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Perspective

Earlier migration timing of salmonids: an adaptation to climate change or maladaptation to fishery?

Kentaro Morita

Hokkaido National Fisheries Research Institute, Japan Fisheries Research and Education Agency, 2-2 Nakanoshima, Toyohira-ku, Sapporo 062-0922, Japan.

E-mail: moritak@affrc.go.jp

Abstract:

Recent studies reporting shifts in the timing of salmonid migrations have suggested global warming to be a cause. However, the specific mechanisms underlining the evolution of earlier-migration timing in salmonid fishes are unknown. In this paper, I present a hypothesis by which fishery-induced selection works to advance the timing of salmonid migration, given the timing of migration and breeding are genetically controlled heritable traits. Although late-spawning salmon brood lines enter rivers after early spawning brood lines, there is evidence that all brood lines arrive in coastal fishing grounds at similar times. As such, late-spawning brood lines would be fished for longer periods of time, with their increased harvest rate imposing directional selection on earlier-spawning brood lines. Thus, fisheries-induced evolution could favor the earlier timing of river entry to escape coastal fisheries. Should earlier migration timing not be an adaptation to global warming—should it be a maladaptation to fisheries-induced selection instead—then it will have a negative impact on the sustainability of salmonid resources.

26 **Introduction**

27 A major consequence of climate change is the phenological shift in life-history events in
28 organisms. Though flowering time of plants, breeding and migration time of animals, and timing
29 of phytoplankton blooms have shifted in relation to global climate change, it often remains
30 difficult to interpret these shifts (Visser and Both 2005). In commercially exploited fishes, other
31 life-history traits, such as age and size at maturity, have often shifted due to fisheries-induced
32 evolution, but the relative importance of environmental changes versus fisheries-induced
33 evolution can be difficult to disentangle (Kuparinen and Merilä 2007).

34 Recent studies have confirmed noticeable shifts in earlier migration timing of multiple
35 salmonid species (*Oncorhynchus*, *Salmo*, and *Salvelinus* spp.) in North America (Quinn and
36 Adams 1996; Taylor 2008; Juanes et al. 2004; Kovach et al. 2013), in addition to genetic change
37 in earlier migration timing of an Alaskan pink salmon (*O. gorbuscha*) population (Kovach et al.
38 2012). These shifts are often accompanied by a decrease in the duration of migration timing,
39 indicating a loss of late-spawning brood lines (Kovach et al. 2015). Advanced timing of adult
40 migrations have also occurred synchronously in Asian pink salmon populations in multiple
41 regions since 1990 (Fig. 1; Kaev et al. 2007; Kaev and Romasenko 2007). From 1990 to the
42 beginning of the 2000s, the peaks of catch timings were advanced about 10 days in Asian pink
43 salmon stocks, though there was no further shift in catch timing in Hokkaido, Japan, from 2000

to present. Selection against a late-migrating phenotype of an Alaskan pink salmon population during its ocean life, coinciding with increasing sea-surface temperature, was thought to represent an adaptation to climate warming (Manhard et al. 2017). However, as salmon are cold-water fish and spawning takes place from late summer to autumn, their earlier upstream migration may in fact increase their risk of encountering elevated water temperature, leading to spawning failure. The specific mechanisms underlining the evolution of earlier migration timing were unknown.

Fishery-induced selection could change the timing of migration and breeding in commercially exploited fishes (Tillotson and Quinn 2018). Both selective fishing towards later migrants of Alaskan sockeye salmon (*O. nerka*), and shifts for earlier migration timing over the last quarter of the 20th century, were demonstrated by Quinn et al. (2007). However, the direction of fishery-induced selection on the timing of migration and breeding is likely to differ, depending on the way in which each fishery occurs (Tillotson and Quinn 2018). If so, it may not be possible to explain the general tendency towards temporally advanced migration in salmonids. In this paper, I describe the general mechanism by which fishery-induced selection might work to advance the migration timing in these fishes.

Inheritance of the timing of migration and breeding

'Isolation by time' is prevalent in some organisms, even in sympatric populations, due to high heritability of breeding time (Hendry and Day 2005). While the environmental conditions such as discharge provided a stimulus for upstream migration (e.g., Davidson et al. 1943), the timing of upstream migration and breeding in salmonid fishes is genetically controlled (e.g., Quinn et al. 2000). Consequently, artificial selection in hatcheries could change the timing of salmon migration (Sato et al. 2000; Quinn et al. 2002; Miyakoshi et al. 2013). In Japanese hatchery-reared chum salmon (*O. keta*), a series of experiments using different otolith thermal marks (depending on the time of egg collection and fertilization) have confirmed that offspring migrate upstream just prior to their parent's breeding period (Takahashi 2009; Takahashi 2013). For example, in Shari River hatchery-reared chum salmon, time-specific otolith-thermal-marks attached between October and December reveal offspring migrate into rivers prior to their parent's breeding period (Fig. 2). Therefore, the timing of upstream migration and breeding are highly correlated between parents and offspring, indicating the two are genetically controlled, heritable traits.

How fishery selection shapes timing migration

As the timings of migration and breeding are highly heritable, potential exists for fisheries-induced evolution (Tillotson and Quinn 2018). In most salmon fisheries, fishing occurs

in coastal areas rather than on spawning grounds, it is important to know the timing of arrival of each breeding line to the coast to be fished, and whether any lag exists between the timing of coastal arrival and upstream migration. If the timing of river entry and coastal arrival are independent—that is, if late-spawning brood lines arrived in coastal areas early in the season—then late-spawning brood lines would be fished for longer periods of time than earlier-spawning brood lines. This extended residency within fishing grounds would lead to disproportionate fishing mortality of late-spawning individuals.

Given otolith-thermal-marked hatchery-reared Japanese chum salmon of late-spawning brood lines occur in coastal catch early in the season (Fig. 3), the hypothesis that some late-spawning brood lines reside within fishing grounds for extended periods of time is supported. In Shari River hatchery-reared chum salmon, brood lines from December fertilization groups were fished in the coast from late September to November, whereas brood lines from October fertilization groups were fished only in September (Fig. 3). In Akka River hatchery-reared chum salmon, brood lines from December fertilization groups were also fished in the coast from September to November (Sato et al. 2000). As with other Pacific salmon, Japanese chum salmon migrate to offshore areas, but return to the coast of Japan in summer via the Bering Sea (Kondoh et al. 1965; Yonemori 1975). Currently, the commercial fishery targeting Japanese chum salmon occurs only in coastal areas (not in offshore areas). Despite

late-spawning brood lines entering the river later in the season (Fig. 2), the timing of their coastal arrival differs little from that of early spawning brood lines (Fig. 3). If all brood lines arrived in coastal fishing grounds at similar times, regardless of their river entry or parent-spawning dates, late-spawning brood lines would be fished for extended lengths of time, effectively increasing their harvest rate and imposing directional selection on earlier-spawning salmon (Fig. 4). Thus, fisheries-induced evolution would favor earlier timing of river entry.

A given number of each brood line is collected throughout the entire period of river entry, regardless of differences in numbers of fish caught in Japanese hatchery programs. Consequently, no selection is intended for the timing of migration or breeding within hatchery populations, though in the past, the timing of migration has changed due to hatchery selection (Miyakoshi et al. 2013). However, for wild populations, fishery selection will favor earlier migration into rivers because fish are less vulnerable to fishing. Paradoxically, fry-to-adult survival rates to the point of river re-entry were relatively high in the earliest Shari River spawning brood line (early Oct: 0.8%, vs. late Oct to Dec.: 0.5% on average), despite fry-to-adult survival rates to the point of entry into coastal waters being low in early spawning brood lines (early Oct: 2.7%, vs. late Oct to Dec.: 9.2% on average) (Fig. 4). What this means is that when fishing mortality is high, the fry-to-adult survival rate to the point of river re-entry may not be representative of natural survival rates. Even though the fry-to-adult survival rate in the early

116 spawning brood line is high, it does not necessary mean lower natural mortality; this brood line
117 may be merely subject to lower fishing mortality. A similar paradox was also shown in a
118 population of Atlantic salmon (*Salmo salar*), wherein the rate of survival to fresh water was not
119 an indication of natural marine survival, but rather an indication of marine exploitation rate
120 (Crozier and Kennedy 1999).

121 From the 1950s to the 1970s the major fishing grounds of Japanese salmon fishery were in
122 high-sea areas, but these high-sea fisheries reduced in the 1980s, and grounds were closed in
123 1993 as a consequence of the Convention for the Conservation of Anadromous Stocks in the
124 North Pacific (Eggers et al. 2005; Morita and Fukuwaka 2007). Since the moratorium on
125 high-sea fisheries, the major salmon fishing grounds have shifted to coastal regions. Whereas
126 fisheries-induced selection might once have favored maturation at smaller size, given former
127 offshore fisheries had targeted immature fish using size-selective gillnets (Fukuwaka and Morita
128 2008), selection today might now operate on the timing of migration, given fisheries target adult
129 salmon returning for spawning. As an aside, recent increases in marine-mammal predation in
130 coastal areas on both sides of the Pacific Rim (Velikanov and Radchenko 2013; Shuntov and
131 Ivanov 2015; Chasco et al. 2017; Thomas et al. 2017) might indicate natural predation has a
132 similar effect to coastal fishing on salmon population mortality.

Implications and conclusion

It is not my intention to discount the possibility that salmon migrate earlier into rivers because of climate change, but to introduce an alternative hypothesis equally worthy of consideration. If the loss of late-spawning brood lines is not a direct consequence of or an adaptation to climate change—that it is a maladaptation to fisheries-induced selection—then it will negatively impact the sustainability of salmonid resources.

Diversity in life-history traits is important for the longer-term viability of populations, buffering them from environmental fluctuations (Greene et al. 2010). Accordingly, the loss of diversity in timing of migration might reduce the resilience of salmonid populations to recover from or respond to environmental change. As Pacific salmon also provide nutrients and energy for aquatic and terrestrial ecosystems (Cederholm et al. 1999), and late-spawning salmon are particularly important foods for overwintering animals such as eagles (Hunt et al. 1992; Ueta et al. 1999; Kamauchi et al. 2012), conserving diversity in the timing of their migration is necessary for maintenance of ecosystem services.

Additional research on relationships between the timing of breeding, river entry, and arrival to the coastal area (i.e., fishing ground) for each salmon brood line with different spawning time, is necessary. It would also be useful to identify fry-to-adult survival rates for each brood line, and to disentangle natural mortality and fishing mortality in marine survival rates. Future

sustainable exploitation of salmon resources will require population management that also incorporates maintenance of diversity in the timing of salmon breeding and migration.

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Figure captions

Fig. 1. Temporal changes in median date of coastal catches of Asian pink salmon in Hokkaido Island (●), Iturup Island (□), Kunashir Island (+), southeastern Sakhalin (▲), and Aniva Bay (○). Data from Kaev et al. (2007), Kaev and Romasenko (2007), and Morita and Suzuki (2018).

Fig. 2. Timing of river entry for hatchery-reared chum salmon broods with different otolith thermal marks (depending on the time of egg collection and fertilization) in Shari River (data from Morita 2017). Arrows indicate the time of egg collection and fertilization of their parent. Data based on thermal marked fry released in 2009–2010, and adults caught in 2014, aged 4–5 years. Numbers of thermal-marked fry released are 0.8 to 2 million per brood, with recoveries 319 individuals from 1084 specimens from river hatchery catch. Fish were collected at the hatchery weir, near the river mouth.

Fig. 3. Timing of coastal catch for hatchery-reared chum salmon broods with different otolith thermal marks (depending on the time of egg collection and fertilization) in Shari River (data from Morita 2017). Arrows indicate the time of egg collection and fertilization of their parent. Data based on thermal-marked fry released in 2009–2010, and adults caught in 2014, aged 4–5 years. Numbers of thermal-marked fry released are 0.8 to 2 million per brood, with recoveries

278 155 individuals from 5104 specimens from coastal catch.

279

280 Fig. 4. Fry-to-adult survival rates to coastal waters (■) and to river (▲), and exploitation rate by

281 coastal fishery (○) in relation to parent breeding time for hatchery-reared chum salmon in Shari

282 River (data from Morita 2017).

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Fig. 1

Fig. 2

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Fig. 4