined the threshold size of male salmon and white-spotted charr at the watershed scale and found that, in both species, the threshold sizes to become resident were smaller in tributaries located farther from the sea. This result supports the above prediction based on the increased cost of migration (Fig. 6b).

Under hatchery conditions in which selective breeding is used, the outcome is different. If residents are not used as parents in the hatchery, only the expected lifetime reproductive success of migrants would be increased, and it would be more adaptive to become migrants without maturing, no matter how well they grow (Fig. 6c). In this case, the threshold size is predicted to shift to the right, making it more likely that fish become migrants. Sahashi and Morita (2018) found support for this prediction by showing that, in hatchery masu salmon, the threshold size to become resident was larger than that of wild fish in the Shari River system in Hokkaido, Japan, where the hatchery had only used migrants as parent fish for approximately 80 years. Contrary to this case, some Japanese hatcheries of masu salmon use only residents as parent fish. For this style of hatchery management, Ohkuma et al. (2016) have confirmed that hatchery fish are less prone to smoltification and that many individuals become residents.

How long will partial migration be maintained in a population if conditions continue to favor one migration tactic over the other? In white-spotted charr, populations above dams where only residents have reproduced for five or six generations smolt at about one-tenth the frequency of those below dams with migrants, and only females smolt (Morita et al. 2000, 2009a). Moreover, in the Imsa River in Norway, some Arctic charr migrate to the sea even though migrants are unable to return upriver (Jonsson et al. 1989). By contrast, smolts do not appear in a brown trout population that was land-locked between 6000 and 7000 years ago (Jonsson 1982). Prof. Tatsuro Kubo, a leading expert on salmonid breeding in Japan, stated that he had bred and smoltified a variety of salmonids in Japan, including masu salmon, amago salmon (*O. masou ishikawae*), southern Asian Dolly Varden charr (*Salvelinus curilus*), nikko-iwana (*Salvelinus leucomaenis pluvius*), and Sakhalin taimen (*Parahucho perryi*). Kubo could not, however, smoltify the subspecies kirikuchi (*Salvelinus leucomaenis japonicas*), which is distributed at the southern limit of the charr range and is considered to have been land-locked for a relatively long period. In a modeling study using a species of bird, Eurasian blackcaps (*Sylvia atricapilla*), when a migratory-only population was subjected to directional selection favoring residents, it took six generations for the population to show partial migration, but 98 generations before the population became residents only (De Zoeten and Pulido 2020). These results suggest that partial migration may be maintained in a

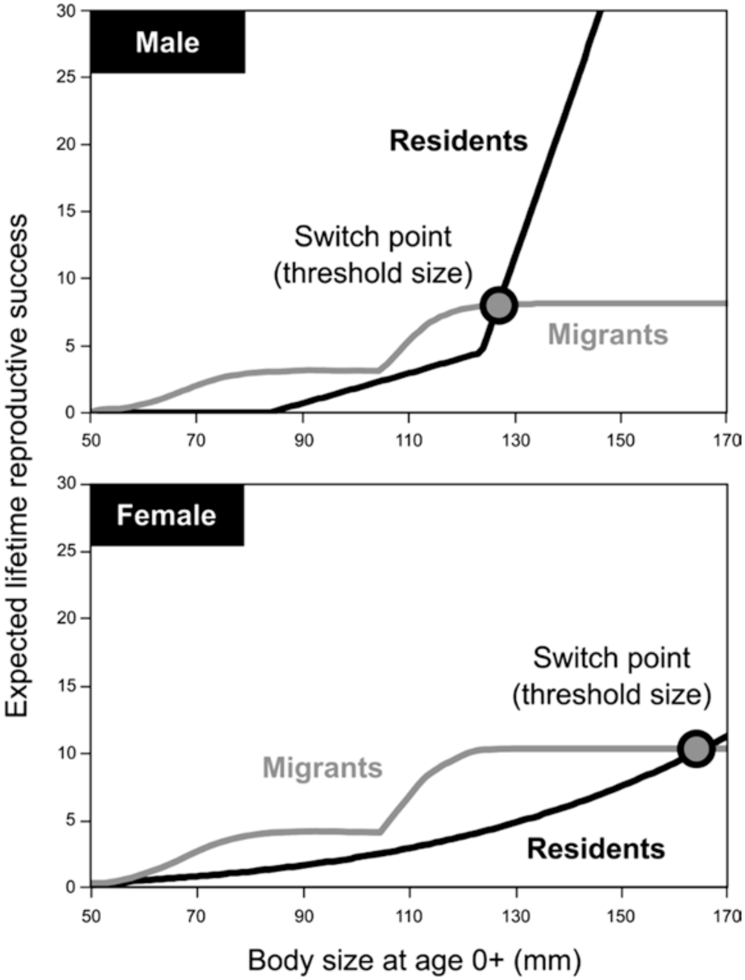
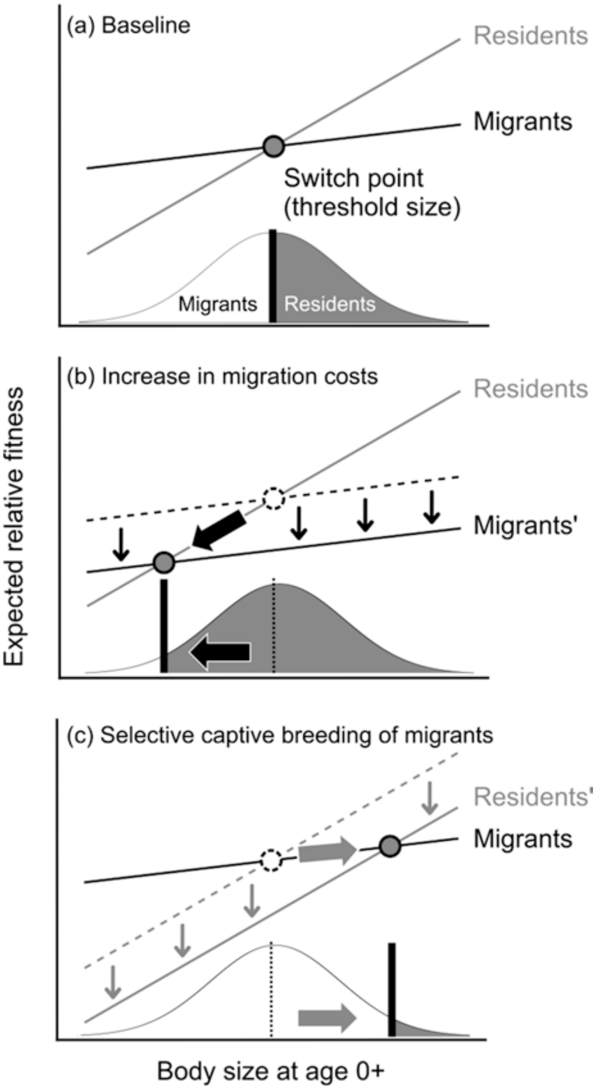


Fig. 5 Curves depicting the expected lifetime reproductive success for alternative migratory tactics in male and female masu salmon, as a function of body size during the breeding season at age 0+ years. The switchpoint is further to the right in females than males (modified from Morita et al. 2014)

population for a long time, over tens of generations, even if the situation continues to favor one migration tactic over the other.

As a general rule for masu salmon and white-spotted charr, the fastest-growing individuals of both sexes become residents (Yamamoto et al. 1996; Morita and Nagasawa 2010), but this does not mean that all other individuals will become migrants. In the case of male masu salmon, the group of fish with the third-fastest growth rate will also become residents (Fig. 7). In other words, individuals that belong to the second- or fourth fastest-growing groups become migrants. In fact, in rearing experiments using masu salmon, it has been shown that the fastest-growing

Fig. 6 Status-dependent fitness functions of alternative migratory tactics in three situations: (**a**) Baseline. When evolutionary factors influence migrants or residents, the switchpoint (i.e., size threshold) at which the fitness of each tactic is equal will shift right or left, and the proportion of the alternative migratory tactics will change with the size threshold; (**b**) Increase in migration costs. Higher migration costs reduce migrant fitness, and the size threshold will shift left and promote residency; (**c**) Selective captive breeding of migrants. Selective captive breeding of migrants reduces resident fitness, and the size threshold will shift right and promote migration (modified from Sahashi and Morita 2018)



group becomes the age 0+ years residents; the second-fastest-growing group becomes the age 1+ years smolts (migrants), and the third fastest-growing group becomes the age 1+ years residents (Tamate and Maekawa 2002).

However, the fastest-growing group may not always become residents, as average growth varies with geographic location. For example, as described above, at southerly latitudes, average growth is good because temperatures are high, so the fastest-growing group becomes residents, and the second-fastest-growing group becomes migrants. By contrast, at northerly latitudes, average growth is poor as temperatures are low, so the relationship between growth and life history discussed above is different. Namely, the fastest-growing group becomes migrants, and the second-fastest-growing group becomes residents (Gruzdeva et al. 2013). Therefore, even for the same species, it is important to recognize which life-history divergence of a target population you are focusing on, as the relationship between growth and life history varies by location. This raises the question as to why the relationship between growth and life history might flip, becoming opposites, in different populations.

4 Exploring Mechanisms of Life-History Divergence, with Careful Interpretation of Cause and Effect

There has been a great deal of interest in the factors underlying life-history divergence between residents and migrants. It goes without saying that body size is only one indicator, and that many more traits are involved in the life-history divergence. Many studies have compared traits between mature individuals in the river (mature parr, residents) and immature individuals (prospective migrants), or compared traits (e.g., growth, morphology, and behavior) between smolting individuals (migrants) and non-smolting individuals (prospective residents). However, since both smoltification and maturation are physiologically determined more than 6 months prior (Hunt et al. 1982; Ikuta et al. 1987; Yamamoto and Nakano 1996; Tamate and Yamamoto 2004), care should be taken in interpreting cause and effect. For example, in masu salmon, individuals smolting at age 1+ years have poor growth in the river before switching to smolts, but good growth after the switching. It is difficult to interpret cause and effect when considering whether individuals smolt because they are growing well and are active, or whether they begin to grow well and become active due to smolting.

As migrant masu salmon are more valuable to fisheries than residents, hatchery release projects have aimed to produce juveniles that do not become residents but smolt instead. Therefore, hatchery technicians are well aware of how to increase smoltification rates by producing certain growth conditions for specific periods of development (Akaishi 1992; Toda 1992; Matsumura et al. 1995). By suppressing growth with low water temperature until July when fish are age 0+ years, fork length can be kept at or below 7 cm and body weight at 10 g or less, which reduces the appearance of aged 0+ years residents in September (Fig. 7). By accelerating growth from July to November (when fish are aged 0+ years) to reach a fork length of 9 cm and a body weight of 10 g or more, then inhibiting growth again during the winter, smoltification rates are increased in the spring when fish are aged 1+ years (Fig. 7). This rearing method can produce a 85–90% age 1+ smoltification rate, even in unselected groups (Japan Fisheries Resource Conservation Association 2008). Thus, by controlling growth just before the onsets of maturation and smoltification, hatcheries have produced an artificially high percentage of migrants (i.e., age 1+

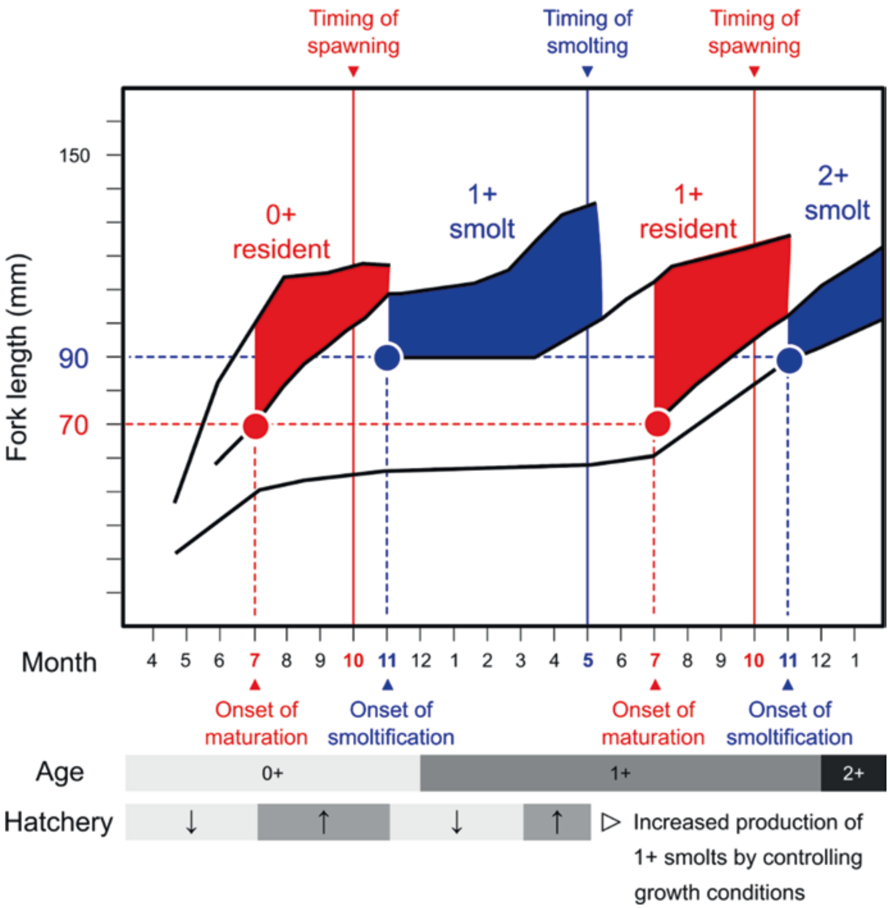


Fig. 7 Schematic diagram of the life-history divergence of male masu salmon in southern Hokkaido, Japan. In order of fastest growth, life histories diverge into 0+ residents, 1+ smolts, 1+ residents, and 2+ smolts, where numbers denote years of age. Dashed and solid lines indicate the approximate onset and timing of each life-history event. The resident life history is determined in early summer (July), whereas the migrant life history (smolts) is determined in autumn (roughly November). Individuals with a fork length of 70 mm or more in July become residents in October, and those with a fork length of 90 mm or more in November become smolts in following May. The bottom row (Hatchery) indicates a proposed rearing method to artificially increase the production of 1+ smolts (i.e., migrants) in the hatchery. Upward arrows indicate periods of accelerated growth, and downward arrows indicate periods of inhibited growth for this method (modified from Kubo 1974; Utoh 1981; Japan Fisheries Resource Conservation Association 2008)

smolts). It should be noted that there is a gap of about 3–6 months between the onset of maturation and spawning periods and between the onset of smoltification and the seaward migration/smolting periods.

5 Stream Life of Prospective Migrants (Prior Preparation)

Interesting ecological features of smolt-switching individuals (i.e., individuals on a migration trajectory) have been mainly studied in Atlantic salmon. Groups that will smolt the following spring (i.e., smolt-switching individuals) are known to have higher growth than other individuals in winter, resulting in a bimodal distribution of body size in the juvenile stage (Thorpe 1977; Metcalfe et al. 1988). Such "catch-up-growth"—increasing consumption and growth rates following a period of slowed development—is thought to be a precaution against size-dependent mortality in the ocean (Nicieza and Metcalfe 1997; Futamura et al. 2022b). This has also been confirmed in masu salmon and white-spotted charr, where after the decision to smolt but immediately prior to smolting, there is higher growth of prospective migrants compared to other individuals in rivers (Hirata et al. 1986, 1988; Takami et al. 1998; Yamamoto and Nakano 1996).

Studies suggest that changes in behavioral patterns of Atlantic salmon following smolt-switching can lead to increased growth. Normally, when water temperatures are low, metabolism and foraging efficiency decrease, and individuals shift to nocturnal behavior that reduces predation risk (Fraser et al. 1993). However, a higher proportion of prospective migrants are diurnal even when water temperatures decrease (Metcalfe et al. 1998). In masu salmon, prospective migrant individuals are also active during the daytime, even in winter when water temperatures are low (Kubo 1976). It has also been shown that smaller prospective migrants grow more and approach a certain threshold size by the time they descend to the sea (Futamura et al. 2022b).

Masu salmon and white-spotted charr migrating to the sea tend to have a similar body size across populations, although there is some interpopulation variation (Tanaka 1965; Yamamoto and Morita 2002), and there seems to be a threshold (Yamamoto et al. 1999b). A larger body size does not always increase the probability of survival in the ocean (Shimoda et al. 2003; Miyakoshi 2006). The expected probability of survival increases with body size up to a certain threshold size, but smolts larger than that of threshold benefit less. This may be because body size-dependent salinity tolerance and escape from predators become critical below a certain threshold (Misaka et al. 1998; Futamura et al. 2022a). This relationship is crucial in the above-mentioned calculation of the expected lifetime reproductive success for residents and migrants. If the survival rate in the ocean increases with smolt size, then individuals that have grown well in the river should descend to the sea and become migrants. No matter how large an individual's body size, there is no guarantee of survival in the ocean, and the effect of large body size has an upper limit; these factors are important for assessing lifetime reproductive success.

6 Beyond Dichotomous Life Histories

In the previous sections, we discussed life-history divergence as a dichotomous pattern, with residents and migrants. In recent years, however, it has become clear that migration patterns cannot simply be divided into two groups; they are complex and diverse. Migrants were thought to spend several years in the river (i.e., the parr stage) before becoming smolts in the spring and descending to the sea. Some individuals of Atlantic salmon and brown trout, however, do not smolt and instead migrate to the ocean as parr in the autumn (Birnie-Gauvin et al. 2019). In coho salmon (*O. kisutch*), some individuals enter estuaries as fry, where they survive and grow well (called "nomads"). However, instead of migrating to offshore waters, the nomads return upstream to freshwater to overwinter before migrating to the ocean as smolts (Koski 2009; Bennett et al. 2015). Nomad-like individuals have also been found in masu salmon and white-spotted charr (Arai and Morita 2005; Matsubayashi et al. 2017; Kuroki et al. 2020). In iteroparous Dolly Varden (*Salvelinus malma*), some migrants remain in the river, essentially becoming "retired" migrants (i.e., previously migratory fish that have returned to a resident life history following one or more migrations to the sea and back) (Bond et al. 2015). Since life-history diversity results in spreading of risk (den Boer 1968, 1981) and contributes to population persistence and fishery stability (Schindler et al. 2010), dividing life-history polymorphisms into a simple dichotomous pattern may overlook something essential. Thus, the study of the full diversity of migration tactics is likely to be a fruitful avenue for future research.

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