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Long-term shifts in the growth and maturation size of Miyabe charr *Salvelinus malma miyabei*

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Abstract

Overfishing can affect life-history traits, resulting in population collapse, and oftentimes a decrease in length-at-age and maturation size in fish populations. However, little is known about these traits recovery mechanisms and time scales in exploited wild populations. In this study, we documented long-term shifts in growth and mature size in Miyabe charr *Salvelinus malma miyabei* associated with recreational lake fishing history in Lake Shikaribetsu for approximately 80 years. Downsizing in the charr was observed when charr population was collapsed due to intensive recreational fishing; however, moratoriums and introduction of fishing regulations, especially catch-and-release implementation, would help to recover population size, length-at-age and mature fish size over the next 10–30 years. This study provides important insight into the biological changes and required recovery time scales of a heavily harvested population, in support of management and conservation strategies.

Keywords: life-history trait shifts, Miyabe charr, overfishing, recreational fishing pressure, recreational fishing regulations

Introduction

Shifts in the life-history traits of some fish populations, including age and size at maturity (Heino et al. 2002; Grift et al. 2003), reproductive effort (Yoneda and Wright 2004) and growth rate (Handford et al. 1977; Thomas and Eckmann 2007), have been reported to be caused by human activities such as fishing. These reproductive parameters are particularly critical for the estimation of stock reproductive capacity, and subsequently the determination of acceptable harvest levels (Tenbrink and Spencer 2013). Thus, understanding the long-term trends in these life-history traits is important for evaluating fish population dynamics and stability, and for supporting effective fishery management strategies (Kendall and Quinn 2011).

Growth is an important life-history trait that is affected by various factors such as physical environmental changes, life-history options, competition and density, integrating many dimensions of environmental influence with physiological function (Begon et al. 2006). Fishing activity can potentially affect traits related to growth indirectly, for example, by decreasing fish population to allow an increase in prey abundance (Enberg et al. 2012). Growth is also influenced by intrinsic factors like growth capacity (i.e. the ability of fish to transform energy intake into body mass) and reproductive investment (i.e. the ratio of gonad mass to somatic mass) (Heino et al. 2008; Nusslé et al. 2009). Reallocation of resources from growth capacity to reproductive investment is likely due to selection against fast growers (Heino et al. 2008; Gadgil and Bossert 1970), thus changes in growth can be linked to changes in these factors (Nusslé et al. 2009).

Both intensive-size selection and density-dependent effects can potentially influence trends in size and maturity schedule in exploited stocks (Beverton and Holt 1957; Ricker 1981), however, in completely different ways. Empirical and modelling studies suggest that intensive-size selection favours individuals that grow slower, mature at smaller sizes and increase their reproductive investment (Gadgil and Bossert 1970; Conover and Munch 2002; Enberg et al. 2009; Sharpe and Hendry 2009). A recent study showed recreational angling also selects for life-history traits that promote downsizing of adults in coastal marine fish (Alós et al. 2014). In salmonid fish, Hard et al. (2008) reviewed the cases of reduction in maturation size caused by overfishing (see also exceptional case in Morita and Fukuwaka (2007)). In contrast, a negative relationship between fish length and population size by density-dependent effects has been documented including salmonid species (Kaeriyama 1998; Jenkins et al. 1999).

Miyabe charr *Salvelinus malma miyabei* is a four-to-six-year generation time endemic subspecies of Dolly Varden *S. malma* that inhabits Lake Shikaribetsu and its inlet streams in Hokkaido, Japan (Kawanabe and Mizuno 1989). Miyabe charr is a popular recreational fishing target in Lake Shikaribetsu, and its fishing history can be divided into seven periods corresponding to changes in fishing styles and regulations (Table 1). Historically Miyabe charr was commercially exploited (period I, by 1959), but it gradually shifted to become a recreational target. As the popularity of recreational fishing surged, the lake population declined because of overfishing without fishing regulations in 1960–68 (period II), which resulted in an entire fishery closure for seven years (period III, during 1969–75). It was said that if fishing had continued to be unregulated, the lake population would have completely collapsed (Shikaoi Town 1994). Even after the first lake moratorium, fishing pressure was still high under regulations that allowed an estimated two-thirds or more of the charr population to be captured every year during 1976–80 (period IV) (Hokkaido Fish Hatchery 1980, 1981), resulting in population collapse (Hirata 1993). As a result, the lake was closed again for 11 years from 1981 to 1992 (period V). Although it was re-opened in 1993 with fishing regulations including a bag-limit, the population remained at a low level during 1993–2004 (period VI) (Hokkaido Fish Hatchery 1997, 1998, 1999, 2000, 2001); however, stricter regulations and a catch-and-release rule introduction helped the lake population to recover (period VII, from 2005) (Yoshiyama et al. 2017).

To date, a number of studies have documented long-term shifts in life-history traits due to fishing selectivity (Olsen et al. 2004), but reports on life-trait recovery from heavy exploitation is limited (Fukuwaka and Morita 2008; Conover et al. 2009; Feiner et al. 2015). In the current study, we re-evaluated growth and maturation size of Miyabe charr and compared the results with historical data from the last 80 years. This study aims to evaluate shifts in growth and mature size of Miyabe charr over time and to investigate life-history trait changes associated with fishing activities in Lake Shikaribetsu to support future management and conservation strategies.

Materials and methods

Study site

Lake Shikaribetsu is a small, enclosed, oligotrophic lake located in the middle of Hokkaido, Japan (43.27˚N, 143.12˚E, area of 3.6 km^2, maximum depth of 108 m). Originally Miyabe charr was the only fish inhabiting the lake; however, various fish species have been introduced, mainly during the 1950s to 1970s (Maekawa 1977). Most notably the introductions were rainbow trout *Oncorhynchus mykiss* in 1929 (Shikaoi Town 1994), Japanese smelt *Hypomesus nipponensis* in 1966 (Shikaoi Town 1994) and masu salmon *Oncorhynchus masou* (first observation in 1981, Hokkaido Fish Hatchery 1982), which thought to have big ecological impacts on the Miyabe charr (Maekawa 1977; Shikaoi Town 1994; Yoshiyama et al. 2017).

The recreational fishing is currently managed by the 'Great Fishing in Lake Shikaribetsu' program provided by the non-profit organization Hokkaido Tourism Union. Detailed fishing regulations are summarized by Yoshiyama et al. (2017) and is also available on the website http://www.shikaribetsu.com/c/en/.

Description of previously published data

Growth and maturation size of Miyabe charr has been documented over the years (Table 2a; 2b). Previous studies by Kubo (1967) and Maekawa (1978) analysed growth using mixed-sex mean length-at-age. The pooled-sex age-length composition data was provided on Hokkaido Fish Hatchery (1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003), which enabled us to evaluate growth during 1993–2001. In terms of maturation size, data on the length of mature fish was available from the listed references in Table 2b. To compare the mature charr size over time, we used data only for lake-run charr captured from inlet streams, considering its complicated life history (Yoshiyama et al. 2017). We assumed that all spawning-migrated lake-run charr captured in the inlet streams were mature in case maturity data was unavailable (i.e. Inukai and Sato 1943; Hokkaido Fish Hatchery 1978, 1994).

Sampling

Miyabe charr were sampled in Lake Shikaribetsu as well as in an inlet stream, the Yambetsu River (Fig. 1). Lake samples (n = 89) were collected by angling in July and September 2015, and river samples (n = 19) were sampled by a casting net (mesh size 16 mm) under a special permission from the Hokkaido government in September 2015. Fish were frozen, brought back to the laboratory, and sex, fork length (FL, mm) and total length (TL, mm) were measured. The paired sagittal otoliths were removed, cleaned with water and stored dry in plastic cases.

Age determination

In the previous studies, ages were determined using otoliths or scales (Table 2a). In the current study, otoliths were used because its usage was suggested in ≥ 6+ Dolly Varden individuals (Stolarski and Sutton 2013). For consistent analysis, we sanded a longitudinal side of otoliths with waterproof 1000-grade sandpaper until it was approximately 400 μm without mounting like Maekawa (1978) did with a whetstone (Maekawa K, pers. comm., 2015). The otoliths were observed under a binocular microscope at 40x magnification with transmitted or reflected light (Fig. 2), and the number of opaque bands were counted using photographs taken with a MacromaX camera (GOKO camera, Kanagawa, Japan) connected to the microscope.

To remove potential bias, the band counts were conducted by three readers without access to the counts of others and fish size. Counts were then compared and accepted if at least two readers got the same counts. In case the counts differed, we assigned a consensus count based on discussion or ultimately excluded it from the analysis if a consensus could not be reached. Ages were finally determined from the number of opaque bands and the capture date assuming the birth date as January 1st.

Growth curve estimations and growth comparisons with previously published data

For our 2015 data, von Bertalanffy growth curves (Eq. 1) were fitted to the sex-stratified age-length data set using the R package FSA (Ogle 2017), and differences in growth curve parameters between sexes were tested by the *F*-test.

$$L_t = L_\infty\left(1 - \exp^{-k(t-t_0)}\right) \qquad \text{(Eq. 1)}$$

where L_∞, k and t_0 are the parameters of von Bertalanffy growth curve.

Growth comparisons with previously published data were made using mixed-sex data. We combined the pooled-sex age-length composition data from Hokkaido Fish Hatchery (1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003), and estimated von Bertalanffy growth curve in 1993–2001 using the total of 3,219 specimens (Table 2a). For 2015 samples, another von Bertalanffy growth curve was estimated using pooled-sex data set for comparisons. These growth curves were compared with the previously published mean length-at-age data in 1955–66 (Kubo 1967) and 1970–74 (Maekawa 1978). Note that fish length in Kubo (1967) was calibrated to FL using the following linear regression equation (Eq. 2) obtained from our data ($R^2 = 0.998$, $n = 107$, 125–355 mm in FL range) since only TL data was provided.

$$FL\ (\text{mm}) = 1.00 \times TL\ (\text{mm}) - 5.00 \qquad \text{(Eq. 2)}$$

Also mean FL (mm) by age and 95% confidence intervals were calculated in each 1993–2001 and 2015 data for support of the growth comparisons with previously published data.

Mature charr size comparisons with previously published data

For 2015 data, both sex-specific and pooled-sex mean FL were calculated using river samples. To compare average pooled-sex mature charr size over time, Tukey-Kramer Honestly Significant Difference (HSD) test was implemented in R among pairs of the following years ($p < 0.05$); 1930, 1960–61, 1970–74, 1983 and 2015 (refer to Table 2b). Note that only those of data sets were available for the statistical comparisons.

Results

Ages were identified for 102 specimens out of 108 fish collected in 2015. The estimated von Bertalanffy growth curves are illustrated in Fig. 3 and its parameters in male and female were following;

Male: $L_t = 356.4\left(1 - \exp^{-0.408(t-1.126)}\right)$, ($n$ = 51)

Female: $L_t = 330.9\left(1 - \exp^{-0.477(t-1.511)}\right)$, ($n$ = 51)

Von Bertalanffy parameters were significantly different between sexes (F = 2.730, d.f. = 3, p = 0.048); males grew larger than females.

Von Bertalanffy parameters in 1993–2001 and 2015 were following;

1993–2001 pooled-sex: $L_t = 365.8\left(1 - \exp^{-0.321(t-0.475)}\right)$, ($n$ = 3,219)

2015 pooled-sex: $L_t = 348.7\left(1 - \exp^{-0.411(t-1.221)}\right)$, ($n$ = 102)

These von Bertalanffy growth curves and previously published mean length-at-age data were illustrated altogether in Fig. 4, showing that the length-at-age in 1970–74 (period III) clearly plateaued at a smaller size comparing with other years

(Table 3). Note that downsizing in the charr in period III was not affected by ongoing fishing activities, because fishing was already closed due to the overfishing in period II (Table 1). The length-at-age increased in 1993–2001 (period VI) when major fishing regulations were introduced after the second lake closure. Currently, stricter regulations are applied, and population has recovered (Table 1), while the shape of the growth curves remained similar through 1993–2001 (period VI) to 2015 (period VII).

Average mature fish size and its FL-range (shown in parentheses) in 2015 were 311 (295–335) mm in male (n = 9) and 298 (264–351) mm in female (n = 10). The shift in mean and range of mature charr size are illustrated in Fig. 5, indicating that mature fish size increased in 1992 (period V) and 2015 (period VII) after lake fishing pressure decreased (Table 1). The pooled-sex average mature fish size was 304 mm (n = 19) in 2015 (period VII), which was significantly larger than any of other years (range 215–242 mm in other four years, all $p < 0.001$).

Discussion

The current study documented life-history trait shifts in Miyabe charr linking to the fishing history in Lake Shikaribetsu over the past 80 years. Specifically, length-at-age and mature charr size increased after fishing pressure was greatly reduced (Table 1; Fig. 4; Fig. 5). After recreational fishing popularity surged in the early 1960s, overfishing and subsequent moratorium introductions were repeated without proper regulations and managements during 1960–92 (period II–V), which led to population collapse (Hirata 1993). In 1993, the lake was re-opened under new fishing regulations designed to reduce fishing pressure (period VI). By the end of this period, growth has greatly improved compared to 1970–74 (periods III). Since 2005 (period VII), stricter regulations have been introduced, including the catch-and-release of all charr, contributing to a three to seven-fold increase in the charr population size compared to period VI (Yoshiyama T, unpubl. data, 2015; Yoshiyama et al. 2017). Yet observed growth remained unchanged between periods VI and VII when fishing pressures were controlled at a lower level; mortality due to recreational fishing was estimated to be less than 0.1 % of lake population (Yoshiyama et al. 2017). In terms of average mature fish size, it became significantly larger in period VII compared to other periods (Fig. 5), possibly due to fishing mortality reduction attributed to fishing regulation change in period VII, especially catch-and-release implementation. Although the short lake closure periods existed, fishing mortality was high overall by the beginning of the 1980s. In addition, it is known that larger individuals are likely be caught by angling (Tsuboi and Morita 2004), and indeed larger and older charr were selectively captured by the recreational fishing in Lake Shikaribetsu (i.e. the mode was 290 mm in recreational fishing catch in 2001) (Hokkaido Fish Hatchery 2000, 2003), which could induce the observed mature fish size shift. Taken together, Miyabe charr would grow slower and mature at a smaller size due to intensive fishing selectivity during periods II and IV, and these life-history traits would recover with reducing the fishing pressure.

The time scale of population, growth and other life-history trait recovery after overfishing provides key information for implementing management and conservation strategies; however, little data is currently available. Our results suggest that altered life-history traits by recreational overfishing, growth and mature fish size, gradually recovered in 10–30 years after fishing pressure reduced (Fig. 4; Fig. 5). Although the detailed mechanism and potential causes are unknown, lake moratoriums and proper fishing regulation introduction could potentially help to reverse these traits. Generally, recovery of these traits from fishery-induced changes is thought to be very slow after fishing pressure is reduced (Pinsky and Palumbi 2014). It is supported by multiple modelling studies which shown that maturation schedule recovery can take centuries with evolutionary changes (Dunlop et al. 2009; Enberg et al. 2009; Kuparinen and Hutchings 2012). Whereas rapid recovery in fish size after fishery closure has recently been reported, for example, in 12 generations in silverside fish *Menidia menidia* (Conover et al. 2009) and approximately 10–20 years in yellow perch *Perca flavescens* (Feiner et al. 2015). This case study thus provides important insights into the changes and time scale of recovery of life-history traits from heavy exploitation. It is noteworthy that few studies have focused on shifts in these traits in freshwater fish species under heavy fishing pressure, and that data from recreational fisheries are rarer than from commercial fisheries (Kendall and Quinn 2011).

The described growth and maturation size shift is highly likely to be attributed to fishing pressure and fishing selectivity rather than shift in the environmental effects such as prey densities, productivity or temperature. Regarding the prey abundance, we could expect the fish transplantations induce negative influence on growth or maturation size during the growth recovery periods, which was opposite to what we observed (Fig. 4; Fig. 5). Recently introduced species such as rainbow trout, Japanese smelt and masu salmon thought to have big ecological impacts on prey of Miyabe charr (Maekawa 1978; Shikaoi Town 1994; Yoshiyama et al. 2017). Miyabe charr mainly feed on planktons in addition to aquatic and terrestrial insects and small fish (Maekawa 1977; Hokkaido Fish Hatchery 1982, 1983, 1985), and potentially compete for common prey with the introduced fishes (Hokkaido Fish Hatchery 1974; Kobayashi H, www.noastec.jp/kinouindex/data2003/pdf/01/01_30.pdf "Accessed 24 Sep 2017"). In terms of lake productivity and temperature, it is difficult to evaluate these effects due to a lack of quantitative monitoring data. However, the fragmentary records indicate that they might not affect growth and mature fish size seriously, or even have a negative influence. Firstly, the stop of direct domestic-sewage inflow in the 1990s could have resulted in a decrease in nutrient supply, which could subsequently lead to a decrease in plankton. Secondly, the lake surface temperature has not seemed to change greatly over time (Hokkaido Fishery Experiment Station 1933; Kubo 1967; Hokkaido Fish Hatchery 1996). Therefore, it is plausible to claim that the effects of fishing pressure and selectivity outweigh that of the environmental changes in regard to our observed downsizing and maturation size reduction of the charr. Other factors, for example, differences in sampling gears and time, may influence the life-history trait shift in addition to recreational fishing pressure, fishing selectivity and the lake environment (Wang et al. 2009). However, it is difficult to evaluate these effects due to a lack of or inconsistency in historical data (Table 2a; 2b).

The current lake population level was estimated to be below the carrying capacity when considering the population and growth data over time with density-dependent effects. Firstly, estimated population size in previous years was larger than the current population size, like population size in 1979 was 95 % larger than 2015 (Table 1) (Hokkaido Fish Hatchery 1980; Yoshiyama T, unpubl. data, 2015). Secondly, the growth in 1993–2001 (periods VI) and 2015 (period VII) did not changed greatly (Fig. 4), even though the estimated population size in period VI was approximately three to eight times larger compared to period VII (Table 1) (Hokkaido Fish Hatchery 1997, 1998, 1999, 2000, 2001; Yoshiyama T, unpubl. data, 2015; Yoshiyama et al. 2017). Recently introduced new regulations, including catch-and-release, should be important for the recovery of the Miyabe charr population, contributing to the conservation of this endemic species (Yoshiyama et al. 2017).

In summary, the current study documented the life-history trait shifts over time in Miyabe charr that would correspond with shifts in recreational fishing activities. Based on a four-to-six-year generation time for this species, our results suggest that altered life-history traits due to overfishing could potentially be reversed within 10–30 years after fishing pressure has been reduced. Appropriate fishing regulations, such as regulating the fishing effort and/or catch-and-release implementation, can contribute to the conservation of both population size and the life-history traits of wild fish populations. Long-term records of these traits provide key information for management and conservation of fish populations and facilitate evaluation of current population state or dynamics. Our study thus provides an important insight into the biological changes caused by overfishing and the time scales required to reverse them in a wild fish population.

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References

Alós J, Palmer M, Catalan IA, Alonso-Fernández A, Basterretxea G, Jordi A, Buttay L, Morales-Nin B, Arlinghaus R (2014) Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. Mar Ecol Prog Ser 503: 219-233

Begon M, Harper JL, Townsend CR (2006) Ecology: From Individuals to Ecosystems, 4th Edition. Blackwell Publishing Ltd, Oxdord

Beverton RJ, Holt SJ (1957) On the dynamics of exploited fish population. MAFF Fish Invest Ser II vol. 19, London

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. Science 297: 94-96

Conover DO, Munch SB, Arnott SA (2009) Reversal of evolutionary downsizing caused by selective harvest of large fish. Pro R Soc Lond B Biol Sci 276: 2015-2020

Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. Ecol Appl 19: 1815-1834

Enberg K, Jørgensen C, Dunlop ES, Heino M, Dieckmann U (2009) Implications of fisheries-induced evolution for stock rebuilding and recovery. Evol Appl 2: 394-414

Enberg K, Jørgensen C, Dunlop ES, Varpe Ø, Boukal DS, Baulier L, Eliassen S, Heino M (2012) Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar Ecol 33: 1-25

Feiner ZS, Chong SC, Knight CT, Lauer TE, Thomas MV, Tyson JT, Höök TO (2015) Rapidly shifting maturation schedules following reduced commercial harvest in a freshwater fish. Evol Appl 8: 724-737

Fukuwaka M, Morita K (2008) Increase in maturation size after the closure of a high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*. Evol Appl 1: 376-387

Gadgil M, Bossert WH (1970) Life historical consequences of natural selection. Am Nat 104: 1-24

Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar Ecol Prog Ser 257: 247-257

Handford P, Bell G, Reimchen T (1977) A gillnet fishery considered as an experiment in artificial selection. J Fish Res Board Can 34: 954-961

Hard JJ, Gross MR, Heino M, Hilborn R, Kope RG, Law R, Reynolds JD (2008) Evolutionary consequences of fishing and their implications for salmon. Evol Appl 1: 388-408

Heino M, Baulier L, Boukal DS, Dunlop ES, Eliassen S, Enberg K, Jørgensen C, Varpe Ø (2008) Evolution of growth in Gulf of St Lawrence cod? Pro R Soc Lond B Biol Sci 275: 1111-1112

Heino M, Dieckmann U, Godø OR (2002) Measuring probabilistic reaction norms for age and size at maturation. Evolution 56: 669-678

Hirata T (1993) Lake Shikaribetsu in Hokkaido; How do we treat a rare species Miyabe charr. Mag Fly Fish 23: 41-43 (in Japanese)

Hokkaido Fish Hatchery (1974) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1978) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1980) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1981) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1982) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1983) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1985) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Sapporo (in Japanese)

Hokkaido Fish Hatchery (1994) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (1995) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (1996) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (1997) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (1998) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (1999) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (2000) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (2001) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (2002) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fish Hatchery (2003) Annual report of Hokkaido Fish Hatchery. Hokkaido Fish Hatchery, Eniwa (in Japanese)

Hokkaido Fishery Experiment Station (1933) Lake survey. Fisheries survey report 29: 1-48 (in Japanese)

Inukai T, Sato S (1943) Spawning habit of Miyabe charr (*Salvelinus miyabei* Oshima) in Lake Shikaribetsu. Zool Mag 55: 78-79 (in Japanese)

Jenkins Jr TM, Diehl S, Kratz KW, Cooper SD (1999) Effects of population density on individual growth of brown trout in streams. Ecology 80: 941-956

Kaeriyama M (1998) Dynamics of chum salmon, *Oncorhynchus keta*, populations released from Hokkaido, Japan. N Pac Anadr Fish Comm Bull 1: 90–102

Kawanabe H, Mizuno N (1989) In: Maekawa. K. (ed) Miyabe charr. Nippon no tansuigyo (Japanese freshwater fishes). Yama-Kei PUN, Tokyo (in Japanese)

Kendall NW, Quinn TP (2011) Length and age trends of Chinook salmon in the Nushagak River, Alaska, related to commercial and recreational fishery selection and exploitation. Trans Am Fish Soc 140: 611-622

Kubo T (1967) Ecological and physiological studies on the Dolly Varden charr (*Salvelinus malma*) in Lake Shikaribetsu, Hokkaido. Sci Rep Hokkaido Salmon Hatch 21: 11-33 (in Japanese with English abstract)

Kuparinen A, Hutchings JA (2012) Consequences of fisheries induced evolution for population productivity and recovery potential. Pro R Soc Lond B Biol Sci 279: 2571-2579

Maekawa K (1977) Studies on the variability of the land-locked Miyabe charr, *Salvelinus malma miyabei* Oshima, I: Development and early life history. Jpn J Ecol 27: 91-102 (in Japanese with English abstract)

Maekawa K (1978) Growth and development of *Salvelinus malma miyabei* compared with other forms of *S. malma*. Jpn J Ichtyol 25: 9-18

Maekawa K, Onozato H (1986) Reproductive tactics and fertilization success of mature male Miyabe charr, *Salvelinus malma miyabei*. Environ Biol Fishes 15: 119-129

Morita K, Fukuwaka M (2007) Why age and size at maturity have changed in Pacific salmon. Mar Ecol Prog Ser 335: 289-294

Nusslé S, Bornand CN, Idekind C (2009) Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. Evol Appl 2: 200-208

Ogle DH (2017) FSA: Simple fisheries stock assessment methods. R package version 0.8.16.

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428: 932-935

Pinsky ML, Palumbi SR (2014) Meta-analysis reveals lower genetic diversity in overfished populations. Mol Ecol 23: 29-39

Ricker I (1981) Changes in the average size and average age of Pacific salmon. Can J Fish Aquat Sci 38: 1636-1656

Sharpe DM, Hendry AP (2009) Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol Appl 2: 260-275

Shikaoi Town (1994) The 70 years history of Shikaoi Town. Shikaoi Town Government, Shikaoi (in Japanese)

Stolarski JT, Sutton TM (2013) Precision analysis of three aging structures for amphidromous Dolly Varden from Alaskan Arctic rivers. N Am J Fish Manag 33: 732-740

Tenbrink TT, Spencer PD (2013) Reproductive biology of Pacific ocean perch and northern rockfish in the Aleutian Islands. N Am J Fish Manag 33: 373-383

Thomas G, Eckmann R (2007) The influence of eutrophication and population biomass on common whitefish (*Coregonus lavaretus*) growth-the Lake Constance example revisited. Can J Fish Aquat Sci 64: 402-410

Tsuboi JI, Morita K (2004) Selectivity effects on wild white-spotted charr (*Salvelinus leucomaenis*) during a catch and release fishery. Fish. Res 69: 229-238

Wang HY, Cook HA, Einhouse DW, Fielder DG, Kayle KA, Rudstam LG, Höök TO (2009) Maturation schedules of walleye populations in the Great Lakes region: comparison of maturation indices and evaluation of sampling-induced biases. N Am J Fish Manag 29: 1540-1554

Yoneda M, Wright PJ (2004) Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. Mar Ecol Prog Ser 276: 237-248

Yoshiyama T, Tsuboi J, Matsuishi T (2017) Recreational fishery as a conservation tool for endemic Dolly Varden *Salvelinus malma miyabei* in Lake Shikaribetsu, Japan. Fish Sci 83: 171-180

Figure Caption

Fig. 1 Sampling locations. Samples were collected from Lake Shikaribetsu and its inlet stream, Yambetsu River (map revised from Maekawa 1978)

Fig. 2 Photomicrograph of a Miyabe charr sagittal otolith taken with reflected light, showing the annulation pattern in a four-year-old individual. Black triangles represent the end of opaque zones

Fig. 3 Estimated von Bertalanffy growth curves for male and female Miyabe charr. Crosses and open circles represent male and female individuals, respectively

Fig. 4 Growth shift of Miyabe charr over time. Roman numbers represent the fishing history periods in Lake Shikaribetsu (refer to Table 1). Note that 1956–66 (period II) and 1970–74 (period III) are mean length-at-age from previously published data, and 1993–2001 (period VI) and 2015 (period VII) are von Bertalanffy growth curves

Fig. 5 Shift in mature Miyabe charr size over time. Vertical bars and solid squares represent the range of mature charr by FL (mm) and its average size, respectively. Note that fish size was standardized to FL and outliers were excluded. Alphabetical letters above the bars show statistical differences of mean mature fish size between years; sharing the same letter indicates no significant differences ($p < 0.05$, Tukey-Kramer HSD test). The horizontal bars below the year represent the periods related to the fishing history in Lake Shikaribetsu, while the black bars indicate periods of high fishing pressure (refer to Table 1)

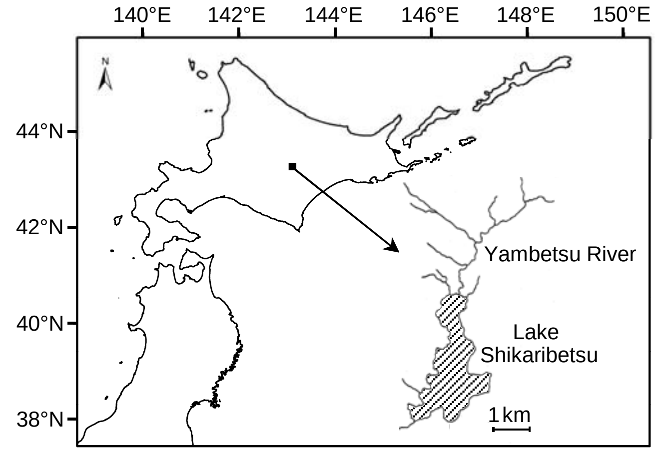
140°E
142°E
144°E
146°E
148°E
150°E
44°N
42°N
40°N
38°N
N
Yambetsu River
Lake
Shikaribetsu
1 km

Fig.1

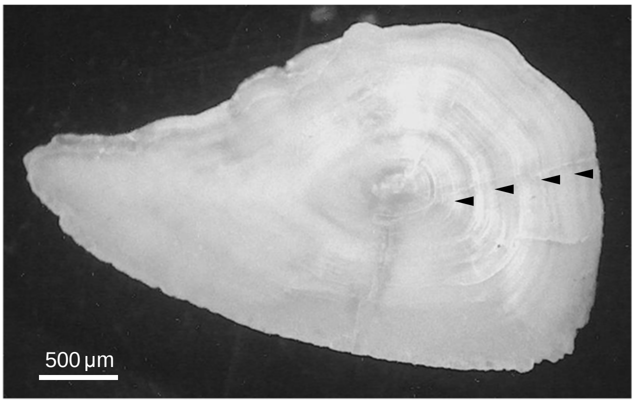

Fig.2

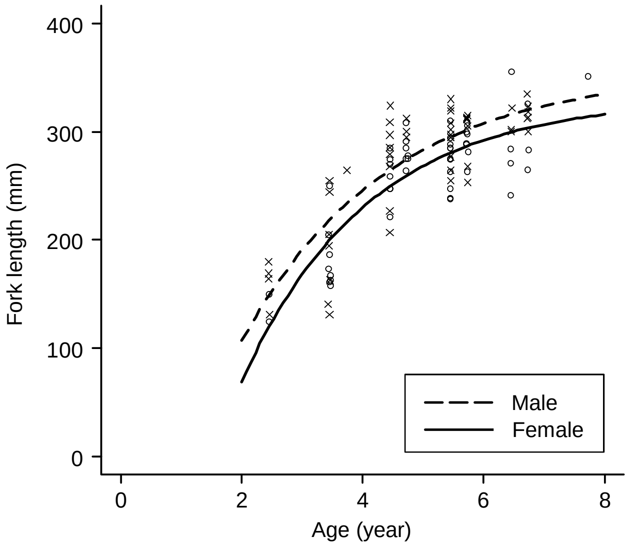

Fig.3

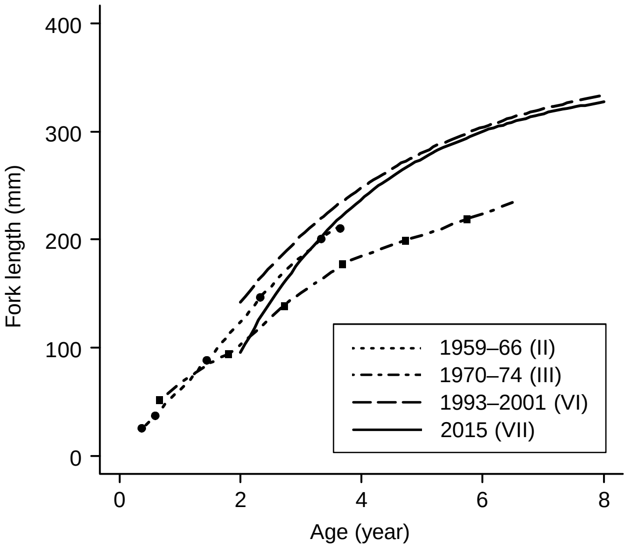
400
300
200
100
0
Fork length (mm)
0
2
4
6
8
Age (year)
1959–66 (II)
1970–74 (III)
1993–2001 (VI)
2015 (VII)

Fig.4

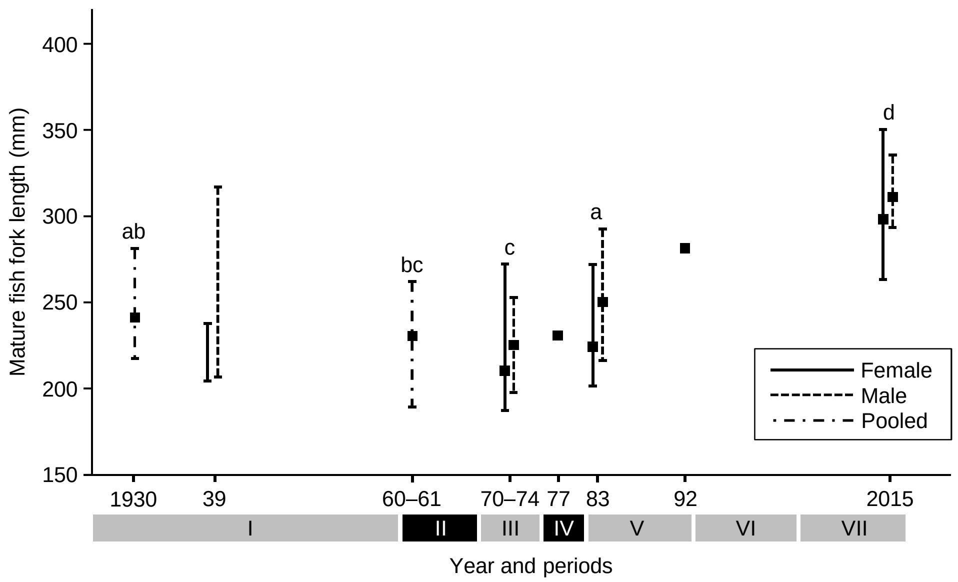
Mature fish fork length (mm)
400
350
300
250
200
150
ab
bc
c
a
d
Female
Male
Pooled
1930
39
60–61
70–74
77
83
92
2015
I
II
III
IV
V
VI
VII
Year and periods

Fig.5

Table 1 Fishing history in Lake Shikaribetsu and fishing regulations over time

Period	Year	Event	Major Fishing Regulations				Bag limit	Total catch/year	Estimated population size (year and method)
			Area	Open (/year)	Entry (/day)	Gears			
I	~1959	Commercially exploited	Free	Free	Free	Free	None	N.A.	N.A.
II	1960–68	Recreationally overfished	Free	Free	Free	Free	None	N.A.	N.A.
III	1969–75	Closure	–	–	–	–	–	–	N.A.
IV	1976–80	Reopen/Recreationally overfished	Restricted[1]	61 days	Free	One rod/person	None	127,994 (1979)[3] 42,100 (1980)[4]	181,000 (1979, DeLury Method)[3] 68,400 (1980, DeLury Method)[4]
V	1981–92	Closure	–	–	–	–	–	–	N.A.
VI	1993–04	Experimental open for recreational fishing	Restricted[1]	10–30 days	30 persons	One rod/person	10–20 fish/day	2,078–4,910 (1994–2001)[5]	13,880–31,635 (1995–99, Petersen Method)[6]

VII	2005~	Special open for recreational fishing	Restrected[1]	50 days	50 persons	One rod/person Lure/Fly only[2]	0[7]	4,865 (2014)[7, 8] 7,092 (2015)[7, 9]	105,300 (2014, Schnabel Method)[8] 92,790 (2015, Schnabel Method)[9]

N.A.: No Data

[1] Partially open except for designated natural monument area

[2] No bait fishing allowed. Barbless hook only

[3] Hokkaido Fish Hatchery (1980)

[4] Hokkaido Fish Hatchery (1981)

[5] Hokkaido Fish Hatchery (1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003)

[6] Hokkaido Fish Hatchery (1997, 1998, 1999, 2000, 2001)

[7] All Miyabe Char should be released under the catch-and-release regulation

[8] Yoshiyama et al. (2017)

[9] Yoshiyama T, unpubl. data, 2015

Table 2a Summary of previously published data on growth of Miyabe charr

Sampling year(s)	Sampling site(s)	Sampling method(s)	*n*	Age determination	Reference(s)
1959–66	Inlet stream, lake	Angling and drive-in net (stream samples), angling (lake samples)	606	Scales	Kubo (1967)
1970–74	Lake	N.A.	N.A.	Otoliths	Maekawa (1978)
1993	Lake	Gill nets	243	N.A.	Hokkaido Fish Hatchery (1995, 1996)
1994	Lake	Experimental gill nets*	365	N.A.	Hokkaido Fish Hatchery (1996)
1995	Lake	Experimental gill nets*	540	N.A.	Hokkaido Fish Hatchery (1997)
1996	Lake	Experimental gill nets*	621	N.A.	Hokkaido Fish Hatchery (1998)
1997	Lake	Experimental gill nets*	218	N.A.	Hokkaido Fish Hatchery (1999)
1998	Lake	Experimental gill nets*	365	N.A.	Hokkaido Fish Hatchery (2000)
1999	Lake	Experimental gill nets*	319	N.A.	Hokkaido Fish Hatchery (2001)
2000	Lake	Experimental gill nets*	218	Scales	Hokkaido Fish Hatchery (2002)
2001	Lake	Experimental gill nets*	325	Scales	Hokkaido Fish Hatchery (2003)

N.A.: No Data

*Mesh size: 30, 36, 45, 54, 66, 80 and 93 mm

Table 2b Summary of previously published data on maturation size of Miyabe charr

Sampling date	Sampling location	Sampling method(s)	*n*	Reference
Oct. 1930	Inlet stream	N.A.	9	Hokkaido Fishery Experiment Station (1933)
Oct. 1939	Inlet stream	Fish weir	♀: 92, ♂: 78	Inukai and Sato (1943)
Oct. 1960 and Oct. 1961	Inlet stream	Angling and drive-in net	97	Kubo (1967)
1970–74	Yambetsu River and Kohan River (inlet streams)	N.A.	♀: 34, ♂: 17	Maekawa (1978)
1977	Inlet stream	N.A.	199	Hokkaido Fish Hatchery (1978)
Aug. 1983	Yamada creek (inlet stream)	Fish weir	♀: 99, ♂: 120	Maekawa and Onozato (1986)
Sep. 1992	Yambetsu River (inlet stream)	N.A.	134	Hokkaido Fish Hatchery (1994)

N.A.: No Data

Table 3 Mean fork length (FL) by age in Miyabe charr over time

Age	Mean FL (mm)*			
	1960–61	1970–74	1993–2001	2015
1+	88 (54–124)	94 ± 8		
2+	152 (119–178)	143 ± 13	182 (178–187)	153 (130–176)
3+	201 (159–227)	181 ± 24	233 (231–235)	191 (169–214)
4+		200 ± 26	270 (268–271)	274 (263–286)
5+		219 ± 24	296 (294–298)	289 (281–297)
6+			318 (312–324)	303 (287–318)

*Mean FL (mm) measurements show with FL ranges in 1960–61, with standard deviations in 1970–74, and with 95% confidence intervals in 1993–2001 and 2015.