



# The past, present, and a future for native charr in Japan

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## Abstract

Charrs (*Salvelinus*) reach their southernmost distribution in Japan, and are uniquely adapted to the short, steep streams of this island archipelago. Southern Asian Dolly Varden (*Salvelinus curilus*) occur only in Hokkaido Island, whereas white-spotted charr (*Salvelinus leucomaenis*) range to southern Honshu. Both species diverged from an ancestral lineage during the late Pliocene/early Pleistocene, when lowered sea levels created semi-enclosed water bodies in the seas of Japan and Okhotsk. Genetic analyses showed *S. curilus* represents the most ancient divergence from the Dolly Varden (*Salvelinus malma*) - Arctic charr (*Salvelinus alpinus*) group, and revealed five lineages of *S. leucomaenis* which align differently than traditional subspecies. Japanese charr display diverse and flexible life histories including anadromous fish with partial migration, and fluvial, affluvial, and resident forms. In Hokkaido, Dolly Varden are distributed upstream and white-spotted charr downstream. They coexist in narrow sympatric zones through adaptive shifts by Dolly Varden in behavior and morphology that facilitate benthic foraging. Both species hybridize with native and nonnative salmonids, and are displaced from microhabitats and decline in abundance when rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) invade. Japan streams contain over 95,000 erosion control dams which create short stream fragments (medians ~200 m). This has increased extirpation of charr populations via lower genetic diversity and stochastic and demographic factors. Tributaries provide complex rearing habitats, afford refuges from floods, and supply recruits that sustain populations in mainstem fragments and create metapopulations in connected riverscapes. Charr play central roles in linked stream-riparian food webs, and cause direct and indirect effects that cascade to streambed algae and riparian predators when linkages are disrupted by anthropogenic effects or altered by native parasites. Many charr populations are threatened by habitat fragmentation and introgression or invasion by nonnative forms, but efforts to conserve charr are growing. These include restoring connectivity among pure populations above barriers that prevent invasions, protecting tributary nurseries, and instituting angling regulations to protect headwater populations. Key steps include inventorying pure populations, identifying conservation units, selecting appropriate management based on connectivity and biotic interactions, and engaging stakeholders and youth to engender an ethic for conserving irreplaceable charr lineages.

**Keywords** Conservation · Ecology · Food webs · Phylogeography · Spatial ecology

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## Introduction

The charrs native to Japan are both beautiful and unique. In autumn 1988, when the senior author attended the International Symposium on Charrs and Masu Salmon in Sapporo, Japan (Noakes 1989), relatively little was known about these fishes. Several of the 85 papers published in the symposium volume concerned the complexities of charr systematics in Japan, but only six other papers and five abstracts addressed the biology, ecology, evolution, or management of Japanese charr (Kawanabe et al. 1989). In contrast, 26 papers and abstracts concerned specifically Arctic charr (*Salvelinus alpinus*).

Charrs of the genus *Salvelinus* reach their southernmost distribution in Japan, and are uniquely adapted to aquatic ecosystems of the island archipelago. The region is geologically young and tectonically active, so streams on the relatively narrow island chain are short and steep (Yoshimura et al. 2005), and habitats for charr are often fragmented by natural waterfalls. Charr populations must also contend with wide seasonal variation in flow owing to high annual precipitation (ca. 1–2 m) and flooding from monsoons and typhoons, although other populations occupy more benign environments in lakes or are anadromous in coastal watersheds. This broad array of habitats occupied has led to wide variation in appearance and life history (Morita 2019).

Why is a review of Japanese charr needed now? The 1988 symposium catalyzed much research on charrs in Japan, and collaborations among Japanese and international researchers who became fascinated with these fishes. This led to a proliferation of publications on their evolution, ecology, and conservation during the intervening 35 years, including more than 140 papers reviewed here. This research provides important information relevant to the conservation and management of charrs in Japan and other regions, and yet key challenges remain. The purpose of this paper is to briefly review this literature, and provide an overview of the past and present for native charr in Japan. We then compare them to two charr in North America that span the range of habitat connectivity and biotic interactions found on that continent, and suggest conservation actions that could promote a better future for the unique and beautiful charr in Japan.

## Species and forms of charr in Japan

Two species of charr are native to the Japanese archipelago (Fig. 1), southern Asian Dolly Varden (*Salvelinus curilus*, syn. *Salvelinus malma krascheninnikovi*; Markevich and Esin 2019), called “Oshorokoma” in Japanese (a word

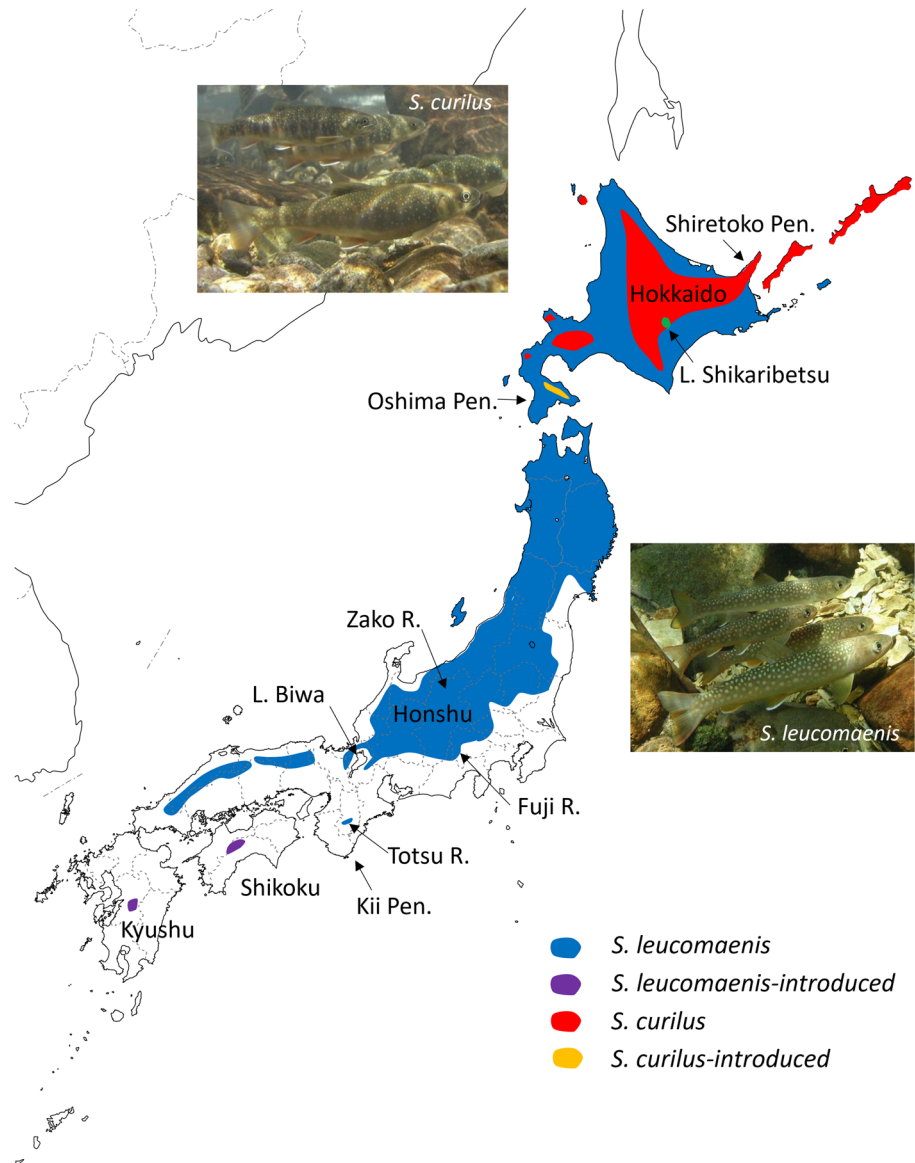
from the original Ainu inhabitants of Hokkaido), and white-spotted charr (*Salvelinus leucomaenis*) or “Iwana” (meaning rock fish; Morita 2019). In Japan, southern Asian Dolly Varden are distributed only in Hokkaido, but they range north to nearly the tip of Kamchatka, on Sakhalin Island, and along the Russian Far East coast from Uda Bay south to the northern border of South Korea, including in northern tributaries of the Yellow Sea (Mori 1936; Sato 1980; Markevich and Esin 2019). They are now considered a separate species from sister lineages of Dolly Varden (*Salvelinus malma*) distributed east around the Pacific rim to Washington state in the USA (Yamamoto et al. 2014). Miyabe charr (*Salvelinus curilus miyabei*), a lacustrine-adapted subspecies consisting of subpopulations that home to separate tributaries (Maekawa 1985), is endemic to Lake Shikaribetsu, Hokkaido (Maekawa 1984).

White-spotted charr are distributed throughout most of Honshu Island and all of Hokkaido except Shiretoko Peninsula (Fig. 1). They extend north throughout Sakhalin and to all watersheds of the Kamchatka Peninsula and Sea of Okhotsk, and south along the Sea of Japan coast to northern North Korea (Mori 1936; Markevich and Esin 2019). The traditional taxonomy recognized four subspecies, arrayed from north to south: resident “Ezo-iwana” and anadromous “Amemasu” (rain trout, *Salvelinus leucomaenis leucomaenis*) in Hokkaido, “Nikko-iwana” (*Salvelinus leucomaenis pluvius*) in northern Honshu, “Yamato-iwana” and “Kirikuchi” charr (*Salvelinus leucomaenis japonicus*) in southern Honshu, and “Gogi” (*Salvelinus leucomaenis imbricus*) in western Honshu (Fig. 2; Kawanabe 1989; Morita 2019). Kirikuchi charr are genetically distinct southernmost populations restricted to seven small, isolated headwater tributaries on the Kii Peninsula (Sato et al. 2010). Introductions have established populations of southern Asian Dolly Varden and Miyabe charr in rivers of southern Hokkaido (Morita 2019) and white-spotted charr farther south in Shikoku and Kyushu islands (Kondou et al. 1999; Inoue et al. 2023).

## Evolution and zoogeography of charr in Japan

Japan is at or near the center of origin for southern Asian Dolly Varden and white-spotted charr, both of which diverged from an ancestral lineage in the late Pliocene through early Pleistocene epochs (Esin and Markevich 2018). The region was not ice covered during Pleistocene glaciation, but sea level declines of 120–140 m isolated the seas of Japan and Okhotsk as semi-enclosed bodies of brackish or fresh water, promoting genetic divergence. Analysis of mtDNA from throughout the range of Dolly Varden revealed three main lineages (Yamamoto et al. 2014). The western lineage, identified as southern Asian Dolly Varden,

**Fig. 1** Distribution of charr in Japan (after Morita 2019; K. Morita images). Southern Asian Dolly Varden (*Salvelinus curilus*) inhabit only Hokkaido and nearby islands. White-spotted charr (*S. leucomaenis*) co-occur with them in all these regions except on Shiretoko Peninsula where only Dolly Varden are present. Miyabe charr (*S. c. miyabei*) occur only in Lake Shikaribetsu, located at the green oval. Locations of introduced populations of each species are also shown



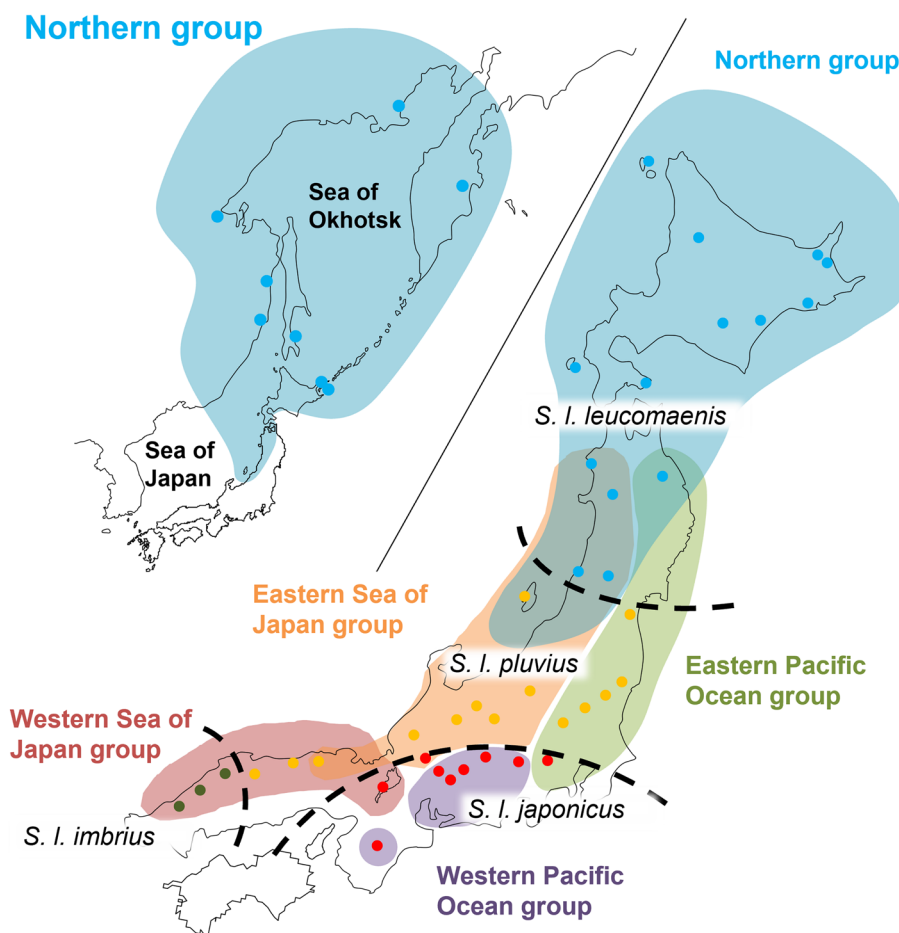
represents the most ancient divergence from the ancestral lineage, dated to 3.5–1.2 MYA (Million Years Ago; Esin and Markevich 2018) in a center of origin in the southern Sea of Okhotsk. This lineage is considered basal to the more derived sister clades of central Dolly Varden (*Salvelinus malma malma*), eastern Dolly Varden (*Salvelinus malma lordi*), and all Arctic charr.

White-spotted charr diverged from an ancestral lineage about 3.3–2.4 MYA in the Sea of Japan, and later colonized northward (Esin and Markevich 2018). A wide-ranging study of 588 single nucleotide polymorphisms (SNPs) revealed five geographic groups, several with slightly overlapping boundaries (Fig. 2; Yamamoto et al. 2023). However, these do not align perfectly with the four traditional subspecies, especially in central and southern Honshu where, based on SNPs, two groups assign to basins draining

east to the Pacific Ocean and two others to basins draining west to the Sea of Japan. The northern lineage is largely congruent with *S. l. leucomaenis* in Hokkaido and northward, probably because migratory forms allowed gene flow among rivers. However, for the four southern lineages the evidence indicates that repeated colonization and isolation of landlocked forms, coupled with inter-drainage gene flow via stream capture caused by processes like uplift, erosion, and movement of active faults (Masuda et al. 2023) probably explains the complex zoogeography. Given this complex genetic structure and lack of contemporary gene flow, the most appropriate units for conservation are populations within river basins, rather than traditional subspecies (Yamamoto et al. 2023).

Southern Asian Dolly Varden (simply Dolly Varden hereafter, when referring to Japan) and white-spotted charr

**Fig. 2** Distribution of five genetic groups of white-spotted charr determined by Bayesian population assignment of 394 individuals from 48 river systems throughout their range based on 588 single-nucleotide polymorphisms (modified from Yamamoto et al. 2023, with permission). Dashed curves and colored location markers show the distributions of the four traditional subspecies: *Salvelinus leucomaenis leucomaenis* (blue), *S. l. pluvius* (yellow), *S. l. japonicus* (red), and *S. l. imbricus* (green)



co-occur in Hokkaido (Fig. 1), although they overlap in relatively short stream segments. Dolly Varden are more cold-adapted and colonized river headwaters, whereas white-spotted charr are more warm-adapted and inhabit downstream segments and lowland habitats (Ishigaki 1984). The two species co-occur only in narrow zones of sympatry, or abut in parapatry, and the boundary is closely aligned with temperature isotherms (Fausch et al. 1994). For example, in streams of northeast Hokkaido on Shiretoko Peninsula, which extends into the cold North Pacific Ocean (mean annual air temperature [MAT] 5 °C), Dolly Varden dominate throughout and white-spotted charr are largely absent. Temperatures warm across the island toward the southwest, and the downstream limit of Dolly Varden and upstream limit of white-spotted charr gradually increase in elevation. On Oshima Peninsula of southwest Hokkaido (MAT 8–9 °C) white-spotted charr dominate and Dolly Varden are native only to one cold spring stream. Yamamoto et al. (2006a) reported evidence of introgression of white-spotted charr mtDNA into some Shiretoko Dolly Varden populations. They suggested hybridization was owing to smaller resident male Dolly Varden fertilizing eggs of a few large anadromous female

white-spotted charr that entered rivers there, either by paired mating or sneaking.

### Individual behavior and ecology

During the 35 years since the Charr and Masu Salmon Symposium, Japanese charr have been studied intensively at the individual level, especially factors shaping their life history, the structure of dominance hierarchies and mechanisms driving foraging mode shifts, interactions with nonnative salmonids, and patterns of and mechanisms causing hybridization with nonnative species.

*Life history.* Dolly Varden and white-spotted charr have diverse and flexible life history patterns, based on costs of migration, food resources, and temperatures in different habitats. Like other salmonids, charr in Japan display more anadromy to the north and residency to the south (i.e., are landlocked), owing to more resources in marine environments to the north and in freshwaters to the south (Gross et al. 1988). Charrs are iteroparous and express life histories that include anadromous, fluvial, adfluvial, and resident fish, and precocious male parr. In white-spotted charr populations

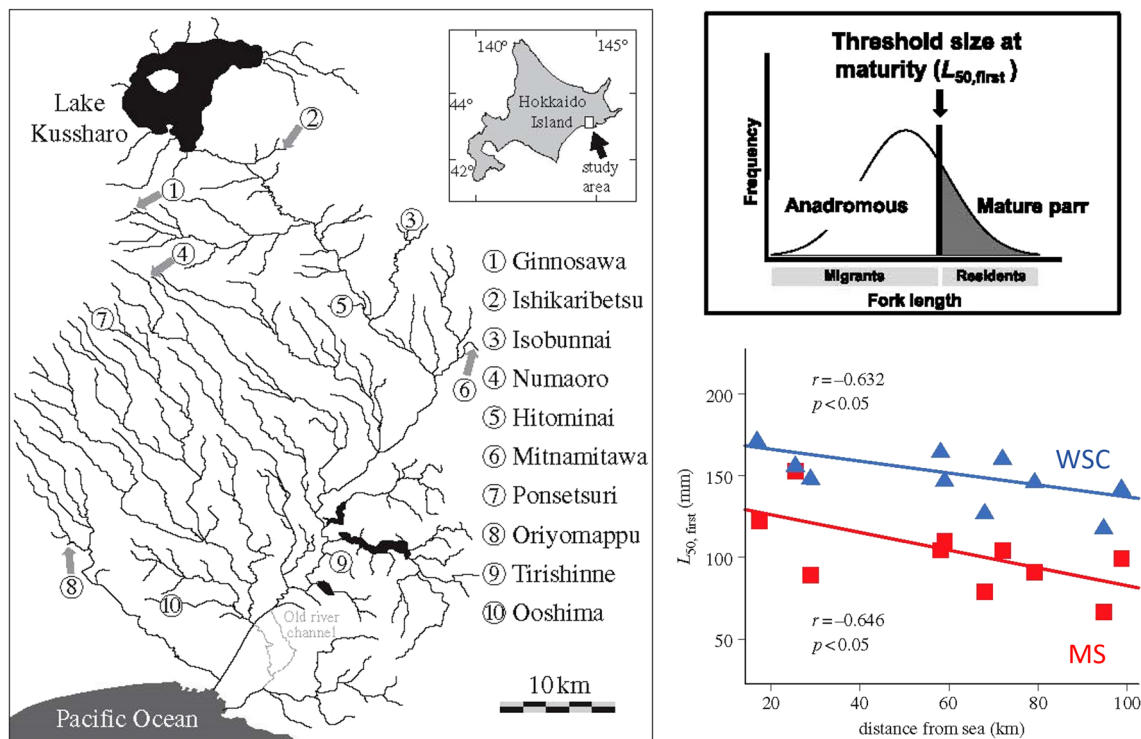
of Hokkaido that have both resident and migratory individuals (i.e., partial migration), males that exceed a threshold size attain sexual maturity, become resident, and fertilize eggs via sneaking behavior. This size threshold is a key life-history trait shaped by tradeoffs among migration costs and the benefits that determine fitness, and is highly variable and potentially locally adapted in salmonine fishes (Sloat et al. 2014). Migration costs increase with distance from the ocean, so male parr mature at a smaller size far from the ocean compared to near, about 145 mm versus 170 mm fork length in tributaries of the Kushiro River in eastern Hokkaido (Fig. 3; Sahashi and Morita 2013). A common garden experiment in the field revealed that male parr also matured at smaller sizes in narrower streams, probably because a greater number of visual refuges in small streams allows greater success for small sneaking males (Morita et al. 2009a).

Anadromy of white-spotted charr in Hokkaido is also complex and flexible. Data from archival tags and analysis of otolith Sr:Ca ratios showed that in eastern Hokkaido these charr made annual migrations, descending rivers to feed in the ocean in May–June and ascending to spawn and overwinter in rivers in August through November (Morita et al. 2013). However, in southwestern Hokkaido some adults

can overwinter in the ocean (Kuroda and Miyashita 2022) because of warmer water temperatures brought by ocean currents and opportunities for growth (Takami et al. 1996).

In contrast, most Dolly Varden populations in Hokkaido are predominately resident, although anadromous forms occur in Shiretoko Peninsula (Maekawa 1973; Morita et al. 2009b; Morita 2019). Dolly Varden also show partial migration within a large river system in central Hokkaido. A majority of females adopted a fluvial life history and migrated from tributaries to the mainstem, whereas faster-growing males remained residents in tributaries (Koizumi et al. 2006b; Ayer et al. 2018), a pattern similar to other partially migratory salmonids that migrate to oceans or lakes (e.g., Jonsson and Jonsson 1993; Morita et al. 2014).

**Spawning.** Charr in Japan typically spawn from late September to late November, depending on water temperature (e.g., Taguchi et al. 2022). In Hokkaido, white-spotted charr spawning peaks in mid-October, about one month earlier than that of Dolly Varden in early November, but the 6-week spawning periods of the two species overlap (Ishigaki 1969; Komiyama 1987). Females excavate redds in water about 10–20 cm deep, with 10–15 cm  $\cdot$  s<sup>-1</sup> velocity and in 10–30 mm diameter substrate (Kitano and Shimazaki 1995; Nakamura 1999a; Kishi and Tokuhara 2018). Male



**Fig. 3** A threshold model of partial migration in salmonids describing the size at which male parr remain resident vs. migrating to sea (upper right). The length at which half the parr are mature at first reproduction ( $L_{50}$ ) is reduced in populations farther from the sea (lower right) for both white-spotted charr (WSC; *Salvelinus leuco-*

*maenis*) and masu salmon (MS; *Oncorhynchus masou*) across 10 populations in the Kushiro River basin of eastern Hokkaido (left), demonstrating the flexibility of this life-history attribute with changes in migration cost (from Sahashi and Morita 2013, with permission)

and female Dolly Varden in an isolated reach of a Shiretoko stream established dominance hierarchies during spawning, and larger females spawned earlier and excavated deeper redds than smaller fish (Kitano 1996). The largest male monopolized three-quarters of all spawning opportunities, whereas only half the subordinate males (the larger individuals) spawned, and several of those only by sneaking. Maekawa et al. (2001) reported a similar mating system among white-spotted charr in central Honshu, where relatively few large males monopolized most spawnings. Genetic analysis of offspring of Miyabe charr revealed that subordinate males that spawned by sneaking (about 1.5 satellite males per spawning event) fertilized about 25% of eggs (Maekawa and Onozato 1986).

Synchronous spawning within populations has been reported for both Dolly Varden (Koizumi and Shimatani 2016) and white-spotted charr (Sato and Harada 2008). An individual-based model of female Dolly Varden spawning dates among populations in 30 small tributaries supported the hypothesis that synchrony can be caused by social interactions rather than environmental factors or predator swamping, and may be a strategy to reduce subdominant males per female and hence egg cannibalism (Koizumi and Shimatani 2016).

**Movement and mesohabitat selection.** Stream salmonids including charr have been reported to move across stream segments to access habitats for spawning, feeding, and refuge (Gowan and Fausch 1996; Fausch et al. 2002; Rodríguez 2002). Movements of white-spotted charr detected by marking and recapturing fish multiple times per year over 4 years indicated about half remained in the same pools, whereas the other half moved to many different distances up to 1–3 km away (Nakamura et al. 2002). The investigators reported that this leptokurtic distribution of movement distances (cf. Radinger and Wolter 2014) suggested fish selected either sedentary or a range of mobile behaviors. Moreover, given that only 33% of tagged fish were recaptured, fish that moved longer distances outside the study area could have been missed, so the true proportion of long-distance movements could be even greater. In the same stream, more white-spotted charr were recaptured over year-long periods in pools that had refuges beneath boulders than pools without such refuges (Nakamura 2011). In an artificial stream, white-spotted charr selected overhead cover closer to the stream bed (10–20 cm) and cover with lateral visual isolation compared with cover farther from the bed or above the water surface (Terada et al. 2020).

**Dominance and foraging behavior.** White-spotted and Dolly Varden charr set up interspecific size-structured linear dominance hierarchies with each other, and with resident masu salmon (*Oncorhynchus masou*) in mesohabitats where they are syntopic in Japanese streams (Nakano and Furukawa-Tanaka 1994; Nakano 1995a; Fausch et al. 2021; see

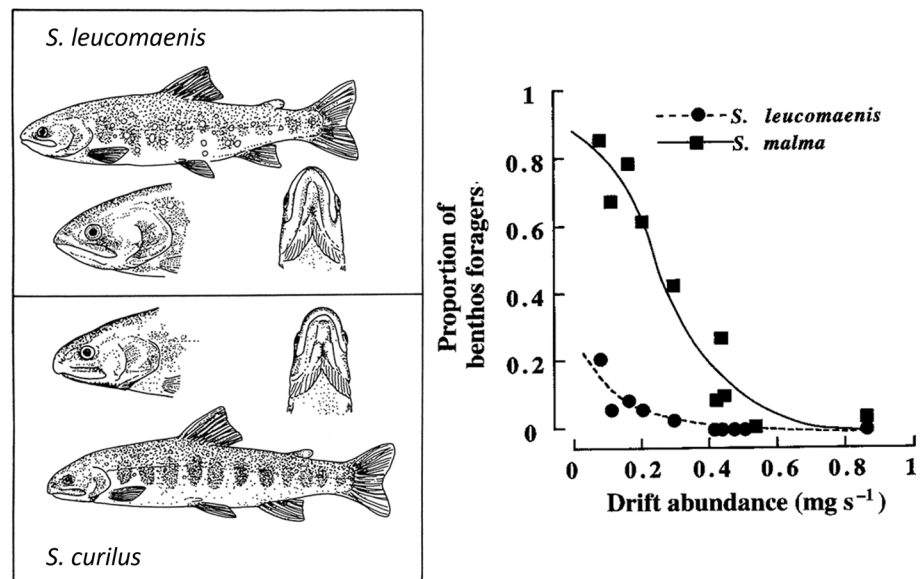
Fausch 2018 for a review of Nakano's work). Within these local social groups, larger more dominant charr have the highest foraging success and growth, similar to dominance hierarchies of resident red-spotted masu salmon ("Amago", *Oncorhynchus masou ishikawae*; Nakano 1995b). Dominance allows larger fish to select focal positions in velocity refuges near the upstream ends of pools, which provide access to the most drifting invertebrates for the least swimming cost and yield the highest net energy intake (Fausch 2014; Fausch et al. 2021).

Research by Shigeru Nakano and collaborators along a Hokkaido riverscape revealed mechanisms allowing coexistence of Dolly Varden and white-spotted charr in syntopy. Knockout experiments and statistical analysis of dominance hierarchies measured by snorkeling showed that for drift-foraging individuals neither species was dominant over the other, so dominance was based on size alone (Fausch et al. 2021). However, as streamflow and drifting invertebrates declined throughout summer, smaller Dolly Varden shifted from drift feeding to picking invertebrates from benthic substrates, a behavior facilitated by their subterminal mouth position (Fig. 4; Nakano and Furukawa-Tanaka 1994). The proportion of Dolly Varden that shifted to benthic foraging increased throughout summer, and the drift-rate threshold at which the shift occurred was nearly identical when measured by field experiment (Fausch et al. 1997) and an observational study over four summers in the same stream (Nakano et al. 1999a). In contrast, white-spotted charr, which have a terminal mouth position, switched to benthic feeding only at very low drift abundance.

The shift to benthic foraging by Dolly Varden is a mechanism of resource partitioning that stabilizes coexistence between the two species in zones of sympatry (Nakano et al. 1999a; Fausch et al. 2021). Moreover, this foraging-mode shift is facilitated by character displacement, whereby Dolly Varden in sympatry develop more subterminal mouths than those in allopatry, resulting in a shift in diet to forage more on benthic organisms (Nakano et al. 2020). This phenotypic plasticity is similar to other charrs across the Holarctic which produce two to seven distinct morphs that fill different trophic niches and habitats (e.g., Skúlason et al. 1999; Bertrand et al. 2008; Chavarie et al. 2015; Markevich et al. 2018). Current evidence indicates that the mechanism stems from environmental influences on gene regulation during development such that, for example, foraging by fry on benthic prey promotes development of blunt head shapes and subterminal jaws (Parsons et al. 2011; reviewed by Skúlason et al. 2019).

**Behavioral interactions with other salmonids.** White-spotted charr were subordinate to other native and non-native salmonids in natural and laboratory streams. In a central Honshu stream, individual resident masu salmon ("Yamame", *Oncorhynchus masou masou*) dominated charr

**Fig. 4** Comparison (left) of head and jaw morphology of white-spotted charr (*Salvelinus leucomaenis*) and southern Asian Dolly Varden (*S. curilus*; illustration by S. Nakano; from Fausch 2015, with permission). Proportion of benthos foragers (right) of white-spotted charr and Dolly Varden (originally designated *S. malma*) measured by snorkeling during 10 periods over four summers in a 1.5-km segment of Poroshiri Stream, Hokkaido (from Nakano et al. 1999a, with permission)



up to 40% greater in mass, and the salmon grew faster during summer surpassing some charr in dominance rank (Nakano 1995a). In laboratory streams, nonnative brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) clearly dominated white-spotted charr in individual pairwise contests (Hasegawa et al. 2004). When together, these nonnatives also forced the white-spotted charr and masu salmon to compete for similar microhabitats, and the competitively inferior charr were relegated to inferior foraging positions downstream (Hasegawa and Maekawa 2006). Visual isolation reduced interspecific aggression by brown trout on white-spotted charr, and allowed the charr to forage much more often on drifting prey (Hasegawa and Maekawa 2009). In two small headwater streams in central Honshu that had been invaded by nonnative brown trout and brook charr (*Salvelinus fontinalis*), about 25% of foraging attempts by white-spotted charr and brook charr were toward the benthos, probably owing to aggression by brown trout (Peterson et al. 2023). Moreover, the diet of white-spotted charr and brook charr overlapped almost completely. These interactions help explain why densities of white-spotted charr declined drastically in the region, and why they disappeared from four other streams studied.

**Hybridization with other species.** White-spotted and Dolly Varden charr hybridize with several native and nonnative salmonids, producing hybrid swarms that can be sustained by movement. Reports of hybrids with nonnative salmonids are common, including white-spotted charr with brook charr or brown trout (Kitano et al. 2009, 2014; Fukui et al. 2016, 2018; Fukui and Koizumi 2020), Dolly Varden with brook charr (Fukui et al. 2021), and Miyabe charr with introduced masu salmon (Koizumi et al. 2005). The first hybrids are often asymmetrical, between male nonnative salmonids and female native charr (e.g., Kitano et al. 2009,

2014). Nonnative salmonids spawn later than native charr, so early-maturing male nonnative salmonids spawn with native female charr. As hybridization continues, later hybrids can be backcrosses with either species (Fukui et al. 2016).

Hybrids of white-spotted charr and brook charr in Hokkaido are less successful at reproduction but more successful at spreading nonnative genes. Based on parentage analysis, hybrids had much lower reproductive success than either pure species (Fukui et al. 2018). Male hybrids had much lower success than male brook charr owing to less pronounced secondary sexual characteristics (color, height of hump, kype) as well as outbreeding depression caused by other undetermined factors probably operating at multiple life stages. However, hybrid males also had more pronounced characteristics than white-spotted charr males, which increased asymmetrical backcrosses with female white-spotted charr. Despite their lower reproductive success, the survival, growth, and movement of hybrids was as high or higher than the parental species, which is believed to sustain introgression by continuing to spread nonnative genes (Fukui and Koizumi 2020).

Natural hybridization also occurs between white-spotted charr and masu salmon where their ranges overlap in Japan. For example, hybrids have been reported among Kirikuchi charr at the southern extent of the white-spotted charr range. Red-spotted masu salmon are expanding upstream into small, isolated populations of the charr, creating mating opportunities that produce intergeneric hybrids (Sato et al. 2008a, 2010). Similarly, in a river basin in central Honshu, 6% of 153 matings observed across 16 sites were between red-spotted masu salmon and white-spotted charr (Taguchi et al. 2022). Matings occurred during the period of overlap in the spawning seasons (salmon spawn earlier than charr), and females of both species engaged in intergeneric mating

behavior. Sneaking behavior by smaller males of the two species is one mechanism causing hybridization.

## Population ecology

Research on charr in Japan includes extensive studies over large spatial scales of factors influencing their distributions, as well as intensive studies over decade-long temporal scales and kilometer-long spatial scales of metapopulations and spatial ecology. Each revealed important information about how populations use habitat and persist across multiple spatial scales.

*Effects of habitat at mesohabitat to riverscape scales.* Swimming ability, thermal tolerance, and condition-specific competitive ability can explain the distribution of charrs and masu salmon in Hokkaido streams. In southern Hokkaido where Dolly Varden are scarce, white-spotted charr are more prevalent upstream and masu salmon downstream (Morita et al. 2016), a pattern of altitudinal niche partitioning correlated with water velocity and swimming stamina. Masu salmon are superior swimmers, and held positions in higher velocities that are prevalent downstream. In contrast, the charr held positions closer to the streambed and at lower velocities, microhabitats prevalent in upstream reaches.

The altitudinal niche partitioning of Dolly Varden and white-spotted charr described earlier (Fausch et al. 1994) can be accounted for by condition-specific competition, whereby different species dominate under different environmental conditions (Dunson and Travis 1991). A laboratory experiment revealed that white-spotted charr survived poorly at lower temperatures, with or without Dolly Varden, helping explain the upstream limit of their distribution and why it shifts with temperature across Hokkaido Island (Taniguchi and Nakano 2000). In contrast, at higher temperatures Dolly Varden were dominated by white-spotted charr and grew poorly in the laboratory and a field experiment (Watz et al. 2019), which can explain the downstream limit of their distribution. Dolly Varden also showed superior swimming performance over white-spotted charr at cold temperatures found upstream, whereas the two were equal at warmer temperatures found downstream, indicating that Dolly Varden can dominate in cold, steep headwaters where maximum velocities are high (Yamada et al. 2020). These equalizing mechanisms of temperature-dependent survival and condition-specific competition create the narrow zones of syntopy in which the stabilizing mechanisms of foraging mode shifts and character displacement by Dolly Varden can further balance fitness and promote coexistence when food resources are scarce (Nakano et al. 2020; Fausch et al. 2021).

Temperature and foraging opportunities also influence the life history and distribution of white-spotted charr in other locations. At the southern end of their distribution

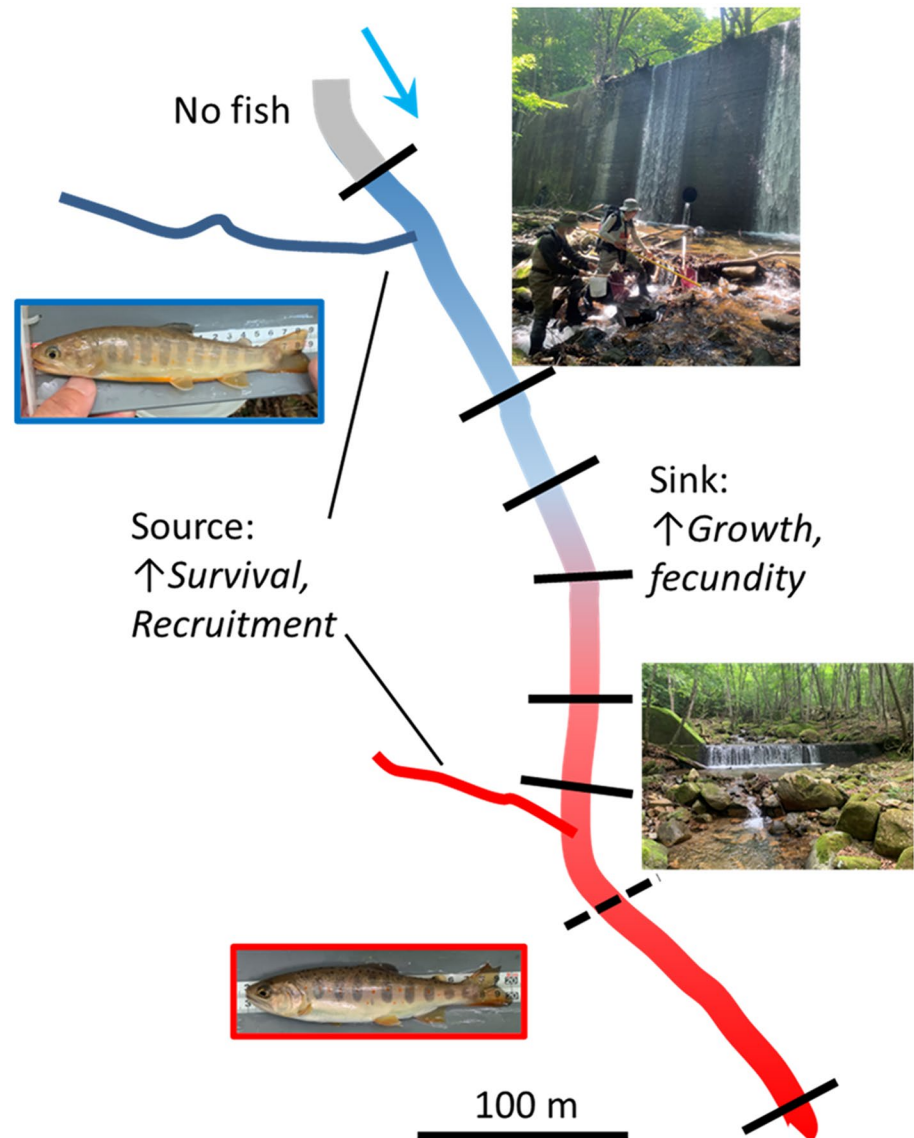
in Honshu, white-spotted charr landlocked at high elevations (>2,000 m) spawned earlier, grew slower, lived longer, and were older and larger at maturity compared to those in lower-elevation streams (Tsuboi et al. 2013a). In southwest Hokkaido, the rate of net energy intake calculated from a bioenergetic model as an index of habitat quality accounted for more than three-quarters of the variation (77%) in biomass of drift-feeding salmonids in 20 reaches of 4 streams (Urabe et al. 2010). White-spotted charr composed up to 70% of the biomass among reaches, and masu salmon the rest.

*Spatial ecology.* The spatial ecology of Japanese charr across mainstems and their tributaries is complex, driven by differences in relative survival, growth, and recruitment in habitats with contrasting disturbance regimes. A decade of research on small populations of Dolly Varden in 100 tributaries of a Hokkaido river using genetics and population surveys revealed a complex metapopulation structure (Koizumi and Maekawa 2004; Koizumi et al. 2006a, 2008; reviewed in Koizumi 2011). Subpopulations were largely independent, based on significant genetic divergence and little demographic synchrony among them, and showed many types of dynamics. These included a few large tributaries that acted as sources, dispersal among smaller ones that could rescue neighbors, and outlying small populations prone to extirpation, often from human effects like culverts and other barriers.

A decade-long study in central Honshu showed the importance of tributaries for sustaining small populations of white-spotted charr in the highly fragmented habitats found there (Tsuboi et al. 2020, 2022). More than 95,000 erosion-control dams that block upstream fish movements have been constructed throughout Japan, about 20,000 in Hokkaido alone (Morita and Yamamoto 2004; Tamate and Hayajiri 2008). In the 1-km stream network studied, these barriers occur about every 75 to 150 m in the mainstem, but not in two tributaries 145 and 280 m long (Fig. 5). Nursery habitat was more prevalent, and survival was higher in the more complex tributary habitats than the simpler mainstem habitats, but the higher density in tributaries resulted in lower growth than in the mainstem (Tsuboi et al. 2020). A matrix metapopulation model of these demographic data showed that the two small 2-m wide tributaries, which made up less than 20% of the total habitat area for charr, were source habitats critical to persistence of the entire metapopulation in this highly fragmented stream network. Without emigration of charr from tributaries to the mainstem, population growth rate would drop far below replacement ( $\lambda = 0.88$ ) and charr would be extirpated from sink habitats in the mainstem (Tsuboi et al. 2022). The mechanisms responsible for higher survival in tributaries are probably greater habitat complexity (more large wood and undercut banks) and providing a refuge from floods (Koizumi et al. 2013). This negative



**Fig. 5** Spatial demographics of white-spotted charr (*Salvelinus leucomaenis japonicus*; upstream, blue) and red-spotted masu salmon (*Oncorhynchus masou ishikawae*; downstream, red) in Sabusawa Stream, central Honshu (after Tsuboi et al. 2020, 2022; Y. Kanno images). Images show examples of high (solid lines) and low (dashed) erosion control dams along the mainstem (arrow shows flow direction). Higher survival and recruitment of fish in the tributaries (source habitats) prevent extirpation of populations in the mainstem fragments (sink habitats), despite the tributaries being less than half as wide as the mainstem (ca. 2 m vs. 5 m) and making up only 18% of the habitat area for charr and 12% for salmon



covariation in survival and growth between tributaries and mainstem habitats likely confers resilience on spatially structured charr populations (Terui et al. 2018).

In contrast, in a northern-Hokkaido tributary with no barriers to movement, white-spotted charr displayed a leptokurtic distribution of movement distances over a 2-month summer period. Most fish were recaptured or detected within 60 m of their initial capture location, but the rest moved to many different distances up to 500 m away (Kanno et al. 2020). A sixth of the population (17%) moved downstream within 1–3 days and emigrated from the tributary permanently. Movements were influenced by body length and condition, but this varied across scales. Smaller charr were more likely to emigrate permanently. Within the tributary, larger fish in poorer condition were more likely to move to find better pools, whereas smaller fish in good condition were also more likely to move to find better opportunities for growth

(Kanno et al. 2021). Similarly, in a fluvial population of Dolly Varden, migrants from two tributaries to the mainstem were in poorer condition than residents (Ayer et al. 2018).

## Invasion biology

Rainbow trout, brook charr, and brown trout were first introduced in Japan starting nearly 150 years ago. They invaded streams and lakes that provide suitable environmental conditions and have displaced native salmonids. Rainbow trout were imported to a fish hatchery near Tokyo in 1877 from California (Japan Bureau of Fisheries 1927), one of the first two introductions of this species beyond North America (MacCrimmon 1971; Fausch et al. 2001). Brook charr were introduced in 1902 (Japan Bureau of Fisheries 1927). There is no official government record for the introduction of

brown trout (Maruyama et al. 1987), but possible sources are a shipment of 20,000 eggs by the US Fish Commission in 1892–1893 (MacCrimmon et al. 1970) or inadvertent mixing of eyed eggs with those of rainbow trout or brook charr (Hasegawa 2020). Rainbow trout were introduced to Hokkaido in 1914 and began invading in the early 1970s, and brown trout began invading Hokkaido about 1980 (Takami and Aoyama 1999). Rainbow trout are now found in 36 of 47 prefectures in Japan, but reproduce naturally in only 9 of them (Hasegawa 2020), mainly in Hokkaido (Kitano 2004; Inoue et al. 2009). In contrast, brown trout reproduce in nearly three-quarters of the 18 prefectures where they occur. Brook charr are reported to reproduce in only five locations in Japan (Kitano 2018).

Flooding from monsoons and typhoons may be a key disturbance preventing natural reproduction of all three nonnative salmonid species, especially in Honshu. For example, white-spotted charr tend to reproduce and rear in small tributaries where flooding disturbance is less (Tsuboi et al. 2020, 2022). Rainbow trout invasion is limited or absent in streams with snowmelt and monsoon rain-driven flooding regimes that coincide with fry emergence in early summer (Fausch et al. 2001), and tends to be restricted to streams dominated by groundwater discharge, especially in Hokkaido (Inoue et al. 2009). In contrast, the timing of emergence of brown trout fry, which occurs in April through May, is closer to the February-to-April fry emergence of native white-spotted charr and masu salmon. Therefore, although floods in Japanese rivers begin in April (Fausch et al. 2001), brown trout may be better suited than rainbow trout to invade these habitats (Hasegawa 2020). This may be similar to invasions by nonnative brook charr and brown trout in Colorado, USA, where spring snowmelt floods reduce recruitment somewhat, but populations nevertheless reach high densities (Fausch 2008).

Several studies have revealed mechanisms at various scales by which rainbow trout and brown trout exclude white-spotted charr from habitats. An early analysis at pool and riverscape scales (Morita et al. 2004), followed by sophisticated statistical analysis of a 16-year time series (Morita 2018) showed that introduction and invasion first by brown trout followed by expansion of rainbow trout displaced white-spotted charr from a southwest Hokkaido stream (Fig. 6). Torrential rains during summer when fry of the nonnative trout are small and vulnerable to displacement apparently limited the pace of invasions, based on a stock-recruitment analysis of the full 20 years of data (Morita 2022). Hence, the charr are limited by invasion of the nonnative trout, whereas the nonnatives themselves are limited by environmental factors. In another Hokkaido stream brown trout invaded when a dam was breached, and displaced white-spotted charr over a 9-year period (Hasegawa 2017), but the trout were limited upstream by cold temperatures

(Hasegawa and Maekawa 2008a). The charr were relegated to pools with more structural complexity when brown trout were present (Hasegawa and Maekawa 2008b).

In an interesting twist, white-spotted charr have become “native invaders” (Carey et al. 2012) in several locations in the southern islands of Shikoku and Kyushu, beyond their native range (Fig. 1; Kondou et al. 1999; Inoue et al. 2023). In three tributaries of the Shikoku stream, white-spotted charr invaded upstream to an erosion-control dam and a natural waterfall over a 15-year period, using headwater habitats similar to those in their native range and displacing the native red-spotted masu salmon there. Spawning habitat is limited in headwater habitats, so one possible mechanism is superimposition of salmon redds by the later-spawning charr (Togaki et al. 2023).

## Community and ecosystem ecology

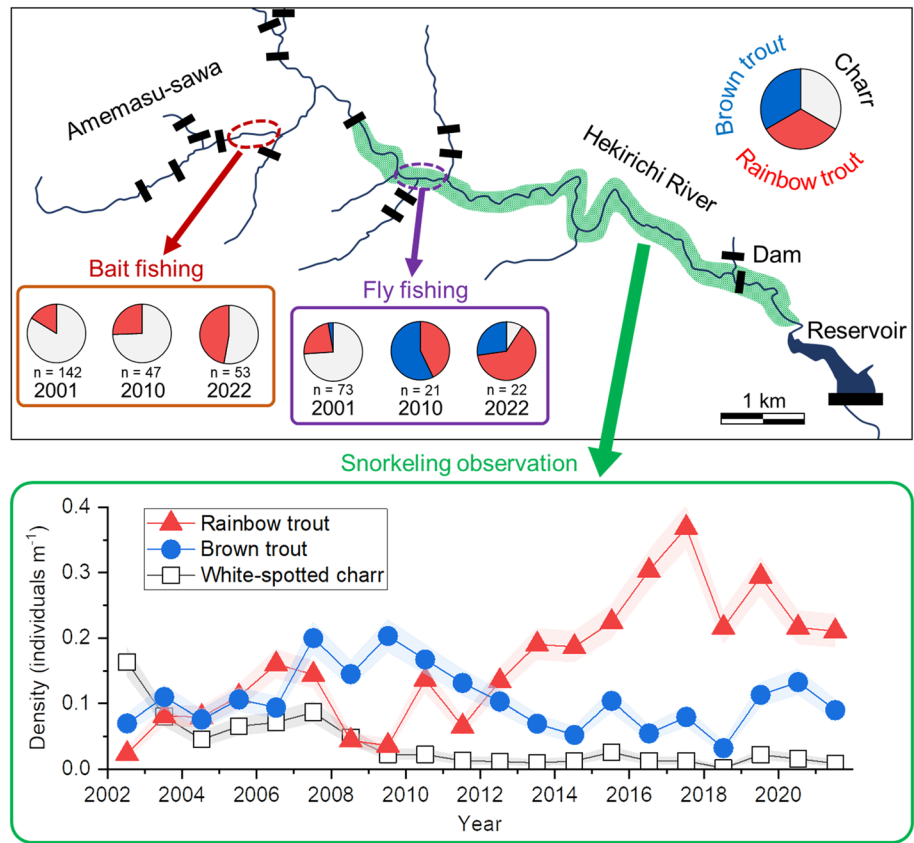
Pioneering studies by Shigeru Nakano and his colleagues using large-scale manipulations in the field to measure effects of charr on reciprocal stream-forest food web interactions made major advances in stream and fish ecology (Fausch 2018). This research inspired other researchers to use a similar approach to study the direct and indirect effects of nonnative trout and nematomorph parasites on terrestrial and aquatic invertebrates that drive these food web effects.

*Charr piscivory.* White-spotted charr prey on hatchery-reared fry of anadromous chum salmon (*Oncorhynchus keta*) and masu salmon that are stocked in Hokkaido rivers, selecting the smaller individuals (Hasegawa et al. 2021). These fry provide a pulsed food resource that temporarily increases the food intake and growth rate of the charr (Hasegawa and Fukui 2022). Experiments revealed that predation on masu salmon fry could be reduced substantially if fry were raised to exceed 40% of the length of white-spotted charr predators (Miyamoto and Araki 2017).

*Role in food webs.* Dolly Varden and white-spotted charr have strong effects on linked stream-riparian food webs through predation on aquatic insects that emerge into riparian zones, and terrestrial arthropods that fall into streams. Terrestrial arthropods are an important resource subsidy for charr, making up 50% of the total annual energy intake for white-spotted charr and 23% for Dolly Varden in a southern Hokkaido stream (Nakano and Murakami 2001). When Dolly Varden alone were enclosed in 25-m long reaches during a field experiment in the same stream, more than half their summer diet was terrestrial arthropods (Nakano et al. 1999b).

Shigeru Nakano and his colleagues pioneered using mesh greenhouses to experimentally exclude this terrestrial arthropod subsidy (Fig. 7), which caused Dolly

**Fig. 6** Densities of native white-spotted charr (*Salvelinus leucomaenis*) and nonnative rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) measured by angling (upper panel; Tsuboi and Morita 2004; J. Tsuboi, National Research Institute of Fisheries Science, Nikko, Japan, written communication of unpublished data, 17 June 2023) and snorkeling (middle panel; modified from Morita 2022, with permission) over two decades in the Hekirichi River, southern Hokkaido (lower panel; K. Morita image). Both sampling methods revealed similar declines in the proportion of charr and increases in nonnative trout

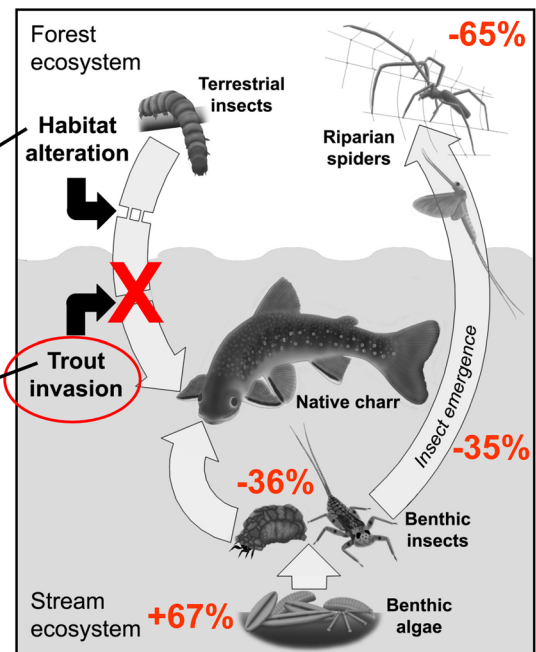


Varden charr to initiate cascading food web interactions sufficient to influence riparian predators through indirect effects (Nakano et al. 1999b; Baxter et al. 2004). When Dolly Varden were enclosed in fenced reaches covered with greenhouses, they switched to foraging on benthic invertebrates, reducing their biomass by 46%. This caused benthic algae to bloom (a 49% increase in biomass), and emergence of adult aquatic insects to decrease by 79% (Fausch et al. 2010). Loss of insect emergence, such as virtually eliminating it using mesh greenhouses, caused most

riparian spiders that rely entirely on this subsidy to leave or die (an 83% decline; see also Kato et al. 2003), and bat foraging to decline drastically (Fukui et al. 2006). In another experiment where fish were free to move, half the biomass of salmonids (including both charr species) left reaches covered by mesh greenhouses compared to control reaches (Kawaguchi et al. 2003), showing the importance of the terrestrial arthropod subsidy.

Nonnative rainbow trout had a similar effect as the greenhouses, usurping most terrestrial invertebrates and

**Fig. 7** Effects of charr in food webs subjected to habitat alteration and nonnative trout invasions. Shigeru Nakano pioneered the use of mesh greenhouses (upper left) to mimic habitat alteration of riparian zones that supply terrestrial arthropods to streams. Nonnative rainbow trout (*Oncorhynchus mykiss*; lower left) have a similar effect, usurping this prey subsidy from Dolly Varden (*Salvelinus curilus*). This treatment resulted in cascading effects throughout the linked stream-riparian food web (shown in red), ultimately causing reduction of riparian spiders by two-thirds, and an increase in benthic algae by two-thirds. Figure and images are from Baxter et al. (2004, with permission)



dominating Dolly Varden, which also caused the charr to shift to benthic feeding (Nakano et al. 1999c; Baxter et al. 2004, 2007). Much like the effect of greenhouses, adding rainbow trout resulted in a 36% reduction in benthic herbivores, a 67% increase in streambed algae, a 35% reduction in emerging aquatic insects, and a 65% decrease in riparian spiders (Fig. 7; Baxter et al. 2004; Fausch et al. 2010).

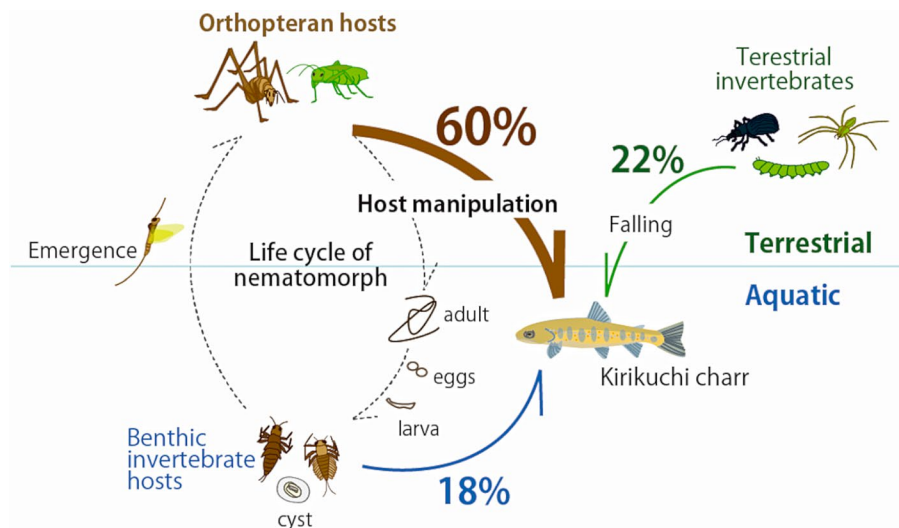
Integrating all the information from studies of this stream-riparian ecosystem in a systems model revealed that the seasonal subsidies of terrestrial invertebrates favored rainbow trout and white-spotted charr, which resulted in exclusion of Dolly Varden. Terrestrial prey inputs in summer and fall supported 95% of the trophic basis of production of rainbow trout and white-spotted charr, increasing their abundance and biomass (Marcarelli et al. 2020). In turn, during winter and spring these fish depleted nearly all the production of benthic insects, which supported about 75% of the production of these two fish species during these seasons. Overall, this forced Dolly Varden to compete with sculpin for scarce benthic prey in summer, so production of these charr fell to nearly zero. The lack of food resources caused by invasion of rainbow trout and their dominance over Dolly Varden likely explains why the nonnative trout have excluded these charr from various spring-fed streams in Hokkaido (Baxter et al. 2007).

Several parasites also can change the foraging of charr, either indirectly or directly, affecting stream food webs. In southern Honshu, nematomorph (horsehair worm) parasites enhance the terrestrial arthropod subsidy to Kirikuchi charr by manipulating behavior of orthopterans (camel crickets and grasshoppers). The final adult stage of the horsehair

worm causes these large terrestrial insects to jump into streams to reach the reproductive habitat of the nematomorph during mid-August to mid-November, supplying 60% of the annual energy intake of charr in one stream (Fig. 8; Sato et al. 2008b, 2011a) and accounting for the variation in terrestrial subsidies and charr and resident masu salmon diets across nine streams studied (Sato et al. 2011b). In turn, a manipulative field experiment showed that this subsidy reduced red-spotted masu salmon foraging on benthic invertebrates. As a result, invertebrate grazers reduced periphyton by approximately 50% in a trophic cascade, and shredders increased leaf breakdown rate by 30% compared to the treatment where crickets were excluded (Sato et al. 2012). Another parasite, a mouth-attaching copepod (genus *Salmincola*) reduced condition of Dolly Varden in Shiretoko Peninsula streams in Hokkaido (Hasegawa et al. 2022), and could potentially alter food-web interactions by changing charr foraging behavior.

## Anthropogenic effects

A series of detailed studies of white-spotted charr populations isolated in short stream fragments are among the best examples worldwide showing effects of habitat fragmentation on stream fish populations. Coupled with studies on the effects of forestry, hydropower production, roads, stocking hatchery fish, recreational angling, and climate change, there is now a rich literature on effects of human activities on Japanese charr.



**Fig. 8** Influence of horsehair worm (nematomorph) parasites in manipulating behavior of terrestrial orthopterans that jump into streams and are eaten by Kirikuchi charr (*Salvelinus leucomaenis japonicus*) in southern Honshu (modified from Sato et al. 2011a, with permission). Percentages of the annual energy intake of charr made

up by infected orthopterans, other terrestrial invertebrates, and benthic invertebrates are shown. A field experiment showed that this subsidy reduces charr predation on benthic insect shredders and grazers, thereby increasing leaf breakdown rate and reducing periphyton

**Habitat fragmentation.** Many streams throughout Japan are highly fragmented by dams of various heights, most constructed for erosion control and nearly all insurmountable by charr. These can cause extirpation of charr populations isolated above them from genetic deterioration, demographic factors, and stochastic environmental events, as well as overfishing. Effective population size ( $N_e$ ) is less than 50 individuals in many fragmented charr populations (e.g., Sato and Harada 2008; Yamamoto et al. 2016, 2019), which can lead to further genetic diversity loss, inbreeding, and consequently increased risk of extirpation. Three case studies highlight the range of effects.

Extensive studies of small, isolated populations of white-spotted charr in Oshima Peninsula showed increased rates of extirpation above dams, owing to reduced egg production, lower growth rates, and stochastic demographic and environmental factors (Morita et al. 2000, 2009c, 2019; Morita and Yamamoto 2002). Predictions from an early incidence function based on watershed area of extirpations in smaller fragments (Morita and Yamamoto 2002) were confirmed by sampling 15 years later (Morita et al. 2019), and an updated incidence function was nearly identical to the original model. In contrast, a fish ladder installed in one stream allowed recolonization of a fishless fragment by charr and masu salmon.

Comparison of the genetic structure of white-spotted charr populations above and below dams at 23 of these locations over a 15-year interval showed that charr populations above dams had lower genetic diversity (heterozygosity and allelic richness) than those below dams, and in

half the cases genetic diversity and effective population size declined through time (Yamamoto et al. 2019). Populations above dams also had higher developmental instability of morphological characters compared to connected populations (Yamamoto et al. 2013a). The reduced genetic diversity in restricted habitats above dams was primarily owing to founder effects just after fragmentation and random genetic drift. Effective population sizes were less than 50, leading to risks of inbreeding to add to those from stochastic environmental effects such as severe floods and debris flows resulting from typhoons (Sato 2006a) and predicted demographic effects (Morita and Yokota 2002).

In a second case study of Fuji River headwater tributaries in central Honshu, more than 30,000 dams have been constructed, most since 1980. Tsuboi et al. (2010) reported that 356 dams had been constructed in 27 streams they surveyed, a density of 3.8 per km. Native red-spotted masu salmon (Amago) and white-spotted charr (Yamato-iwana) are sympatric in this watershed, but genetically pure charr are found only in small headwater streams above the dams (Tsuboi et al. 2010, 2013b) owing to widespread stocking of nonnative Nikko-iwana. Habitat fragmentation apparently disrupts coexistence of native salmon and charr, because in four of five streams with both species in syntopy one species became extirpated from the 1970s to 2004, and in the intensively studied Sabusawa Stream Amago was extirpated or declined over 4 years in the upper sections (Tsuboi et al. 2010). The two native species were found in only about 20 streams each in the entire watershed, and each occupied only 1–2% of thermally suitable habitat. A Population

Viability Analysis (PVA) based on empirical data for survival, maturity, and fecundity yielded estimates of probability of extirpation in 100 years of 48% for the charr (Tsuboi et al. 2013b). However, a modest increase in adult survival rates reduced this predicted extirpation probability to only 5.5%, which could be achieved by saving only two mature female charr per year from angling mortality in the longest fragments of Sabusawa Stream that measured 250–400 m between dams.

A third case study in the Totsu River headwaters on the Kii Peninsula in south-central Honshu showed that endangered Kirikuchi charr (Sato 2007) were lost from most of their range owing to habitat destruction, overharvest, and hybridization with nonnative Nikko-iwana and Ezo-iwana. Kirikuchi charr are genetically distinct from other subspecies and forms. In addition, two genetically pure populations only 40 km apart in reaches isolated above natural waterfalls and erosion-control dams are clearly different genetically, potentially owing to genetic drift during long isolation, founder effects, or invasion by different anadromous populations (Sato et al. 2010; Yamamoto et al. 2023). Effective population sizes were low, ranging only 38–68 and 55–158 for the two populations based on a stochastic individual-based PVA model. An estimated 20–50% of their genetic variation will be lost over 200 years, reducing it far below the 90–95% heterozygosity needed for sustained population viability (Sato and Harada 2008). The incidence of morphological deformities was high (3–17% over 3 years), and annual survival rates were about half those of intact fish (Sato 2006b; see also Morita and Yamamoto 2000, Morita et al. 2009c, Yamamoto et al. 2013a). Sato et al. (2010) proposed that because fish in each stream originated from one population, pure fish could be translocated among isolated reaches within each stream to increase genetic diversity.

*Land and water uses.* Forestry, hydropower production, and road construction also reduce charr populations by increasing road density and erosion control dams, and reducing flows, all of which degrade habitat. Forestry plantations are common in Japan, and forestry activities can increase the number of erosion control dams and road density in the riparian zone, which reduces canopy cover. In streams of Shiretoko Peninsula, one of the most undisturbed regions in Japan, plantations led to higher stream temperatures and lower biomass of periphyton and Dolly Varden (Kishi et al. 2004). Streams on the peninsula with Dolly Varden have been fragmented by 238 dams without fish ladders. Streams with more dams had higher temperatures, more shallow habitats with fine sediment, and fewer Dolly Varden than reference streams with few or no dams (Kishi and Maekawa 2009). In contrast, in southwestern Japan where native vegetation is deciduous broadleaved forest, plantations of coniferous cedar and cypress exclude most light from smaller streams year-round. This leads to little periphyton

production during the leaf-free season (fall through spring) compared to streams draining deciduous forests (M. Inoue, pers. observation). Furthermore, terrestrial arthropod input from conifer plantations is much lower than from natural deciduous forests, resulting in lower fish abundance in streams draining conifer plantation (Inoue et al. 2013).

Depletion of flow for hydropower production, and roads constructed to access the dams also degrade charr habitats. In a central Japan stream, depletion of 83% of the flow from a 1-km segment during about 9 months per year for hydropower production resulted in a 33% decrease in density of age-1 and older white-spotted charr, and a 42% reduction in biomass (Nakamura 2013). A 4-yr mark-recapture study revealed that more than half the charr recaptured had remained in the same pools in a 3-km free-flowing section upstream compared to only about 30–40% of those in the section where flow was depleted (Nakamura et al. 2002). Throughout this segment, white-spotted charr declined to low levels after rocks and sand were dumped into the channel during road construction, which filled pools and homogenized habitat, although abundance rebounded rapidly after angling was prohibited (Nakamura et al. 1994, 2001).

*Stocking hatchery charr.* Stocked charr are larger than wild fish and can dominate them, and likely reduce their survival, but the stocked charr themselves survive poorly. Both in enclosures and two natural headwater streams of central Japan, white-spotted charr that were wild or semi-wild (stocked in the stream as eyed eggs) dominated genetically similar hatchery charr when fish were of equal length. However, the hatchery charr stocked in streams are 14% larger than the semi-wild fish, and dominated wild individuals in enclosures when the hatchery charr were more than 11% larger (Nakamura and Doi 2014). Moreover, the apparent survival rate of hybrids between wild native males and domesticated females was 2.5 times that of domesticated charr in five isolated sections of a central Honshu mountain watershed (Yamashita et al. 2020). This represents a worst-case scenario, where larger hatchery-reared charr dominate less domesticated semi-wild fish and yet survive poorly themselves (Weber and Fausch 2003).

*Response to recreational angling.* Both charr species are susceptible to traditional Japanese fishing in mountain streams, so regulations are required to sustain populations. Dolly Varden and white-spotted charr, along with resident masu salmon, provide popular sport fisheries in Japan, especially for anglers that practice traditional “Keiryu” (mountain stream) fishing using live benthic invertebrates as bait. White-spotted charr are more vulnerable to angling than sympatric Dolly Varden, probably because white-spotted charr orient more toward the water column and water surface whereas Dolly Varden feed more frequently from the benthos when syntopic (Tsuboi et al. 2021).

Larger charr are more vulnerable to angling than smaller ones, and fish caught once are more likely to be caught again (Tsuboi and Morita 2004; Tsuboi et al. 2021). A moderate effort of bait fishing (0.5 min • m<sup>-2</sup> of pool area) captured a third or more of charr in Hokkaido mountain streams, on average, and catchability increased as density decreased (Tsuboi et al. 2021; Hasegawa and Koizumi 2023). Hence, populations of charr in small streams are prone to collapse with unregulated bait fishing, so regulations on harvest will be required to sustain sport fisheries.

Miyabe charr in Lake Shikaribetsu are a popular sport fish, but by 2000 had declined owing to overharvest. Regulations that restrict fishing to about half the lake, restrict gear, and allow catch-and-release angling during only 50 days per year have increased abundance more than seven times and nearly tripled catch rates (Yoshiyama et al. 2017, 2023). Anglers attracted from throughout Japan provide a strong economic boost to the local economy (Yoshiyama et al. 2018).

**Climate change.** Charr are stenothermal fishes, highly susceptible to changes in water temperature. In an early analysis based on simple models of climate warming effects on groundwater temperature, Nakano et al. (1996) predicted that an increase of 2 °C in air temperature would lead to loss of more than 65% of habitat for Dolly Varden and 20% for white-spotted charr in the Japanese archipelago. Moreover, their analysis showed that as charr retreat to higher elevations they become restricted to shorter habitat fragments in headwater streams, further increasing risk of extirpation. Empirical data show that stream drying can also eliminate charr, such as a 2014 drought in central Japan that killed 5% of white-spotted charr and 9% of red-spotted masu salmon in one headwater tributary (Kishi et al. 2020).

## Conservation and restoration of charr

As in most countries, management of charr in Japan occurs on a template of habitat degradation from past activities, ongoing stocking of hatchery fish, invasions of nonnative species, and growing influences of climate change. It also must operate within constraints imposed by local traditions and a complex mixture of jurisdictions over land, water, and fish populations. Overlain on a long history of intensive land and water use, especially in Honshu, various management actions have been used to conserve native charr, and new methods are being proposed.

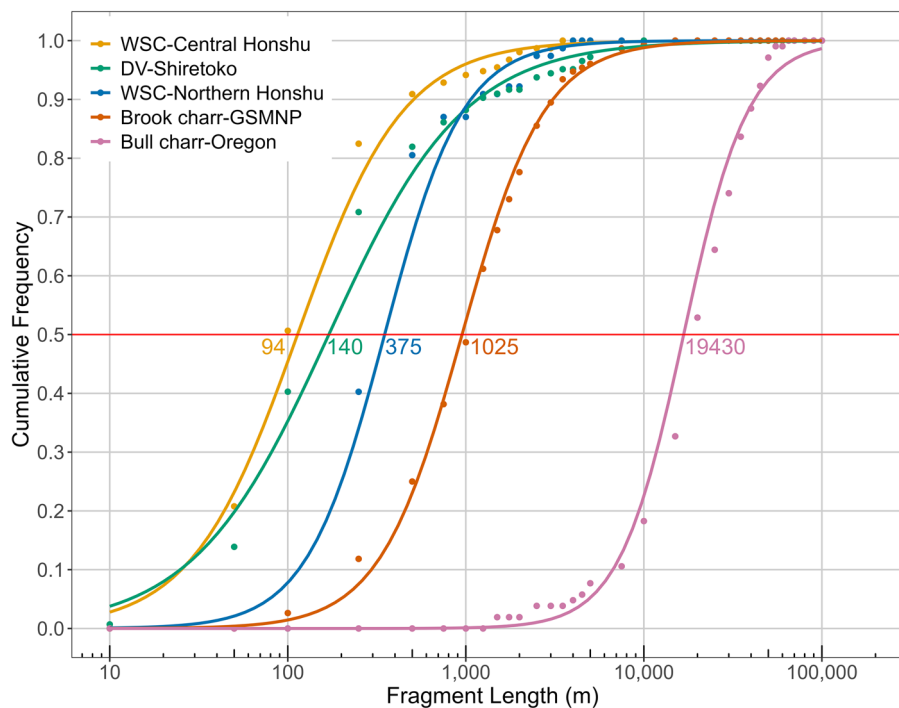
**Status of charr in Japan.** A few rare forms of charr in Japan are considered vulnerable to extinction at the international or national level, and others are listed as such in certain prefectures. The seven remaining populations of Kirikuchi charr are the southernmost in the genus *Salvelinus*, and are listed as Endangered by the International Union

for Conservation of Nature (Sato 2007) and on the Japan Red List (Ministry of the Environment of Japan 2020). The lineage of white-spotted charr called Gogi (*Salvelinus leucomaenis imbricus*), all southern Asian Dolly Varden, and Miyabe charr in Lake Shikaribetsu are listed as Vulnerable on the Japan Red List, indicating an increasing risk of extinction. Most prefectures with native white-spotted charr list their subspecies on the regional Red List as at some level of extinction risk (*S. l. pluvius* are listed in 15 prefectures, and *S. l. japonicus* and *S. l. imbricus* are listed in 5 prefectures each; Japan Red Data Retrieval System 2023). However, charr populations are often not protected in national parks in Japan, where only scenery is protected (Nakamura et al. 1994), and there is no systematic accounting of protected charr populations in Japan.

**Management to conserve and restore native charr.** Four key threats affecting many native charr populations in Japan are habitat fragmentation by erosion-control dams which causes loss of genetic diversity and increased risk of extirpation, introgression from stocking hatchery charr, invasions by nonnative salmonids, and overfishing (Morita 2019). Adding fishways to dams can be effective in restoring upstream migration (Morita et al. 2019) and gene flow and genetic diversity (Yamamoto et al. 2006b). Fishways have been constructed on some dams in various watersheds, including portable fishways and some handmade by citizens (Machida et al. 2019; Sato et al. 2021). Narrow slits have been cut in other dams to allow fish passage (Morita 2019). Nevertheless, the more than 95,000 dams constructed throughout Japan resulted in stream fragments with medians of only 94 and 375 m in two Honshu basins (Fig. 9; Nakamura 2001; Endou et al. 2006), and only 140 m even in relatively undisturbed watersheds of Shiretoko Peninsula (Kishi and Maekawa 2009; but see Nakamura and Komiyama 2010). Nevertheless, breaching barriers must be considered carefully, because in many watersheds specific dams prevent invasions from downstream by hybridized charr or nonnative salmonids, a classic invasion-isolation tradeoff (Fausch et al. 2009).

Artificial spawning channels, and adding gravel to natural channels, are another form of habitat restoration, and have been successful in attracting white-spotted charr to construct redds, and spawn and incubate eggs in several central Honshu mountain streams (Nakamura 1999b; Kishi and Tokuhara 2017). Many anglers participated in creating these spawning sites, which helps engage local stakeholders in conserving wild fish.

In Honshu, hatchery white-spotted charr (primarily Nikko-iwana) have been widely stocked by anglers and fisheries cooperatives, causing introgression with other native forms (e.g., Sato et al. 2010). In Yamanashi Prefecture, anglers are prohibited from stocking salmonids, and in Sabusawa Stream Nikko-iwana were eradicated to help conserve



**Fig. 9** Cumulative frequency distributions of stream habitat fragment lengths (m) occupied by four native charr in Japan and North America. Points for 34 frequency bins were calculated from the empirical data and used to fit logistic curves. An empirical median is shown for each curve. Data for each species and region are from the following sources: white-spotted charr [WSC; *Salvelinus leucomaenis*] in central Honshu (Endou et al. 2006; range: 16–3,245 m,  $N=154$ ), Dolly Varden [DV; *S. curilus*] on Shiretoko Peninsula (Kishi and

Maekawa 2009; range: 10–8,130 m,  $N=144$ ), WSC in northern Honshu (Nakamura 2001; range: 125–3,750 m,  $N=77$ ), southern Appalachian brook charr (*S. fontinalis*; M. Kulp, National Park Service, Gatlinburg, Tennessee, USA, written communication of GIS layers, 25 April 2023; range: 65–11,758 m,  $N=152$ ), and bull charr (*S. confluentus*) in Oregon watersheds (Chelgren et al. 2023; range: 1,400–64,322 m,  $N=104$ ). Fragment lengths from Nakamura (2001) were interpolated from a histogram and so are approximate

native Yamato-iwana. In contrast, for pure populations isolated in short stream fragments genetic restoration (Whiteley et al. 2015) is possible, as demonstrated by translocating white-spotted charr from below dams into isolated populations above barriers in two Hokkaido streams (Yamamoto et al. 2006b). Genetic diversity was restored to the same levels as pure fish below barriers by rapid introgression of genes into the isolated populations.

Nonnative rainbow and brown trout are widespread in Japan and cannot be eradicated from most habitats, but regulations to prevent stocking them are rare. Rainbow trout are officially stocked in 31 of 47 prefectures throughout Japan, and regulations prohibit their stocking only in Saga prefecture in Kyushu (Kitano 2004). Regulations prevent stocking brown trout and brook charr only in Hokkaido and Shiga prefecture around Lake Biwa, but no regulations prevent moving those stocked previously. Artificial ponds for angling are common sources of salmonid invasions because nonnative species and hybrids are widely stocked and can easily escape. Smoltified rainbow trout and anadromous brown trout have been reported in Japan (Hasegawa 2020), which could create another vector causing widespread invasions

into new rivers. Direct eradication is difficult but might be feasible in small streams (but see Meyer et al. 2006), or by targeting spawning or winter aggregations (Kitano 2004; Koizumi et al. 2017; Furusawa et al. 2022). In cases where an invasive species is already widespread, another option could be managing physical and biological factors that modify impacts of invaders, such as modifying temperature and flow regimes to hamper nonnative salmonids (Dunham et al. 2020).

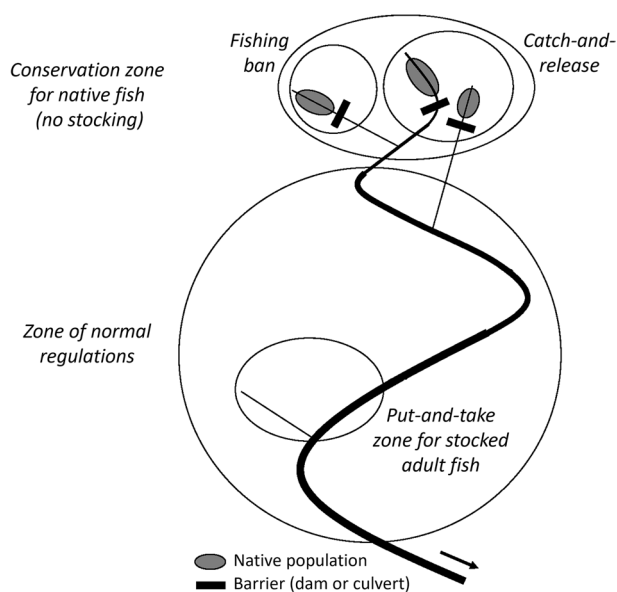
Fishing has long been prohibited in some small headwater tributaries in Japan (termed “Tanezawa”), primarily for rare forms of white-spotted charr such as Kirikuchi, Gogi, and “Nagaremon”, a unique morphotype (Nakamura et al. 1994; Kikko et al. 2022). Spatially arranged fisheries regulations can be a highly successful management option for addressing overfishing and conserving native salmonids. For example, in the Zako River in central Honshu, high catch rates of native salmonids have been sustained in the mainstem by preventing harvest in a group of small tributaries that apparently supply recruits (Yamamoto et al. 2013b), further supporting the importance of tributary habitats (Tsuboi et al. 2022). Nakamura (2008; Nakamura et al. 2012) proposed



a general plan for conserving native charr and salmon in watersheds by creating three zones (Fig. 10): 1) selected headwaters closed to fishing or designated catch-and-release, and not stocked with hatchery charr, 2) middle segments under normal angling regulations, and 3) downstream segments where domesticated fish are stocked as eggs, fry, or adults for angling. Some fisheries cooperatives are now implementing such plans.

## Considering a future for charr in Japan

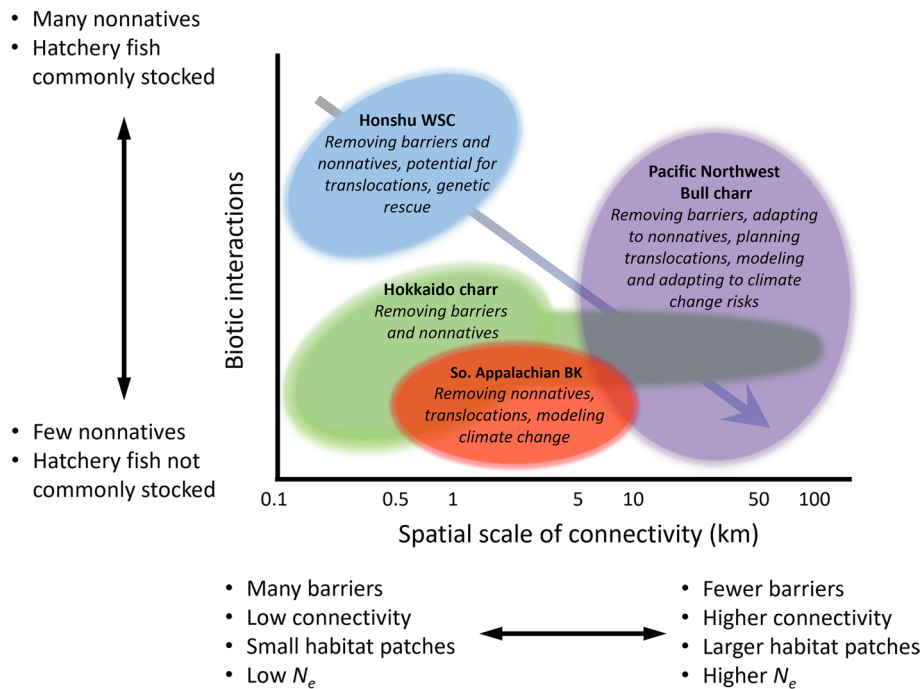
Diligent research by Japanese and some foreign fish biologists has generated a large body of information on the charr of Japan since the 1988 symposium, yet progress to conserve the diversity of forms and their habitats has been modest. Some of this is owing to the declining human population and interest in charr in rural areas of Japan, coupled with reduced numbers of fisheries staff to conduct research or management. In addition, as in many regions it takes time for research to influence management, and some current actions conflict with conservation of native charr. Here we compare the management of charr in Japan to two charr species in North America, and consider what steps and new information might advance the conservation of Japanese charr.



**Fig. 10** A general scheme for managing and conserving native charr in Japan streams (modified from Nakamura 2008, with permission; Nakamura et al. 2012). Headwaters are designated as conservation zones for pure native charr and salmon, with some tributaries protected by fishing bans or catch-and-release regulations. Downstream segments are under normal angling regulations, and some zones are designated for put-and-take angling of stocked adult fish

Bull charr (*Salvelinus confluentus*) of the Pacific Northwest and brook charr of the southern Appalachian Mountains represent ends of a spectrum for charr conservation in North America. Bull charr are listed as a Threatened species under the U.S. Endangered Species Act, and the approximately 600 populations in the conterminous USA typically occupy drainages from less than 10 km to over 200 km in spatial extent (i.e., length of the longest continuous river segment, Figs. 9, 11; U.S. Fish and Wildlife Service 2015). The native range of bull charr includes the Pacific coast from southern Oregon to southeast Alaska, and inland to the Yukon, Northwest Territories, Alberta, Montana, Idaho, and Nevada (Dunham et al. 2008). In the conterminous USA populations are arranged in 6 management units and 109 core areas (subwatersheds) for conservation and recovery, based on substantial genetic diversity among populations and relatively low diversity and low effective population sizes within them (e.g., 76% of U.S. populations sampled had  $N_e < 50$ ; Ardren et al. 2011). No hatchery bull charr are stocked for angling but some populations are invaded by brook charr causing risk of introgression, especially by sneaking males (Kitano et al. 1994; Kanda et al. 2002). Many populations have been inventoried and evaluated for purity (U.S. Fish and Wildlife Service 2015). Their threatened status has fostered active management for more than 25 years, including removing barriers to increase connectivity (Brenkman et al. 2019), removing nonnative brook charr (Buktenica et al. 2013), translocating pure fish into watersheds where they were lost (Hayes and Banish 2017; Benjamin et al. 2019), and modeling climate change risks (Falke et al. 2015; Isaak and Young 2023). Recent research using decision support tools to analyze tradeoffs showed that the greatest benefits will be from targeted translocations coupled with enhancing diverse life histories and spawning and rearing habitat to allow adapting to rather than removing nonnative brook charr (Brignon et al. 2018; Dunham et al. 2022). Nevertheless, removing brook charr can be effective in some cases (Buktenica et al. 2013).

Brook charr are widespread throughout eastern North America, occurring from Labrador, Canada inland to Minnesota, USA and south along the Adirondack and Appalachian mountains to northern Georgia. Similar to white-spotted charr, the phylogeography of brook charr is complex, and populations in the southern Appalachian Mountains are highly divergent from those to the north (Kazyak et al. 2022). They are also highly differentiated from each other, apparently owing to diversity lost through genetic drift in the small headwater stream fragments they inhabit. Introductions of nonnative rainbow trout and brown trout began about 140 years ago, along with stocking hatchery brook charr of northern origin, thereby eliminating pure native charr from most segments downstream from barriers (Hudy et al. 2008). As a result, non-introgressed southern Appalachian brook



**Fig. 11** Comparison of typical domains of spatial connectivity and biotic interactions for bull charr (*Salvelinus confluentus*) and southern Appalachian brook charr (BK; *S. fontinalis*) in North America and white-spotted charr (WSC; *S. leucomaenis*) and Dolly Varden (*S. curilus*) in Japan. Genetically pure populations number about 600 for bull charr and at least 500 for southern Appalachian brook charr, but most charr populations in Japan have not been inventoried. Current and planned management actions are described for each species. A conservation goal represented by the arrow is to move populations towards the lower right, by restoring habitats with greater connectivity and fewer biotic interactions with nonnative species and forms

charr occur in short stream segments about 0.2–10 km in extent above natural waterfalls or barriers that protect them from nonnative trout invasions (Figs. 9, 11). Like charr in Japan, effective population sizes are small, 60% of them less than 30. Many populations have been inventoried and undergone genetic analysis for purity (Kazyak et al. 2018; Pregler et al. 2018), of which at least 500 represent native lineages (M. Kulp and J. Rash, pers. communication). Active management to remove nonnative trout and translocate pure southern brook charr into headwater enclaves has been ongoing for 45 years (Larson and Moore 1985).

By contrast to these charr in North America, most populations of Dolly Varden and white-spotted charr in Japan are isolated in short stream fragments with medians of about 100–375 m and maxima of 3 to 8 km in total extent (Fig. 9), although white-spotted charr in Hokkaido occupy some connected rivers that are much longer (Fig. 11). Most white-spotted charr populations in Honshu have been subjected to introgressive hybridization from nonnative lineages stocked for angling, or competition with masu salmon stocked beyond their native ranges, and some are threatened by invasions of nonnative rainbow trout and brown trout (Morita 2019; Hasegawa 2020). Populations have been inventoried in only a few regions, and except for Kirikuchi charr (Sato et al. 2010) few populations have been tested for genetic purity.

However, in recent years the genetic characteristics of wild charr populations are becoming better understood, and new nation-wide databases of genetic characteristics are being created (e.g., Yamamoto et al. 2004, 2006a, 2014, 2023). Stocking by local fisheries cooperatives and by some anglers is ongoing, but some cooperatives are now focusing on sustaining endemic charr lineages and their local adaptations. Recent efforts are beginning to increase connectivity for pure populations by removing barriers or installing fishways while retaining downstream barriers that prevent invasions by nonnative forms, and a modest number of translocations for reintroduction or genetic restoration above barriers have been accomplished or are planned. Angling regulations are set by local fisheries cooperatives, which typically close fishing from October through February and set minimum size limits, but bag limits are either unrestricted or limited only to large numbers (e.g., 20 stocked fish per day; Rahel and Taniguchi 2019). Catch-and-release regulations are relatively uncommon in Japan, but prohibiting fishing in selected tributaries has been found effective at increasing adult fish densities (Yamashita et al. 2023).

Given this, what options are available for sustaining lineages of native charr in Japan into the future? For regions where pure native charr are less common, such as throughout most of Honshu, a first step is to inventory charr populations

and their genetic purity, as well as the barriers that isolate them in each drainage basin so that management can be prioritized (Fig. 12). At present, in only two prefectures have comprehensive surveys been completed (Tochigi and Yamana-shi) and an eDNA survey is planned in one of the basins as a follow up after two decades. However, local anglers and others may have extensive knowledge, so there may be opportunities to engage these stakeholders in innovative ways to collect or provide data on species distribution and abundance (e.g., Zhou et al. 2022; Chelgren et al. 2023).

A second step is to identify appropriate groups of populations for management, often grouped into conservation units that are substantially reproductively isolated and represent important evolutionary legacies of the species (Waples 1995). The phylogeography of white-spotted charr indicated five such evolutionarily significant units (Fig. 2), and revealed that within each one, drainage basins are the appropriate units of conservation owing to substantial genetic diversity among them (Yamamoto et al. 2023). A similar conclusion was reached for bull charr (U.S. Fish and Wildlife Service 2015) and southern Appalachian brook charr (Kazyak et al. 2022). Though less studied, Dolly Varden also vary across Hokkaido (Yamamoto et al. 2014, 2021), including the unique Miyabe charr, and in most regions have been long isolated in headwater segments, so drainage basins are also the appropriate unit for their conservation. Once conservation units are designated, a key step will be to educate members of fisheries cooperatives, local anglers, and the public about the importance of this genetic diversity and the adaptive life-history variation it supports, and to involve all stakeholders in setting guidelines or regulations to prevent introgression of the remaining pure lineages from stocking hatchery charr.

A third step is to consider options for managing populations within conservation units, which must necessarily consider key factors of the spatial scale of connectivity and biotic interactions (Figs. 11, 12). For example, when stocking has been widespread and invasions are prevalent, as for white-spotted charr in Honshu and southern Appalachian brook charr, downstream barriers that isolate these pure charr populations must remain in place to protect them from nonnative salmonids. Under this scenario, management options include removing nonnatives and introgressed forms, optimizing the number, size, and distribution of these habitat fragments and their tributaries, and restoring habitat quality (Fausch et al. 2009). In contrast, downstream from barriers and in larger watersheds already invaded by nonnative brown trout or rainbow trout where controlling them is not feasible, their impacts might be modified by enhancing the expression of charr life history diversity (e.g., fluvial, adfluvial, and partial-migration life histories) and managing the physical environment to favor the native charr (e.g., restoring coldwater refuges, managing flow regimes), as has

Step 1. Inventory charr populations, genetic purity, and barriers

Step 2. Select groups of populations for conservation based on evolutionarily significant units and core areas

Step 3. Select options for management to fit spatial scales of connectivity and important biotic interactions

Step 4. Engage stakeholders and educate youth about evolutionary legacies of native charr

Goal: Encourage an ethic that is culturally transmitted to future generations

**Fig. 12** Suggested steps for conservation and management to enhance the future of native charr in Japan

been proposed for bull charr (Dunham et al. 2020, 2022). This life-history diversity will be increasingly important for reducing risks of extirpation in a changing environment, as well as providing many other benefits to ecosystems.

The fourth step, and most important, is the early and extensive engagement of stakeholders in the management process, and education of children and youth about the importance of evolutionary legacies of their local biota like native charr. Illegal stocking of nonnative charr or trout by anglers or others can reverse expensive and time-consuming management actions like those described above, so it is critical that this step be taken early and continued throughout (Bamzai-Dodson et al. 2021; Brignon et al. 2023). For example, engaging interested and knowledgeable anglers in inventorying pure native charr populations in their local basin will engender pride in, and knowledge about these irreplaceable ancient evolutionary legacies. Likewise, fisheries cooperatives might become involved in culturing rare lineages for translocation to suitable habitats, with the goal of eventually developing a catch-and-release fishery to allow anglers to see and hold the charr that are native to their home waters. This could engender an ethic for conserving native charr, allowing it to evolve in the minds of those in the community who are interested (Leopold 1949) and be culturally transmitted to future generations.

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## Declarations

**Conflicts of interest** The authors have no relevant financial or non-financial interests to disclose.

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