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Title	Long-term shifts in the growth and maturation size of Miyabe charr <i>Salvelinus malma miyabei</i>
Author(s)	Yamamoto, Yuki; Yoshiyama, Taku; Kajiwara, Keitaro et al.
Citation	Fisheries science, 84(3), 425-433 https://doi.org/10.1007/s12562-018-1186-5
Issue Date	2018-05
Doc URL	https://hdl.handle.net/2115/73849
Rights	The final publication is available at www.springerlink.com
Type	journal article
File Information	Manuscript of FISC_ For print.pdf



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

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21 **Abstract**

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

31

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

33

34 **Introduction**

35 Shifts in the life-history traits of some fish populations, including age and size at maturity (Heino et al. 2002; Grift et al.
36 2003), reproductive effort (Yoneda and Wright 2004) and growth rate (Handford et al. 1977; Thomas and Eckmann 2007),
37 have been reported to be caused by human activities such as fishing. These reproductive parameters are particularly critical
38 for the estimation of stock reproductive capacity, and subsequently the determination of acceptable harvest levels (Tenbrink
39 and Spencer 2013). Thus, understanding the long-term trends in these life-history traits is important for evaluating fish
40 population dynamics and stability, and for supporting effective fishery management strategies (Kendall and Quinn 2011).

41 Growth is an important life-history trait that is affected by various factors such as physical environmental
42 changes, life-history options, competition and density, integrating many dimensions of environmental influence with
43 physiological function (Begon et al. 2006). Fishing activity can potentially affect traits related to growth indirectly, for
44 example, by decreasing fish population to allow an increase in prey abundance (Enberg et al. 2012). Growth is also
45 influenced by intrinsic factors like growth capacity (i.e. the ability of fish to transform energy intake into body mass) and
46 reproductive investment (i.e. the ratio of gonad mass to somatic mass) (Heino et al. 2008; Nusslé et al. 2009). Reallocation
47 of resources from growth capacity to reproductive investment is likely due to selection against fast growers (Heino et al.
48 2008; Gadgil and Bossert 1970), thus changes in growth can be linked to changes in these factors (Nusslé et al. 2009).

49 Both intensive-size selection and density-dependent effects can potentially influence trends in size and maturity
50 schedule in exploited stocks (Beverton and Holt 1957; Ricker 1981), however, in completely different ways. Empirical and
51 modelling studies suggest that intensive-size selection favours individuals that grow slower, mature at smaller sizes and
52 increase their reproductive investment (Gadgil and Bossert 1970; Conover and Munch 2002; Enberg et al. 2009; Sharpe

53 and Hendry 2009). A recent study showed recreational angling also selects for life-history traits that promote downsizing
54 of adults in coastal marine fish (Alós et al. 2014). In salmonid fish, Hard et al. (2008) reviewed the cases of reduction in
55 maturation size caused by overfishing (see also exceptional case in Morita and Fukuwaka (2007)). In contrast, a negative
56 relationship between fish length and population size by density-dependent effects has been documented including salmonid
57 species (Kaeriyama 1998; Jenkins et al. 1999).

58 Miyabe charr *Salvelinus malma miyabei* is a four-to-six-year generation time endemic subspecies of Dolly
59 Varden *S. malma* that inhabits Lake Shikaribetsu and its inlet streams in Hokkaido, Japan (Kawanabe and Mizuno 1989).
60 Miyabe charr is a popular recreational fishing target in Lake Shikaribetsu, and its fishing history can be divided into seven
61 periods corresponding to changes in fishing styles and regulations (Table 1). Historically Miyabe charr was commercially
62 exploited (period I, by 1959), but it gradually shifted to become a recreational target. As the popularity of recreational
63 fishing surged, the lake population declined because of overfishing without fishing regulations in 1960–68 (period II),
64 which resulted in an entire fishery closure for seven years (period III, during 1969–75). It was said that if fishing had
65 continued to be unregulated, the lake population would have completely collapsed (Shikaoi Town 1994). Even after the
66 first lake moratorium, fishing pressure was still high under regulations that allowed an estimated two-thirds or more of the
67 charr population to be captured every year during 1976–80 (period IV) (Hokkaido Fish Hatchery 1980, 1981), resulting in
68 population collapse (Hirata 1993). As a result, the lake was closed again for 11 years from 1981 to 1992 (period V).
69 Although it was re-opened in 1993 with fishing regulations including a bag-limit, the population remained at a low level
70 during 1993–2004 (period VI) (Hokkaido Fish Hatchery 1997, 1998, 1999, 2000, 2001); however, stricter regulations and
71 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 km², 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/>.

91

92 **Description of previously published data**

93 Growth and maturation size of Miyabe charr has been documented over the years (Table 2a; 2b). Previous studies by Kubo
94 (1967) and Maekawa (1978) analysed growth using mixed-sex mean length-at-age. The pooled-sex age-length composition
95 data was provided on Hokkaido Fish Hatchery (1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003), which enabled us
96 to evaluate growth during 1993–2001. In terms of maturation size, data on the length of mature fish was available from the
97 listed references in Table 2b. To compare the mature charr size over time, we used data only for lake-run charr captured
98 from inlet streams, considering its complicated life history (Yoshiyama et al. 2017). We assumed that all spawning-migrated
99 lake-run charr captured in the inlet streams were mature in case maturity data was unavailable (i.e. Inukai and Sato 1943;
100 Hokkaido Fish Hatchery 1978, 1994).

101

102 **Sampling**

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

108

109 **Age determination**

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

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

122

123 **Growth curve estimations and growth comparisons with previously published data**

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

126

127
$$L_t = L_{\infty} \left(1 - \exp^{-k(t-t_0)}\right) \quad (\text{Eq. 1})$$

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

129

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

137

138
$$FL \text{ (mm)} = 1.00 \times TL \text{ (mm)} - 5.00 \quad (\text{Eq. 2})$$

139

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

142

143 **Mature charr size comparisons with previously published data**

144 For 2015 data, both sex-specific and pooled-sex mean FL were calculated using river samples. To compare average pooled-
 145 sex mature charr size over time, Tukey-Kramer Honestly Significant Difference (HSD) test was implemented in R among

146 pairs of the following years ($p < 0.05$); 1930, 1960–61, 1970–74, 1983 and 2015 (refer to Table 2b). Note that only those
147 of data sets were available for the statistical comparisons.

148

149 **Results**

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

152

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

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

155

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

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

159

160 1993–2001 pooled-sex: $L_t = 365.8 \left(1 - \exp^{-0.321(t-0.475)} \right), (n = 3,219)$

161 2015 pooled-sex: $L_t = 348.7 \left(1 - \exp^{-0.411(t-1.221)} \right), (n = 102)$

162

163 These von Bertalanffy growth curves and previously published mean length-at-age data were illustrated altogether in Fig.
164 4, showing that the length-at-age in 1970–74 (period III) clearly plateaued at a smaller size comparing with other years

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

170 Average mature fish size and its FL-range (shown in parentheses) in 2015 were 311 (295–335) mm in male ($n =$
171 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,
172 indicating that mature fish size increased in 1992 (period V) and 2015 (period VII) after lake fishing pressure decreased
173 (Table 1). The pooled-sex average mature fish size was 304 mm ($n = 19$) in 2015 (period VII), which was significantly
174 larger than any of other years (range 215–242 mm in other four years, all $p < 0.001$).

175

176 Discussion

177 The current study documented life-history trait shifts in Miyabe charr linking to the fishing history in Lake Shikaribetsu
178 over the past 80 years. Specifically, length-at-age and mature charr size increased after fishing pressure was greatly reduced
179 (Table 1; Fig. 4; Fig. 5). After recreational fishing popularity surged in the early 1960s, overfishing and subsequent
180 moratorium introductions were repeated without proper regulations and managements during 1960–92 (period II–V), which
181 led to population collapse (Hirata 1993). In 1993, the lake was re-opened under new fishing regulations designed to reduce
182 fishing pressure (period VI). By the end of this period, growth has greatly improved compared to 1970–74 (periods III).
183 Since 2005 (period VII), stricter regulations have been introduced, including the catch-and-release of all charr, contributing

184 to a three to seven-fold increase in the charr population size compared to period VI (Yoshiyama T, unpubl. data, 2015;
185 Yoshiyama et al. 2017). Yet observed growth remained unchanged between periods VI and VII when fishing pressures
186 were controlled at a lower level; mortality due to recreational fishing was estimated to be less than 0.1 % of lake population
187 (Yoshiyama et al. 2017). In terms of average mature fish size, it became significantly larger in period VII compared to
188 other periods (Fig. 5), possibly due to fishing mortality reduction attributed to fishing regulation change in period VII,
189 especially catch-and-release implementation. Although the short lake closure periods existed, fishing mortality was high
190 overall by the beginning of the 1980s. In addition, it is known that larger individuals are likely be caught by angling (Tsuboi
191 and Morita 2004), and indeed larger and older charr were selectively captured by the recreational fishing in Lake
192 Shikaribetsu (i.e. the mode was 290 mm in recreational fishing catch in 2001) (Hokkaido Fish Hatchery 2000, 2003), which
193 could induce the observed mature fish size shift. Taken together, Miyabe charr would grow slower and mature at a smaller
194 size due to intensive fishing selectivity during periods II and IV, and these life-history traits would recover with reducing
195 the fishing pressure.

196 The time scale of population, growth and other life-history trait recovery after overfishing provides key
197 information for implementing management and conservation strategies; however, little data is currently available. Our
198 results suggest that altered life-history traits by recreational overfishing, growth and mature fish size, gradually recovered
199 in 10–30 years after fishing pressure reduced (Fig. 4; Fig. 5). Although the detailed mechanism and potential causes are
200 unknown, lake moratoriums and proper fishing regulation introduction could potentially help to reverse these traits.
201 Generally, recovery of these traits from fishery-induced changes is thought to be very slow after fishing pressure is reduced
202 (Pinsky and Palumbi 2014). It is supported by multiple modelling studies which shown that maturation schedule recovery

203 can take centuries with evolutionary changes (Dunlop et al. 2009; Enberg et al. 2009; Kuparinen and Hutchings 2012).
204 Whereas rapid recovery in fish size after fishery closure has recently been reported, for example, in 12 generations in
205 silverside fish *Menidia menidia* (Conover et al. 2009) and approximately 10–20 years in yellow perch *Perca flavescens*
206 (Feiner et al. 2015). This case study thus provides important insights into the changes and time scale of recovery of life-
207 history traits from heavy exploitation. It is noteworthy that few studies have focused on shifts in these traits in freshwater
208 fish species under heavy fishing pressure, and that data from recreational fisheries are rarer than from commercial fisheries
209 (Kendall and Quinn 2011).

210 The described growth and maturation size shift is highly likely to be attributed to fishing pressure and fishing
211 selectivity rather than shift in the environmental effects such as prey densities, productivity or temperature. Regarding the
212 prey abundance, we could expect the fish transplantations induce negative influence on growth or maturation size during
213 the growth recovery periods, which was opposite to what we observed (Fig. 4; Fig. 5). Recently introduced species such
214 as rainbow trout, Japanese smelt and masu salmon thought to have big ecological impacts on prey of Miyabe charr
215 (Maekawa 1978; Shikaoi Town 1994; Yoshiyama et al. 2017). Miyabe charr mainly feed on planktons in addition to aquatic
216 and terrestrial insects and small fish (Maekawa 1977; Hokkaido Fish Hatchery 1982, 1983, 1985), and potentially compete
217 for common prey with the introduced fishes (Hokkaido Fish Hatchery 1974; Kobayashi H,
218 www.noastec.jp/kinouindex/data2003/pdf/01/01_30.pdf “Accessed 24 Sep 2017”). In terms of lake productivity and
219 temperature, it is difficult to evaluate these effects due to a lack of quantitative monitoring data. However, the fragmentary
220 records indicate that they might not affect growth and mature fish size seriously, or even have a negative influence. Firstly,
221 the stop of direct domestic-sewage inflow in the 1990s could have resulted in a decrease in nutrient supply, which could

222 subsequently lead to a decrease in plankton. Secondly, the lake surface temperature has not seemed to change greatly over
223 time (Hokkaido Fishery Experiment Station 1933; Kubo 1967; Hokkaido Fish Hatchery 1996). Therefore, it is plausible to
224 claim that the effects of fishing pressure and selectivity outweigh that of the environmental changes in regard to our
225 observed downsizing and maturation size reduction of the charr. Other factors, for example, differences in sampling gears
226 and time, may influence the life-history trait shift in addition to recreational fishing pressure, fishing selectivity and the
227 lake environment (Wang et al. 2009). However, it is difficult to evaluate these effects due to a lack of or inconsistency in
228 historical data (Table 2a; 2b).

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

238 In summary, the current study documented the life-history trait shifts over time in Miyabe charr that would
239 correspond with shifts in recreational fishing activities. Based on a four-to-six-year generation time for this species, our
240 results suggest that altered life-history traits due to overfishing could potentially be reversed within 10–30 years after

241 fishing pressure has been reduced. Appropriate fishing regulations, such as regulating the fishing effort and/or catch-and-
242 release implementation, can contribute to the conservation of both population size and the life-history traits of wild fish
243 populations. Long-term records of these traits provide key information for management and conservation of fish
244 populations and facilitate evaluation of current population state or dynamics. Our study thus provides an important insight
245 into the biological changes caused by overfishing and the time scales required to reverse them in a wild fish population.

246

247 **Acknowledgements**

248 This study was supported by the management staff of Great Fishing in Lake Shikaribetsu; Takeda K, Tabata T, Sawada K,
249 Takahashi K and Otagiri H for sampling assistance. The authors also acknowledge Itou M and all the staff of the Commerce
250 and Tourism Department of the Shikaoi Town government for their administrative support. The authors are grateful to
251 Takatsu T for help with age determination, and Shimizu M and Tojo N for constructive comments on the manuscript. This
252 research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

253

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419

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)

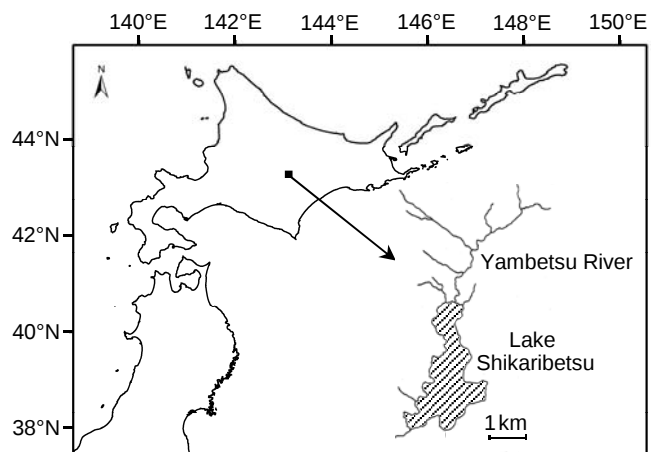


Fig.1

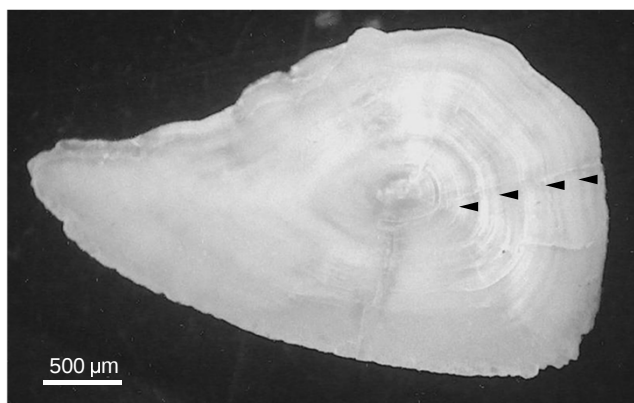


Fig.2

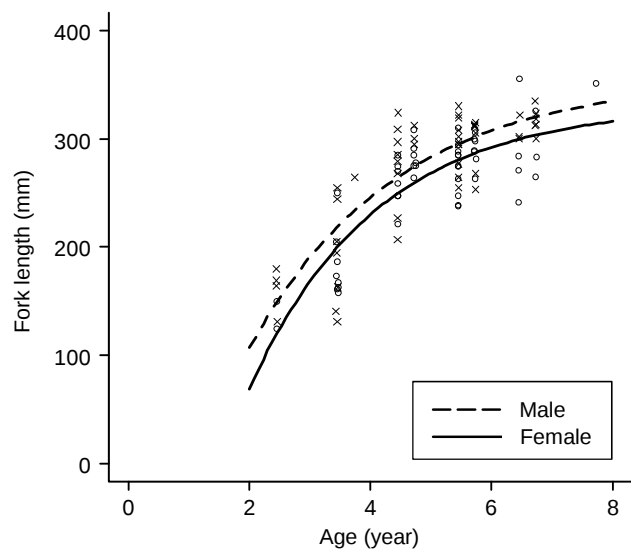


Fig.3

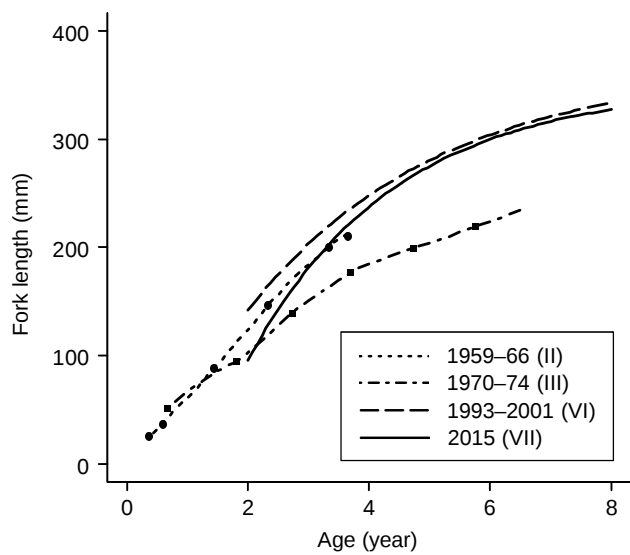


Fig.4

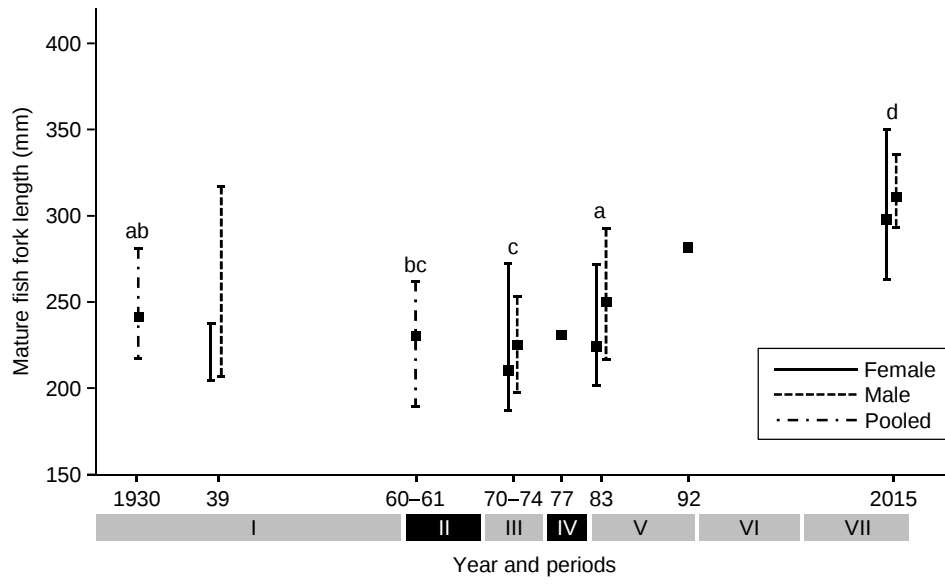


Fig.5

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	Restricted ¹	50 days	50 persons	One rod/person	4,865 (2014) ^{7, 8}	105,300 (2014, Schnabel Method) ⁸
		recreational fishing				Lure/Fly only ²	7,092 (2015) ^{7, 9}	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)	<i>n</i>	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)	<i>n</i>	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.