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Growth and Development of *Salvelinus malma miyabei* Compared with Other Forms of *S. malma*

Koji Maekawa

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Abstract Three forms of the Dolly Varden, *Salvelinus malma*, land-locked form (Miyabe char), river-resident form and sea-run form, were examined with special reference to their growth and development. The growth rate of the Miyabe char was closely similar in early stages of growth to that of the river-resident form, but a remarkable difference of body size appeared from two years of age, when the former descended into the lake and grew rapidly thereafter. The Miyabe char attained maturity at a later and more advanced growth stage than the river-resident form. The most striking difference was that a remarkable inflection corresponding to the fork length of the smolt was recognized in the relative growth line of the sea-run form, but the Miyabe char and river-resident form did not show this inflection in the growth line. The Miyabe char, therefore, might have more neotenous body form and size in relation to its precocity than the anadromous one. The process of land-locking and the subsequent evolution of the Miyabe char might be similar to that of kokanee, *Oncorhynchus nerka*, land-locked in lakes.

In a previous paper (Maekawa, 1977a), some divisions in the developmental stages, especially those in the juvenile stage of the Miyabe char, *Salvelinus malma miyabei* Oshima, a land-locked form in Lake Shikaribetsu in Hokkaido, Japan, were made with special reference to the early life history. A comparison of development and growth between the Miyabe char and other forms of the Dolly Varden, *S. malma* (Walbaum), such as the residual and anadromous forms is important. It is necessary to acount for the relationship between them, since land-locked processes or differentiation of the Salmonidae and closely related species have been discussed in relation to their precocity by many previous authors (Ohno, 1938; Ricker, 1938, 1940; Azuma, 1973; Kubo, 1974; Utoh, 1976, 1977). No such reports, however, have been made on the Miyabe char, except for preliminary reports by Kubo (1967) and Kimura (1976).

This paper describes the development and growth of the Miyabe char in comparison with some other prominent forms of the Dolly Varden.

Material and methods

The materials examined in the present investigation were collected from the following districts from 1970 to 1974. The Miyabe char were collected from Lake Shikaribetsu of the Tokachi River system and the Yambetsu and Kohan Rivers, flowing into the lake. The river-resident forms were collected from the upper reaches of the Nuppun-Tomuraushi River of the Tokachi River system, the Tokoro River, and the Nishitappu River of the Ishikari River system. The anadromous forms were collected in Alaska from the Eagle and Switzer Rivers, a lake (name unknown), the sea surrounding Juneau, and the Sea of Okhotsk. The name of each form is abbreviated as follows.

Lake-run form of the Miyabe char: L-form
River-resident form of the Miyabe char: LR-form
River-resident form of the Dolly Varden in the Nuppun-Tomuraushi River: RNu-form
River-resident form of the Dolly Varden in the Nishitappu River: RN-form
River-resident form of the Dolly Varden in the Tokoro River: RT-form
Sea-run form of the Dolly Varden: S-form

All of the Miyabe char from the Kohan River were resident-form, land-locked by a concrete dam. Data on the body length of the Miyabe char from Lake Shikaribetsu was

obtained from a report by the Hokkaido Fish Hatchery, to compute the relation between body and fork lengths. It was $y=0.93x+0.03$ (y: body length, x: fork length). The following dimensions of the body were measured: fork length, head length, body depth, pectoral fin length, maxillary length, and eye diameter.

In order to compute the relative size of the body parts of the sea-run form, river-resident forms, and the Miyabe char, specimens collected during summer (June, July, and August) were used, to exclude seasonal variation, except for the LR-form which was collected throughout the seasons. A log-log was made of the fork length on the x axis and body part length on the y axis. When inflections were thought to occur, an equation, $\log y=k \log x+\log b$, of each straight-line was

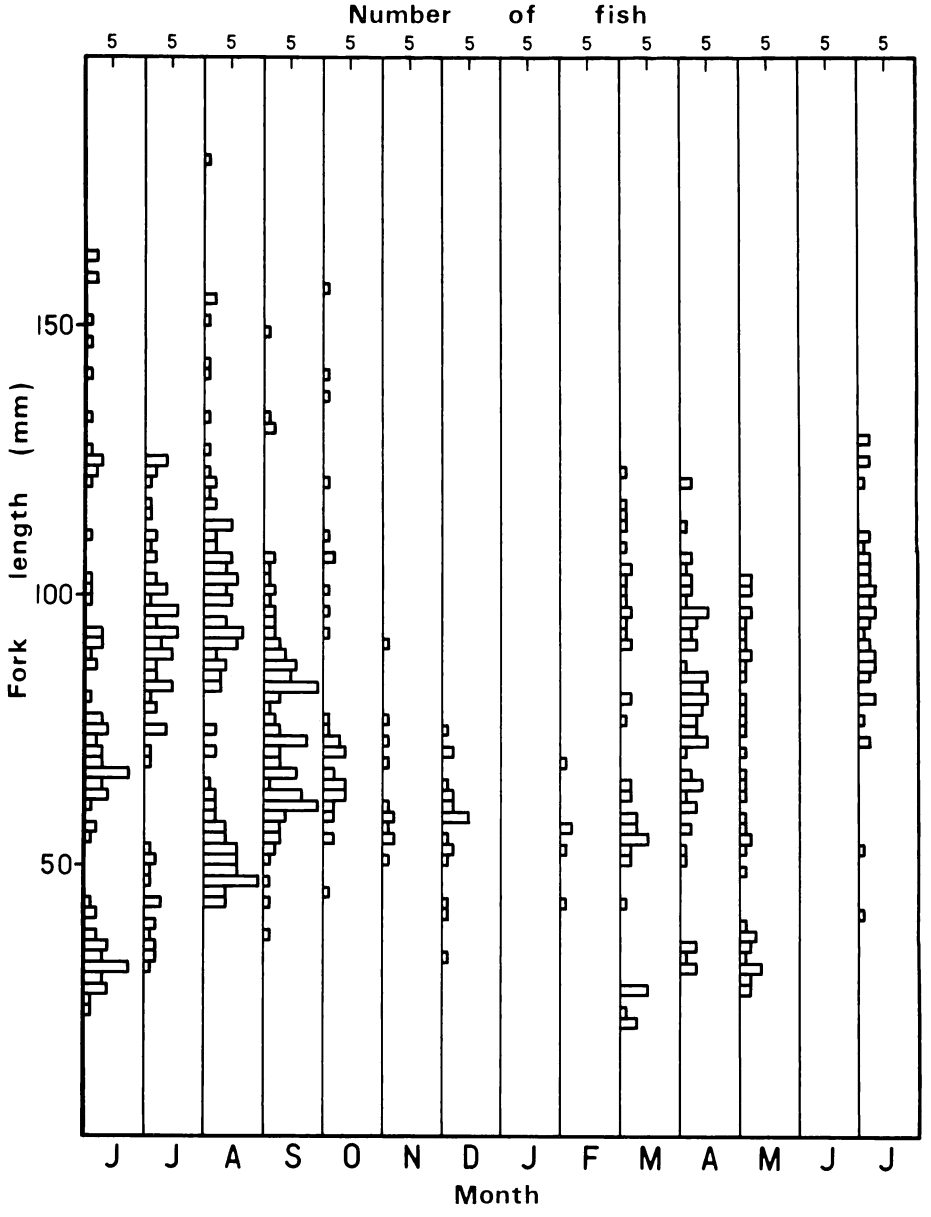

Fig. 1. Monthly length-composition of Miyabe char collected by hand and cast nets at the Yambetsu River in 1971～1972.

computed at the estimated point of the inflection. The statistical significance of the lines was examined (Kondo, 1964) and a possible intersecting point was calculated from the equations.

Otoliths were used for age determination (Grainger, 1953; Heiser, 1966). However, it could not be used for the S-form because they were strongly decalcified from storage in 10% formalin for 1 year or less.

Results

Comparison of growth and body forms of three forms of the Dolly Varden. Comparisons of growth and body forms should be made at the same developmental stage, but there were not sufficient specimens from each locality, except for those from Lake Shikaribetsu, Hokkaido. In considering the developmental stage, the growth aspect of the fork length will be described first in order to compare the S-form, RNu-form, L-form and LR-form.

A) Growth aspect to fork length: The fork length distribution of the Miyabe char collected from the mouth to the middle reaches of the Yambetsu River in 1971～1972 is shown in Fig. 1. The growth trend of individuals of the first year, presumed by the mode and mean of the fork length, showed rapid growth from June (32 mm in fork length in average) to August or September (65 mm in average), and almost no growth occurred after October and during the winter. The larger groups of the fork length distribution in June (Fig. 1) were assemblages of one- and two-year-old individuals, and were assumed to grow to 80～100 mm in fork length in late summer (Maekawa, 1977a).

Histograms (Fig. 2) show the size and age frequency of samples from Lake Shikaribetsu in June, July, August and October. Monthly variation in the age-determined groups of July and October and the mode of the smallest group of fork length indicate that the smallest fish grew rapidly from July to August. Two groups were recognized in the fork length distributions for the two-year-old individuals in October, the smaller one with an average length of 130 mm, which could be fall migrants (Maekawa, 1977a). The histograms of October also indicate that the fork

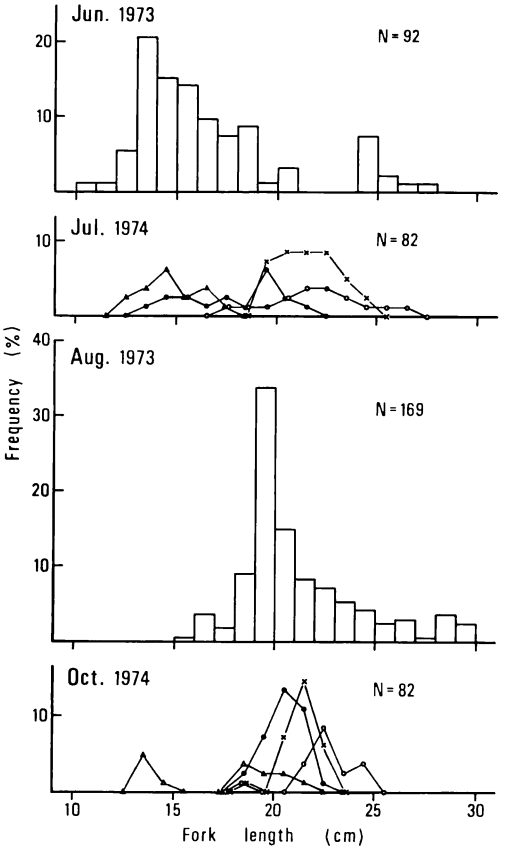

Fig. 2. Monthly length- and age-frequencies of Miyabe char collected by gill nets in Lake Shikaribetsu. Six- and seven-year-old individuals, two samples in July and four in October, 1974, are excluded from the figures shown by age frequency. Symbols indicate as follows: △—△: 2 years old, ●—●: 3 years old, ×—×: 4 years old, ○—○: 5 years old.

lengths overlapped extensively among individuals older than three years of age.

Fig. 3 shows the growth curve of the fork length of the L-form, LR-form and RNu-form. The LR-form in a group of fish is differentiated from the Phase E_2 of the developmental stages of the Miyabe char (Maekawa, 1977a). The growth curve of the LR-form was very slack and the size of five-year-old individuals of this type was smaller than that of other forms. The growth curve of the RNu-form could closely resemble that of the L-form in the early stage of growth, since there was no significant difference in

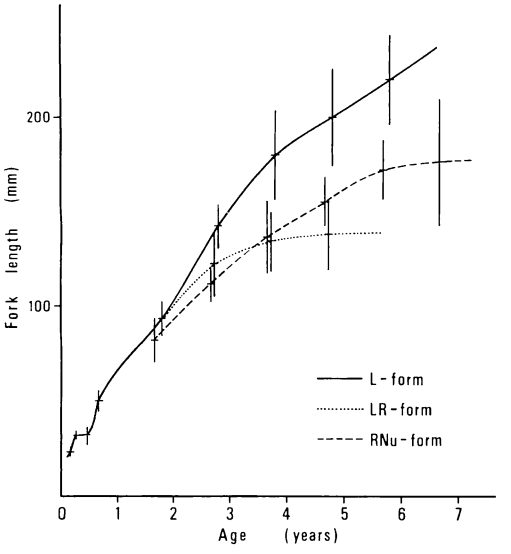

Fig. 3. Estimated growth curves of Miyabe char and river-resident form of Dolly Varden. The bars represent the range of standard deviation.

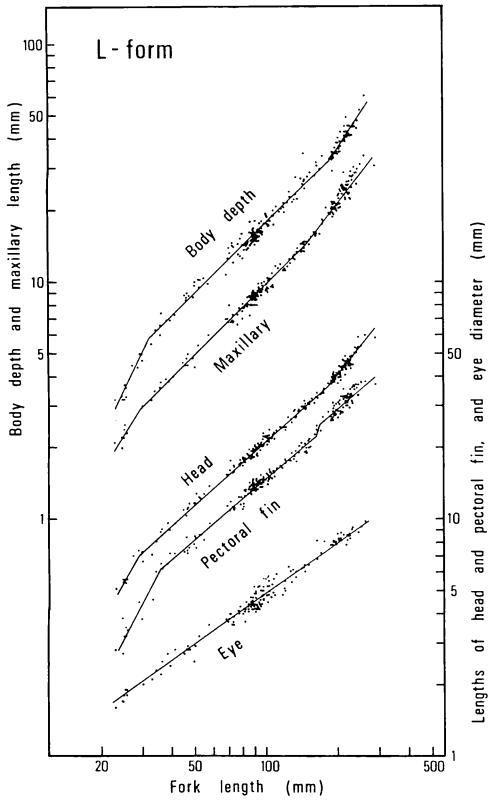

Fig. 4. Relation of body parts to fork length in lake-run form (L-form) of Miyabe char.

the size of one-year-old individuals between the RNu- and L-forms, though the author did not have samples for the first year of life of the RNu-form. The curve of the RNu-form, however, became retarded at the later stages, two years after hatching.

B) Relative growth of body form: The relative growth patterns of the head, body depth, maxillary, pectoral fin and eye to fork length were compared among all forms examined in this study.

The L-form showed two inflections in the relative-growth curves of the head length, body depth, maxillary length, and pectoral fin length but not in the eye diameter (Fig. 4). The first inflection clearly appeared at 29.4～37.0 mm in fork length, and the second at about 130～180 mm. The body, head and maxillary growth ratios showed a remarkable tachyauxesis up to the points of the first inflection, and bradyauxesis between the first and the second, and tachyauxesis again thereafter (Table 1). There is no significant difference in the relative growth coefficient between K_2 and K_3 of the pectoral fin. However, a possible intersecting point of the second inflection of the pectoral fin was estimated from visual observation, not from the equations, since it could be clearly recognized from the line. The inflection of the LR-form was not clear in the growth curve of all the body parts, but individual variation was larger than that of the other forms. This might be due to seasonal or sexual variations.

In the case of the S-form (Fig. 5), however, the relative-growth curves of the dimensions showed more complex patterns, which had clearly two inflections. The possible inflection could have appeared at about 30 mm in fork length as in the L-form, but since only a few samples less than 35 mm in fork length were used, these influections could not be estimated. The growth ratios which showed remarkable bradyauxesis after the first inflections were found in the maxillary, eye and pectoral fin growth. This inflection, however, was somewhat unclear in the body depth and head. Possible intersecting points were observed from about 145.0 to 160.0 mm in fork length. In the eye, the relative growth coefficient of K_2 could be near zero, indicating

Table 1. Fork length at which growth inflection points occur and equations, $\log Y = k \log X + \log b$, of the relative growth curve in body parts to the fork length of the Miyabe char and each form of the Dolly Varden. x denotes $\log X$. There are not statistically significant differences in the coefficients between *1. The intersecting points shown by stars (*) were estimated from visual observations.

		Body depth	Head	Maxillary	Pectoral fin	Eye
L-form	K_1	$2.0255x-1.2695$ ($r=0.94$, $N=12$)	$1.5581x-0.8736$ ($r=0.96$, $N=12$)	$1.4709x-1.2309$ ($r=0.88$, $N=8$)	$1.7422x-1.1906$ ($r=0.96$, $N=14$)	$0.7223x-1.0362$ ($r=0.98$, $N=151$)
	1st inflect.	32.1	29.4	29.6	37.0	
	K_2	$0.9869x-0.7426$ ($r=0.98$, $N=132$)	$0.8917x-0.5615$ ($r=0.99$, $N=156$)	$0.9831x-1.0009$ ($r=0.99$, $N=134$)	$0.8607x-0.6887$ ($r=0.98$, $N=123$)	
	2nd inflect.	184.0	182.5	132.7	170.0*	
	K_3	$1.4010x-1.2666$ ($r=0.90$, $N=49$)	$1.1323x-0.8651$ ($r=0.86$, $N=48$)	$1.3083x-1.3661$ ($r=0.81$, $N=65$)	$0.9290x-0.7434$ ($r=0.83$, $N=61$)	
	LR-form	$1.4548x-1.2202$ ($r=0.86$, $N=43$)	$0.8358x-0.4906$ ($r=0.90$, $N=43$)	$1.1491x-1.1245$ ($r=0.86$, $N=43$)	$0.9702x-0.7740$ ($r=0.94$, $N=39$)	$0.7908x-1.0840$ ($r=0.88$, $N=41$)
R-form	RT-form	$1.0964x-0.8273$ ($r=0.99$, $N=85$)	$0.8808x-0.5477$ ($r=0.99$, $N=85$)	$1.0428x-1.0446$ ($r=0.98$, $N=79$)	$0.9379x-0.7646$ ($r=0.98$, $N=83$)	$0.7461x-1.0574$ ($r=0.97$, $N=78$)
	RN-form	$0.9925x-0.7164$ ($r=0.97$, $N=82$)	$0.9561x-0.5964$ ($r=0.99$, $N=81$)	$1.1261x-1.0822$ ($r=0.97$, $N=83$)	$1.0037x-0.8183$ ($r=0.98$, $N=80$)	$0.8199x-1.1252$ ($r=0.97$, $N=84$)
	RNu-form	$1.1442x-0.8823$ ($r=0.98$, $N=83$)	$0.8816x-0.5526$ ($r=0.98$, $N=83$)	$1.1010x-1.0865$ ($r=0.96$, $N=83$)	$0.8224x-0.6565$ ($r=0.96$, $N=83$)	$0.7203x-1.0548$ ($r=0.92$, $N=82$)
S-form	K_1	$1.0369x-0.7893$ ($r=0.98$, $N=91$)	$0.8892x-0.5540$*1 ($r=0.99$, $N=87$)	$0.9994x-0.9886$ ($r=0.98$, $N=85$)	$0.8904x-0.7399$ ($r=0.98$, $N=84$)	$0.7420x-1.0396$ ($r=0.98$, $N=89$)
	1st inflect.	——	——	149.3	145.3	158.5
	K_2	——	$0.8726x-0.5445$*1 ($r=0.90$, $N=21$)	$0.7960x-0.7498$ ($r=0.81$, $N=22$)	$0.5586x-0.3542$ ($r=0.83$, $N=21$)	$-0.0639x-0.0725$ ($r=-0.15$, $N=13$)
	2nd inflect.	225.0*	357.1	291.5	268.0	210.7
	K_3	$1.0946x-0.8106$ ($r=0.95$, $N=26$)	$1.3860x-1.3417$ ($r=0.97$, $N=10$)	$1.6219x-1.9594$ ($r=0.97$, $N=10$)	$1.3477x-1.4811$ ($r=0.96$, $N=10$)	$0.5098x-0.8319$ ($r=0.89$, $N=14$)

no growth between the first and next inflections. The second inflection occurred in all of the body parts examined, when the fish attained 200~350 mm in fork length, and their growth ratios showed tachyauxesis thereafter, though the intersecting points of the body depth were estimated from visual observation, not from the equations. In contrast with these two forms, all of the river-resident forms did not show remarkable inflections in the relative-growth curve of all the body parts examined.

Between k_2 in the L-form and k_1 in the S-form, the relative growth coefficient showed no significant differences in all the body parts examined. No significant differences were recognized in k between the RT-form and RNu-form, but there were significant differences in k of the body parts examined between the RT-form and RN-form ($P<0.05$). Significant differences also existed between the RN-form and RNu-form in all the body parts examined except the maxillary. Comparing k_2 of the L-form and k of the RNu-form, there was no significant difference in each body part, except for the body depth. However, no difference was recognized in the body depth between L-form and RT- or RN-forms. The most striking difference between the S-form and the other forms was that the S-form has a lower growth ratio in the maxillary, pectoral fin, and eye after the first inflection, and a greater ratio in the maxillary, pectoral fin, and eye after the second inflection.

Fork length, sex ratio, and age at maturity of the Miyabe char. The fork length and age and sex ratios at maturity of both the L- and LR-forms are shown in Fig. 7. All of the L-form were over 180 mm in fork length, but there was no such great length in the

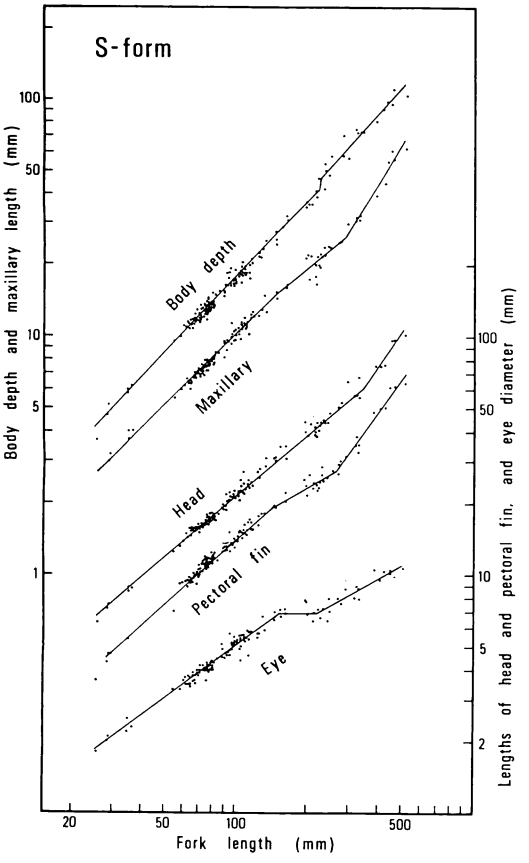

Fig. 5. Relation of body parts to fork length in sea-run form (S-form) of Dolly Varden.

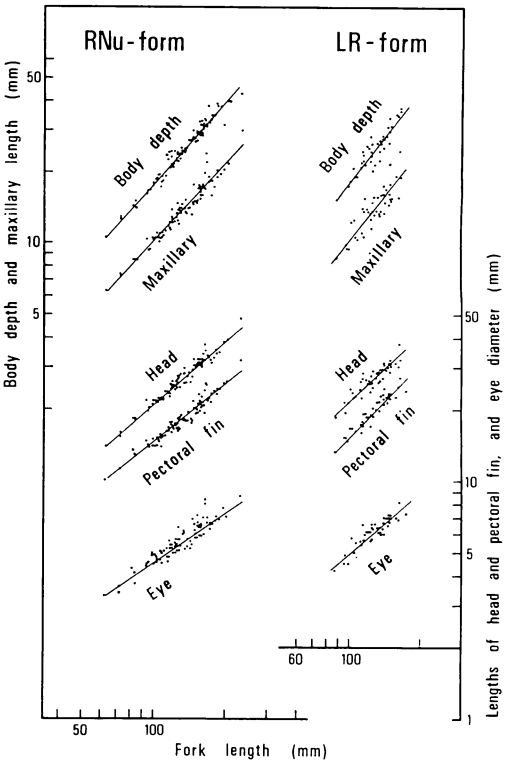

Fig. 6. Relation of body parts to fork length in river-resident form of Miyabe char (LR-form) and river-resident form of Dolly Varden (RNu-form).

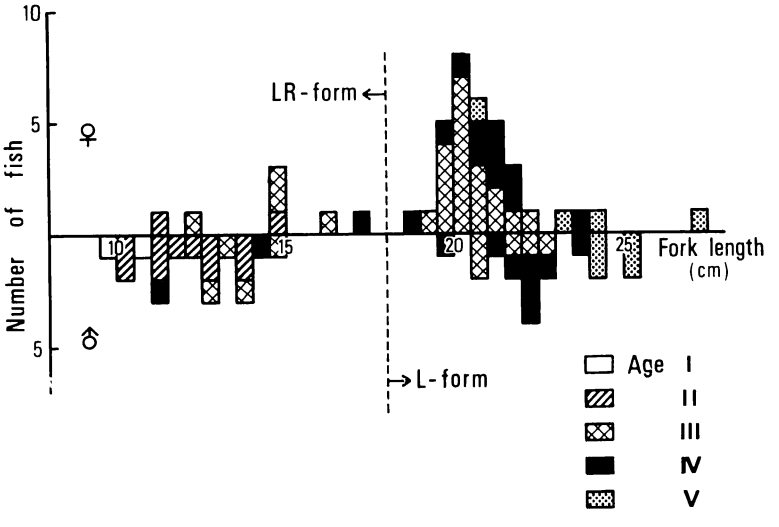

Fig. 7. Size and age compositions of mature Miyabe char collected in the Yambetsu River and the Kohan River.

LR-form. The minimum size of the latter was 95.0 mm in fork length. Therefore, a distinct difference in the fork length at maturity was recognized between the two forms.

The male to female ratio was about 1:2 in the L-form and about 3:1 in the LR-form.

The population sample of the L-form consisted of individuals of age groups of three to five, and those of three (40%) and four (37%) years were predominant. A few samples were seven years old or more with a fork length of 30～35 cm. On the other hand, individuals belonging to the LR-form were younger than those of the L-form, and consisted at age groups of one to four years old, with a mode at two years for male and three years for females.

Discussion

The shape of a fish is modified by different rates of growth, acceleration or retardation and development in various body parts (Hubbs, 1926). In the present study, the growth rate of the Miyabe char (L-form) was similar in the early stage of growth to that of the river-resident form, but the remarkable difference appeared from two years of age, when the former migrated into the lake and grew rapidly thereafter. Heiser (1966), who investigated the age and growth of anadromous Dolly Varden, showed that this char exhibited a slow growth rate before the stage of two or three years of age and a very rapid growth rate after the stage of migration into the sea. Blackett (1968, 1973) and Armstrong and Winslow (1968) studied the fecundity of the resident and anadromous Dolly Varden in southeastern Alaska and reported that the resident char matured sexually a year or more earlier and at a smaller size than did the migratory char (from 5 or 6 years of age). Ishigaki (1969) found that the river-resident form of the Dolly Varden in Hokkaido reached maturity at one year of age, 12 cm in fork length, based on the reading of circuli of scales, but Komiyama (1978), on the basis of the examination of otolith, reported recently that the river-resident form matured from two years of age. The lake-run form of the Miyabe char matured from three years of age at about 180 mm in fork length, while the river-resident form of the Miyabe char matured in one year at 95 mm in fork length. Of the forms of *S. malma* examined, therefore, the greatest retardation of growth and acceleration of maturity were in the river-resident form of the Miyabe char, while in the lake-run form of the Miyabe char muturity was attained at a later and more advanced stage of growth than in the river-resident form of the Dolly Varden, and in the anadromous char in Alaska at the most advanced stage. Therefore, the stage of divergence in the relative body size might be connected with the age of sexual maturity, although the Alaskan forms cannot be compared with Asian races since there is no report on their accurate age of maturity determined by means of otoliths.

Martin (1949) studied the growth rates of many fishes and showed that inflections occurred at the hatching stage, some stages of metamorphosis, ossification, and sexual maturity. He also pointed out that differences in the relative sizes of body parts between fish of the same species were the results of changes in the time of inflections, not in the gradient of the relative growth curves. Many other authors have also investigated growth inflections of fish and have discussed the mechanism of the inflection (cf. Amaoka, 1964). In this study, the relative-growth pattern of each form of the Dolly Varden seemed to be closely similar to that of the brook trout, *S. fontinalis*, from small brooks, from larger bodies of water and of sea-run stocks, which were compared by Wilder (1952). The first inflection observed in the head, body depth, and maxillary occurred at about 30 mm in fork length and corresponded well with the distinguishing point between the phases C_1 and C_2 of development (Maekawa, 1977a). This inflection may probably occur in the growth line in each body part of sea-run form and also river-resident form.

One of the characteristic inflections appeared in the sea-run form between 140 and 160 mm in fork length, though it was not clear in the other forms. The growth ratios showed a remarkable bradyauxesis from this inflection to the next. This may be due to a more rapid growth rate of fork length after the

migration into the sea (Heiser, 1966). Therefore, differences in the relative size of body parts between these three forms become clear after this inflection.

Second inflections of some dimensions in the lake-run form of the Miyabe char and the sea-run form of the Dolly Varden occurred in the area of sexual maturity, though they were somewhat unclear in the river-resident form in Hokkaido. From these considerations as mentioned above, it can be concluded that differences in the relative sizes of body parts among the three forms are results of changes in the timing or the number of times of the inflections, as was pointed out by Martin (1949).

Here, it is interesting to note that the inflection of fork length, which appeared at about 150 mm in fork length in the sea-run form, almost coincided with that of smolts (Armstrong, 1970). The author suggested in an earlier paper (1977a) that the Miyabe char might grow to sexual maturity without transformation to a complete smolt, or if they were transformed, such individuals might be very few. The work of Kubo (1967) is very interesting in that smolt transformation did not occur in the Miyabe char when cultured in a pond under usual conditions, but some juveniles transformed into silvery smolts in the third spring of their life when reared under blue light. This occurrence of smolts suggests that the silvery colour of the Miyabe char could be due to a change in the quality of ambient light or by other unknown factors after the fish migrates into the lake during their young stage (Maekawa, 1977a). This change to smolt did not appear or appeared very seldom in the resident form of the Dolly Varden in Hokkaido (Ishigaki, 1969; Maekawa, 1973). Individuals of the Dolly Varden living in lakes dammed artificially change to a silvery body colour, but they retain juvenile characteristics, such as a reduced lower jaw, even in an adult (Maekawa, in preparation). Therefore, it is supposed that most of the Miyabe char, as in the river-resident form of the Dolly Varden, contnuies to grow without changing to a complete smolt, in contrast with the anadromous form, since the inflection corresponding to the fork length of smolt in the sea-run form does not occur in the relative growth line for the lake-run form of the Miyabe char. As a result, most of the Miyabe char might retain a juvenile body form even as an adult.

The most striking characteristics of the lake-run form of the Miyabe char are, as in the river-resident form, those remarkable parr marks which appear at maturity. A large number of the lake-run and river-resident Miyabe char live to spawn more than twice (Maekawa, in preperation), in contrast with the sea-run form of the Dolly Varden (Armstrong, personal communication). On the other hand, the Miyabe char resembles the anadromous form of the Dolly Varden in some characteristics, i.e. both forms produce river-resident form and have such morphological characteristics as a prolonged lower jaw and relatively large red spots on the body in contrast to the reduced jaw and small red spots of the river-resident form. In other words, the Miyabe char has intermediate characteristics between the anadromous and resident forms of the Dolly Varden and is more precocious and has more neotenous characteristics than the anadromous Dolly Varden. Therefore, the relation between the Miyabe char and the anadromous Dolly Varden might correspond well with that between the land-locked kokanee and the anadromous sockeye, *Oncorhychus nerka* (Ricker, 1938).

Kubo (1967) presumed from ecological and physiological studies that the Miyabe char might be a stock of typical anadromous *Salvelinus malma*. As mentioned above, however, the Miyabe char slightly differs from the anadromous form and/or river-resident form, and differs also in the hemoglobin pattern (Yoshiyasu, 1973) and in the number of gill rakers (Maekawa, 1977b).

It is interesting to note that Ricker (1940) thought that the process of the evolution of the kokanee consisted of two stages of growth: (a) the occurrence of residual or lake-type offspring among the progeny of the anadromous stock; (b) the modification of the progeny of such residuals into the typical kokanee. He postulated that the relation between growth and development in the first stage and natural selection in the second stage played an im-

portant role. The process of evolution of the Miyabe char in relation to land-locking mechanism might be similar to that of the kokanee, as described by Ricker.

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(Department of Oral Anatomy, Faculty of Dental Medicine, Hokkaido University, Sapporo 060, Japan)

然別湖産イワナおよびオショロコマの降海型，河川残留型の生長と発育

前川　光司

然別湖産イワナ，オショロコマの降海型と河川残留型の生長と発育を比較した．然別湖産イワナの稚魚期の生長率はオショロコマ河川残留型によく似ているが，前者は湖に降りる 2^+ から生長率がより高まり，その結果両者の体の大きさは顕著に違ってくる．然別湖産イワナはオショロコマ河川残留型よりも一層生長が進んでから性成熟に達する．体各部の相対生長曲線を比較すると，これら三型の最も大きな違いは，オショロコマの降海型にスモルトの尾叉長と一致するところに顕著な変曲点があるが，その他の型ではこれが明瞭でないことである．それ故，然別湖産イワナはオショロコマの降海型よりも幼形的な体形や体の大きさをもっており，これは前者が後者よりも早熟であることと関係していると考えられる．然別湖産イワナの陸封化が kokanee のそれと対応していることを論議した．

(060 札幌市北区北 13 西 7　北海道大学歯学部口腔解剖学第一講座)