

Individual Growth Variation of Red-spotted Masu Salmon, *Oncorhynchus masou rhodurus*, in a Mountain Stream

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Abstract Individual growth patterns in red-spotted masu salmon, *Oncorhynchus masou rhodurus*, were examined by mark and recapture in a mountain stream, central Japan. The growth pattern varied substantially among individuals of the same age cohort in the stream. Mean absolute growth rates of the individuals were neither significantly different between years, study sections along the stream course, or sexes, but showed significant differences between seasons. No correlation was found between the individual growth rate of fish and the area of pools they inhabited. However, there was considerable growth variation among inhabitants of the same pool. Within a pool, larger individuals grew more rapidly than smaller ones, despite there being no significant relationship between individual growth rates and initial body weights in the stream overall. Individual growth differences probably resulted from growth depensation caused by intraspecific competition within individual pools.

Fishes characteristically show considerable intra-specific variation in individual growth compared with certain other vertebrates. Individuals of many fish species exhibit indeterminate body growth, and continue to grow, even after attaining maturity. This causes particularly pronounced variation in size within a population (Nilsson; 1955; Werner and Gilliam, 1984).

Many investigators have attempted to determine the cause of individual differences in growth (Yamagishi, 1962; Yamagishi et al., 1974; Brett, 1979; Rubenstein, 1981; Elliott, 1989; Goto, 1989a, b). For salmonids, studies on causes of individual differences in growth are essential, as these may be directly concerned with certain aspects of life history such as smoltification and sexual maturation (Thorpe, 1977; Utoh, 1977; Thorpe et al., 1980; Hirata et al., 1986, 1988; Metcalfe et al., 1988; Taylor, 1990), survival (Saito, 1975; Mortensen, 1977; Elliott, 1985, 1990; Nakano and Nagoshi, 1985), and reproductive success in spawning activity (Gross, 1984; Maekawa and Onozato, 1986; Foote, 1988; Hino et al., 1990). However, most observations on the growth and/or size variation of salmonids have been carried out at the populational level or on individual fish in the laboratory, but rarely on individual fish in their natural habitats.

The fluvial form of the red-spotted masu salmon, *Oncorhynchus masou rhodurus*, is distributed throughout mountain streams along the Pacific coastline of south-western Japan. We have previously evaluated the significance of growth differences in relation to population dynamics (Nagoshi et al., 1982; Nakano and Nagoshi, 1985). Like other salmonid populations, there is marked size variation in salmon of the same age, especially among adults (1+ and older). However, there has been little study of the mechanisms causing differences in individual growth.

This paper examines the variations in individual growth pattern for *O. masou rhodurus* in a natural habitat in relation to some environmental factors.

Materials and methods

The study was performed in the Hirakura Stream, a headwater tributary of the Kumozu River, which discharges into Ise Bay on the east coast of Kii Peninsula, central Japan (Fig. 1). The Higashimata Stream, a small tributary of the Hirakura Stream, was used as the study area. This 1.5 km long tributary is 3 m wide on average. The stream arises at an altitude of 600 m and runs through the Mie University Experimental Forest, which consists of secondary deciduous trees and planted cedar, *Crypto-*

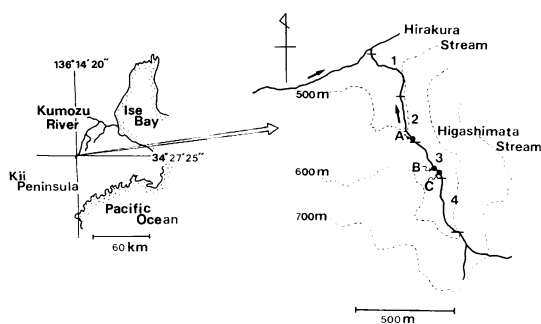


Fig. 1. Map of the Hirakura Stream and location of studied sections (1-4) and pools (A-C) showing contours of 100m elevations. Thick arrows indicate directions of water flow.

meria japonica. The streambed is mainly composed of bedrock and boulder with small areas of sand or gravel. It is a typical mountain stream, with short pools separated by cascades or small waterfalls of about 0.5–3.0m vertical drop.

The whole stream was divided into 4 sections (Fig. 1), and each of the 144 pools numbered so as to record the capture locations for each fish. The mean area of the pools was largest in section 1 and decreased upstream. The gradient as determined from a map, ranged from 11 to 17% between sections. Mean water temperature decreased slightly along the reach, but the difference was significant only between sections 1 and 4 (t-test, $p < 0.05$) (Table 1).

The Higashimata Stream was also inhabited by *Cottus hilgendorfi*, *Phoxinus lagowski*, *Rhinogobius flumineus*, *Linobugurus reini*, and *Anguilla japonica*. The distribution of the first three species was limited to sections 1 and 2 (Table 1), but that of the last two was unknown because of their small population size.

Salmon were marked and/or recaptured in each section from April to November in 1986 and 1987.

Salmon larger than 9.0cm SL were caught by angling and a casting net. From April to September or October 1988, a more intensive mark-recapture program was conducted in pools A, B and C of sections 2 and 3 (Fig. 1). Captured fish were measured to the nearest 0.05mm and weighed to the nearest 0.05g. Fish were individually marked by numbered plastic anchor and ribbon tags, and their scales collected for age determination at first capture. They were then released in the pools in which they were captured. The age of each fish was assessed from their scales following Nagoshi et al. (1982).

In general, the growth potential of fish is considerably different between developmental stages, and it is a delicate subject to compare growth between individuals of different initial sizes. The question of which index should be used is essential in relation to the study purpose. However, for simplicity we calculated absolute growth rate (G) for each individual using the following formula in order to evaluate gain in body weight, which directly influences increases in fecundity, mating success, survival and, therefore fitness.

$$G = (W_2 - W_1)d^{-1}$$

where W_1 and W_2 are body weights (g) at first capture and the recapture, respectively, and d is the number of days between captures.

The numbers of fish in pools A, B and C were estimated by the three points sampling method (Leslie, 1952). The sex of mature fish was determined during the spawning season in autumn (October and November), by pressing lightly on their abdomen to express eggs or sperm.

The population of *O. masou rhodurus* in the Hirakura Stream was mainly composed of three age cohorts (0+ to 2+), and fish older than 2+ were rare (Nagoshi et al., 1982). All marked fish larger

Table 1. Biotic and abiotic characteristics of four study sections in the Higashimata Stream from April to November in 1986 and 1987. Figures in parentheses indicate sample sizes. Plus signs indicate species presence, minus signs their absence.

Section	1	2	3	4
Length (m)	213.1	223.8	254.1	217.3
Mean area of pool (m ²) ± S.D.	24.2 ± 14.0 (23)	22.2 ± 20.9 (32)	13.1 ± 9.8 (45)	10.1 ± 6.3 (45)
Gradient (%)	11	13	17	13
Mean water temperature (°C) ± S.D.	14.9 ± 0.62 (36)	14.5 ± 0.62 (33)	14.1 ± 0.5 (38)	13.3 ± 0.4 (44)
Other fishes present				
<i>Cottus hilgendorfi</i>	+	+	—	—
<i>Phoxinus lagowski</i>	+	+	—	—
<i>Rhinogobius flumineus</i>	+	+	—	—

than 9.0 cm SL were older than 0+ (Nakano et al., 1990). Since the age of fish older than 2+ sometimes could not be determined from scales, all marked fish were classified into two groups, age 1+ (I), and age 2+ or older (II).

Results

A total of 1,165 individuals were marked and released in sections 1–4 during the study periods in 1986 and 1987. However, 10–20% of them showed evidence of tag loss when recaptured. Of the marked individuals, 519 (45%) were recaptured from 1 to 7 times. The periods between successive captures ranged from 1 to 4 months in each year. In 1988, 76 individuals were marked and released, and 28–37 (37–49%) were recaptured each month in pools A, B and C. No fish showed evidence of tag loss in 1988.

Individual growth patterns. The growth patterns of 14 marked individuals, which were captured more than 4 times during a period greater than 4 months, showed substantial variation, even in the same age cohort (Fig. 2). Each individual exhibited a different growth pattern. For example, fish 5 grew rapidly from April to September. Its body weight increment was 75 g, the largest among the 14 examples, for this period. On the contrary, individuals 2 and 11 exhibited little growth from April to September. Their weight increments were about 8 and 5 g, respectively.

Individuals 3, 6, 8, and 10 grew rapidly during spring (from April to June) and little thereafter. The growth curve of fish 4 had some inflections; i.e. growth, which had halted once, apparently occurred again after September. A similar growth pattern was

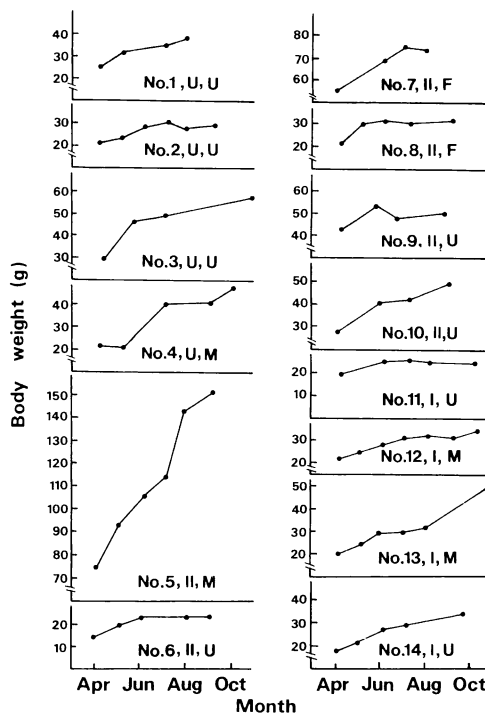


Fig. 2. Growth in body weight of *Oncorhynchus masou rhodurus* recaptured more than four times in 1986 and 1987. I, age 1+; II, age 2+ or older; M, male; F, female; U, unknown age and/or sex.

observed for individual 13.

Among individuals 1, 2, 4, 8, 11, 13, and 14, which had initial body weights of about 20 g in April, fish 13 grew most rapidly during April to November and

Table 2. Comparison of mean growth rate (g/day) of *Oncorhynchus masou rhodurus* between different seasons, years, locations and sexes. Figures in parentheses indicate sample sizes. Analysis of variance (ANOVA) was used to test growth differences. N.S., non-significance.

Category	Mean growth rate ± S.D.				Statistical test	
Season	Spring	Summer	Autumn		ANOVA	p < 0.01
	0.12 ± 0.30 (159)	0.04 ± 0.22 (171)	− 0.06 ± 0.45 (80)			
Year	1986	1987	1988		ANOVA	N.S.
	0.09 ± 0.25 (274)	0.05 ± 0.53 (88)	0.13 ± 0.45 (141)			
Location	Section 1	Section 2	Section 3	Section 4	ANOVA	N.S.
	0.08 ± 0.27 (38)	0.07 ± 0.32 (90)	0.10 ± 0.35 (156)	0.08 ± 0.58 (65)		
Sex	Male		Female		ANOVA	N.S.
	0.12 ± 0.15 (34)		0.11 ± 0.29 (31)			

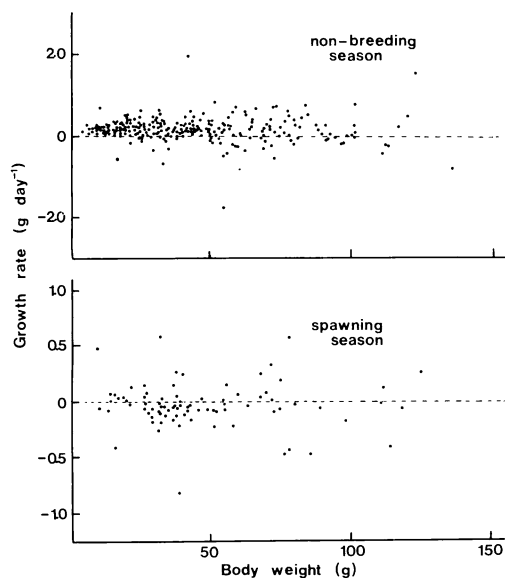


Fig. 3. Relationship between body weight at previous capture and growth rate of *Oncorhynchus masou rhodurus* during the non-breeding season (upper) and the spawning season (lower) in 1986 and 1987.

its weight increment was 28 g. This increment was more than 5 times greater than that of individual 11, which grew only 5 g.

Analysis of growth rate. Fish were classed into several groups, and their mean growth rates were compared between seasons, years, and locations to examine ecological conditions that might cause growth variations. The mean growth rate from April to September (the non-breeding season) was also compared between males and females that could be sexed during the spawning season (Table 2).

No significant differences in fish growth were found for different years, location, or sex. However, the mean growth rate of individuals was significantly different between seasons, being greater in spring (April-June) than in summer (July-September) or autumn (October-November) (Table 2). Both male

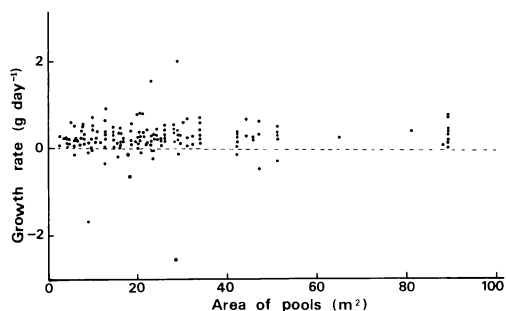


Fig. 4. Relationship between area of pools and growth rate of *Oncorhynchus masou rhodurus* inhabiting them in 1986 and 1987.

and female salmon attain maturity at age 1+ in the Hirakura Stream (Nakano, unpubl. data). The mean growth rate during autumn (spawning season) was therefore negative due to weight loss in mature individuals.

To assess the effect of body sizes on growth, growth rates for each individual between two successive captures during April and September (the non-breeding season) were plotted against their initial body weight for 1986 and 1987 (see below for 1988) (Fig. 3). There was no significant correlation between initial body weight and growth rate of each individual ($r = -0.05$, $p > 0.1$). Similarly, there was no significant correlation when the same analysis was done for captures during the spawning season ($r = -0.09$, $p > 0.1$) (Fig. 3). Thus, the growth rate of individuals for short periods (1–4 months) was not affected by differences in the initial body size.

The relationship between the growth rate of individuals that were always captured in a given pool (Nakano et al., 1990) and the area of the pool was examined (Fig. 4), but no significant correlation was found ($r = 0.021$, $p > 0.1$).

Individual growth in pools. Individual growth variation in pools A, B, and C was examined by mark-recapture in 1988. Pool volume, estimated number of fish in July, and fish density per unit

Table 3. Pool volume, estimated number and density (per unit volume, m^{-3}) in July, and mean growth rate ($g day^{-1}$) of *Oncorhynchus masou rhodurus* in pools A, B and C. Figures in parentheses indicate sample sizes.

Pool	Volume (m^3)	No. of fish \pm S.D.	Density	Mean growth rate \pm S.D.
A	14.2	14 \pm 4	1.01	0.086 \pm 0.34 (10)
B	23.0	22 \pm 5	0.96	0.050 \pm 0.22 (11)
C	26.4	18 \pm 6	0.68	0.078 \pm 0.24 (9)

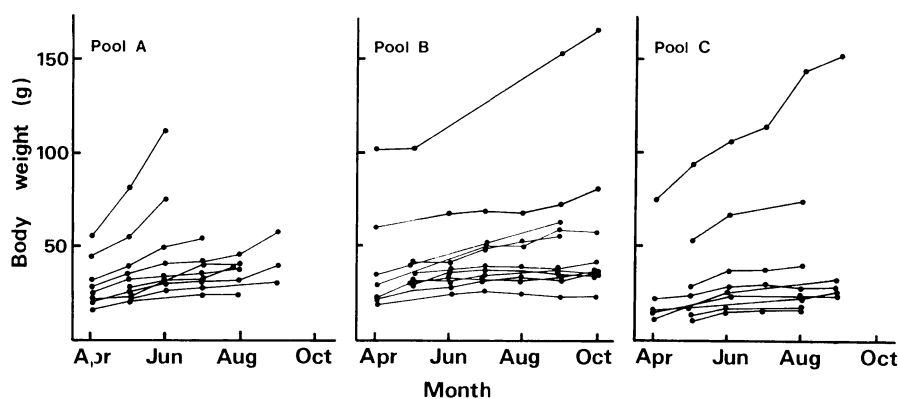


Fig. 5. Body weight changes of individual *Oncorhynchus masou rhodurus* in pools A, B, and C.

volume differed among the pools. Pool A had the highest fish density, followed by pools B and C. The fish density in pool A was 1.5 times higher than that in pool C. However, this minor difference in density was apparently not great enough to affect the mean growth rate of fish, which was not significantly different between pools (ANOVA, $p > 0.1$) (Table 3).

Growth trajectories were drawn for individuals in pools A, B, and C, which were captured more than 3 times during the study period (Fig. 5). Inspection of growth trajectories shows that considerable growth variation occurred even among the individuals inhabiting the same pool. A high positive correlation was obtained between initial weight and growth rate of individuals within each pool (pool A: $n = 10$, $r = 0.85$, $p < 0.01$; pool B: $n = 11$, $r = 0.70$, $p < 0.01$; pool C: $n = 9$, $r = 0.95$, $p < 0.01$) despite there being no significant correlation between weight and growth rate for individuals captured in the entire stream in 1986 and 1987 (see Fig. 3). The largest individuals in each pool grew much faster than the rest.

Discussion

In general, growth of fishes is influenced by water temperature, light, salinity, and dissolved oxygen as abiotic environmental determinants and ration, size, genetics, and competition as biotic ones (Brown, 1957; Brett, 1979). However, we found that the mean growth rate of individual fish varied little along the stream course, despite differences in abiotic characteristics such as stream gradient, water temperature and mean pool area along the reach. Differences in environmental characteristics among the study sections might have been too minor to affect the growth of individuals. The mean growth rate of

fish fluctuated seasonally but not annually. Generally, population density is an important ecological factor accounting for fluctuations in growth rate among fish (Backiel and Le Cren, 1978; Weatherley and Gill, 1987). However, in the Hirakura Stream, Nagoshi et al. (1982) and Nakano and Nagoshi (1985) found that the population density of *O. masou rhodurus* was determined by autumn of the first year of life, so the abundance of age 1+ and older fish fluctuates within a limited range (Nagoshi et al., 1982; Nakano and Nagoshi, 1985). Seasonal difference in growth also seems not to cause great variation among individuals. Moreover, no significant correlation was obtained between individual's growth rate and the area of pools inhabited by them, and considerable growth variation was shown even among inhabitants of the same section and the same pool. Thus, individual growth differences might have resulted from intraspecific competition or from genetic differences in their capacity to grow.

Consideration of genetic factors is beyond the scope of this study. Intraspecific competition, however, is one of the main determinants of individual growth, and induces growth depensation in fish populations (Noakes, 1978; Weatherley and Gill, 1987). In the Hirakura Stream, larger individuals grew more rapidly than smaller ones in each local pool, whereas no significant correlation was found between individual growth rate and initial body weight for the whole population. Thus, the relative size of individuals in each pool appears to be more important as a determinant of individual growth than does absolute body size.

Many authors have reported that stream salmonids in a localized area, such as one pool, form dominance hierarchies (e.g., Newman, 1956; Kalle-

berg, 1958; Chapman, 1962; Jenkins, 1969; Bachman, 1984). Like other stream salmonids, *O. masou rhodurus* in the Hirakura Stream also formed dominance-subordinate relationships within pools on the basis of body size (Nakano, unpubl. data). Thus, the smaller fish were expected to be subordinate in social groups, and their growth was depressed relative to larger fish as a result.

In experimental conditions, it has been widely shown that dominant fish exhibit superior growth rates to subordinates among stream salmonids (Chapman, 1962; Yamagishi, 1962; Wankowski and Thorpe, 1979; Jobling, 1983; Fausch, 1984), and other families (Noble, 1939; Allee et al., 1948; Borowsky, 1978; Rubenstein, 1981). Dominance hierarchies may exert a significant influence on space utilization and/or foraging behaviour of individuals in a social group. Subordinates are excluded from profitable areas for feeding (Yamagishi, 1962; Fausch, 1984; Fausch and White, 1986; Grant, 1990). For example, Fausch (1984) showed that for several species of salmonids dominant fish in an experimental stream held positions affording maximum potential profit (calculated as available energy from drift minus the cost of swimming to maintain position) and, in turn, usually achieved the highest specific growth rate. Puckett and Dill (1985) demonstrated that territorial (dominant) coho salmon in a natural stream had a net energy intake advantage over floaters (subordinate fish) due to reduced cost of search, prey pursuit, and agonistic activity.

Another cause of inferior growth in subordinates is that they may convert food less efficiently than dominants (Jobling and Wandsvik, 1983; Metcalfe, 1986). The physiological costs for stressed subordinates should be higher than for dominants. Thus, dominants grow faster on average than subordinates even if access to, and consumption of, food is equal and subordinates are less active than dominants (Abbott and Dill, 1989).

In the Hirakura Stream, most (63–90%) adult salmon exhibited sedentary behaviour in individual pools (Nakano et al., 1990), which is consistent with observations on many other stream salmonids (Miller, 1957; Burnet, 1969; Solomon and Templeton, 1976; Bachman, 1984; Harcup et al., 1984). Therefore, the dominance status of each member within a local group is likely to remain relatively constant for long periods, once established, so that larger dominant individuals can be expected to grow more rapidly. Reversal of dominance rank seldom

occurs among individuals in the dominance hierarchy either in experimental (Abbott et al., 1985) or wild conditions (Jenkins, 1969; Bachman, 1984; Nakano, unpubl. data). Therefore, stable dominance-subordinate relationships should increase variation in size among individuals in local social groups.

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山地溪流のアマゴにおける成長の個体変異

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本州中央部の山地溪流においてアマゴ *Oncorhynchus masou rhodurus* の個体ごとの成長様式を標識再捕法によって調査した。成長様式は同一年齢群内においても個体によってかなり異なった。個体の1日当りの成長量の平均値は年、流程に沿って配置された調査区および雌雄間では大きな差はみられなかったが、季節間では有意に異なり、春期(4-6月)に最も大きかった。また、個体の成長量は定住している淵の面積とは無関係であった。同一淵内に生息する個体間にも大きな成長変異が認められ、相対的に体の大きい個体ほど成長量が大きかった。調査水域全体では個体の初期の大きさと成長量との間には有意な相関関係は認められなかったことから、個体間の成長変異は主に同一淵内での個体間の競争関係に依存して生じる成長差からもたらされると考えられた。

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