

# Otolith Microstructure in Young-of-the-Year Dolly Varden, *Salvelinus malma*, from American and Asian Populations: Resolution of Comparative Life History Characteristics

R.L. RADTKE,<sup>1</sup> D.P. FEY,<sup>2</sup> A.F. DeCICCO<sup>3</sup> and A. MONTGOMERY<sup>1</sup>

(Received 14 August 1995; accepted in revised form 15 February 1996)

**ABSTRACT.** Sagittal otoliths from young-of-the-year Dolly Varden, *Salvelinus malma*, captured from Cripple River, Alaska and Cha'atam River, Russia were prepared and observed with transmitted light microscopy. Distinct microstructure in samples from both locations indicated daily growth increments, hatching checks and first feeding checks that confirm literature findings in other salmonids. We used increment counts to estimate the ages of individual juveniles and calculated hatch dates and times of first feeding from those ages. Increments deposited before the first feeding mark were significantly smaller than those formed after this mark. Alaskan and Russian fish showed a significant difference in hatching times and the period of first feeding. Summer growth rates of the Russian population, calculated from length-at-age data, were faster ( $0.356 \text{ mm} \cdot \text{day}^{-1}$ ) than those of the Alaskan population ( $0.301 \text{ mm} \cdot \text{day}^{-1}$ ). However, when the average growth rate was calculated with the formula  $GR = (L_{\text{capture}} - L_{\text{hatching}})/\text{age}$ , the values were higher for the Alaskan population ( $0.25 \text{ mm} \cdot \text{day}^{-1}$ ) than for the Russian population ( $0.20 \text{ mm} \cdot \text{day}^{-1}$ ). When otolith radius–fish size relationships were estimated, Alaskan otoliths were found to be larger for the same size fish, because wider increments were deposited in fish from Alaska. Increment width also was related to time of the year: wider increments were deposited during the warmer months. Otolith microstructure provided insights into the early life history of young-of-the-year Dolly Varden from American and Asian populations.

**Key words:** Dolly Varden, *Salvelinus malma*, otoliths, growth, hatch period, Cripple River, Alaska, Cha'atam River, Russia

**RÉSUMÉ.** Des sagittas provenant de Dolly Varden (*Salvelinus malma*) de l'année capturées dans la Cripple en Alaska et dans la Cha'atam en Russie ont été préparées et étudiées au microscope pour examen par transmission. Une microstructure distincte dans les échantillons provenant des deux sites révélait une croissance quotidienne, des repères de l'éclosion et des repères de la première phase alimentaire, qui confirment les résultats consignés dans la documentation sur d'autres salmonidés. On s'est servi du comptage des unités d'accroissement pour estimer l'âge des individus juvéniles et on a calculé la date d'éclosion et la date de la première phase alimentaire à partir de cet âge. Les unités d'accroissement formées avant le repère signalant le début de la phase alimentaire étaient nettement moindres que celles qui se sont formées après ce repère. Les poissons d'Alaska et ceux de Russie montraient une nette différence dans leurs dates d'éclosion et dans celles signalant le début de la phase alimentaire. Les taux de croissance estivaux de la population russe, calculés à partir des données sur la longueur à un âge précis, étaient plus rapides ( $0,356 \text{ mm} \cdot \text{jour}^{-1}$ ) que ceux de la population alaskienne ( $0,301 \text{ mm} \cdot \text{jour}^{-1}$ ). Cependant, quand on calculait le taux moyen de croissance à l'aide de la formule  $TC = (L_{\text{capture}} - L_{\text{éclosion}})/\text{âge}$ , les valeurs étaient supérieures pour la population alaskienne ( $0,25 \text{ mm} \cdot \text{jour}^{-1}$ ) que pour la population russe ( $0,20 \text{ mm} \cdot \text{jour}^{-1}$ ). Lorsqu'on a estimé la relation entre le rayon de l'otolithe et la grosseur du poisson, on a trouvé que les otolithes alaskiennes étaient plus grosses pour la même taille de poisson, parce que les unités d'accroissement chez les poissons alaskiens étaient plus grandes. La taille des unités d'accroissement était aussi reliée à la période de l'année, le plus fort de l'augmentation ayant lieu durant les mois chauds. La microstructure des otolithes a permis de mieux comprendre la première étape de la vie de la Dolly Varden de l'année, venant de populations américaine et asiatique.

**Mots clés:** Dolly Varden, *Salvelinus malma*, otolithes, croissance, période d'éclosion, rivière Cripple, Alaska, rivière Cha'atam, Russie

Traduit pour la revue *Arctic* par Nésida Loyer.

## INTRODUCTION

The salvelinid Dolly Varden, *Salvelinus malma*, is distributed predominately throughout the northern Bering Sea, the southern Chukchi Sea, and along the Beaufort Sea, and its

range includes most of the freshwater tributaries of those seas. Several body forms and life history patterns of Dolly Varden have been described (Armstrong and Morrow, 1980), and northern and southern forms have been distinguished. Spawning takes place in freshwater as early as August or as

<sup>1</sup> School of Ocean and Earth Sciences and Technology, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.

<sup>2</sup> Department of Oceanography, Sea Fisheries Institute, ul. Kollataja 1, Gdynia 81-332, Poland

<sup>3</sup> Alaska Department of Fish and Game, Sport Fish Division, Fairbanks, Alaska 99701-1599, U.S.A.

late as November, and eggs are incubated under ice cover for seven to eight months. The eleutheroembryos, which are 15–20 mm long at hatching, stay in the gravel for a period of 60–70 days until they have absorbed the yolk sac. Emergence takes place around the time of ice break-up, from April to June, and alevins emerge from the nest at a length of about 25 mm. Growth greatly increases as water becomes warmer; by September, the presmolts average about 60 mm in length and 2 g in weight. Young-of-the-year Dolly Varden often inhabit small streamlets only 1–3 cm deep, where water flow is slow (Armstrong and Morrow, 1980).

Few papers exist on the early life history and growth patterns of Dolly Varden. Many early life history processes occur under ice cover and in remote habitats, which makes field studies of the early life history stages forbidding, if not impracticable. Analyses of otolith microstructure may provide a means of sidestepping these difficulties. Pannella (1971, 1974) first discovered daily increment microstructure in otoliths, and daily increment formation has since been verified for a myriad of fish species (see Summerfelt and Hall, 1987; Stevenson and Campana, 1992). A number of investigations have shown daily increment deposition in salmonid otoliths (Wilson and Larkin, 1980, 1982; Neilson and Geen, 1982; Volk et al., 1984; Radtke and Fey, in press). For salmonids it is possible to determine the date of hatching (Marshall and Parker, 1982; Neilson and Geen, 1982) and emergence (Wilson and Larkin, 1980) by interpreting otolith marks and daily increments. Otolith microstructure is an excellent source of information about habitat conditions affecting growth and possibly even success early in life.

Here we examine habitat-dependent growth of Dolly Varden by comparing growth of young-of-the-year populations that occur at the same latitude, but on different continents. We used otoliths to retrospectively describe differences in the early growth rates of Dolly Varden presmolts of different populations. In the process, we assessed the potential of otolith microstructure to record the early life history of Dolly Varden, such as hatching and first feeding dates.

## MATERIALS AND METHODS

We collected samples from the Cripple River, Seward Peninsula, Alaska and the Cha'atam River, Chukotskiy Peninsula, Russia, chosen for their wide geographic separation along the same line of latitude. Dolly Varden samples from these two rivers allow us to examine first-year growth in North American and Asian populations living in similar climatic conditions (Fig. 1). Both rivers, of similar size, offer spawning and overwintering habitat for anadromous Dolly Varden. The Cha'atam River is a tributary of the Kurupka River and flows south into the Gulf of Anadyr, while the Cripple River is an independent drainage flowing south into Norton Sound. Juvenile Dolly Varden were captured using minnow traps baited with fish eggs (chum salmon eggs in the Cripple River and Dolly Varden eggs in the Cha'atam River) and a small dip net. Collections in both rivers were made from

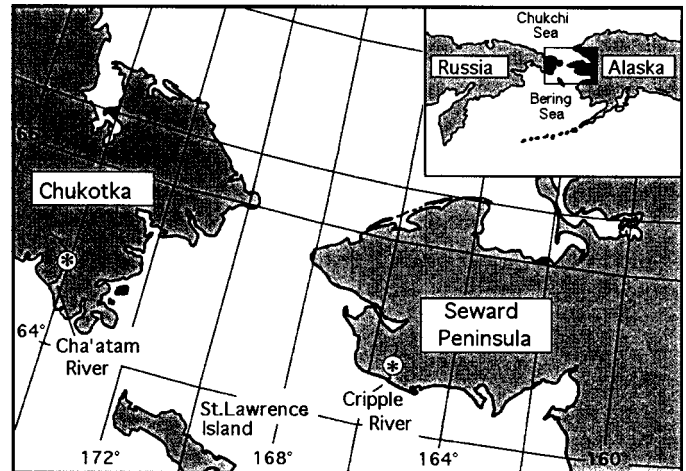


FIG.1. Locations where the juvenile Dolly Varden were collected: Cripple River, Seward Peninsula, Alaska (64°41'N, 165°44'W) and Cha'atam River, Chukotskiy Peninsula, Russia (64°58'N, 174°03'W).

small side-channel nursery areas near known Dolly Varden spawning areas. Eleven juvenile fish were captured in Alaska (64°41'N, 165°44'W) on 23 August 1993, and thirty juvenile fish were captured in Russia (64°58'N, 174°03'W) on 13 September 1993.

The standard length (SL) (nose to caudal peduncle) of all fish was measured, the otoliths were extracted, and the left sagitta from each fish was mounted sulcus side down on a glass slide using Petropoxy resin (Palouse Petro Products, Palouse, Washington). Mounted otoliths were ground to mid-plane with wet sandpaper (600 grit) and polished with alumina paste (0.3  $\mu$ m and 0.05  $\mu$ m) until all increments between the core and the outer edge were visible. Detailed procedures are described in Radtke (1989). Prior to visualization by light microscopy, and after grinding and polishing, otoliths were embedded within a mounting medium that has a refractive index similar to that of glass, and covered with a glass cover slip.

Otoliths were observed with transmitted light at 1000 $\times$  magnification. All measurements and increment counts were taken along the medial rostral plane from the center to the otolith edge (Radtke, 1987, 1989). An increment was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean, 1982). The hatching and first feeding checks, as defined by Neilson and Geen (1982) and Zhang et al. (1995), were recognizable in most samples. Increment images were digitized and enhanced using image analysis software. Increments were enumerated twice by the same person at different times, without knowledge of the prior results. The maximum variability was a difference of five increments, and the majority of counts varied by two increments or less. The average of the two counts was used for subsequent analyses.

Several additional otolith dimension measurements were taken for comparison: distance to the hatching check, distance to the first feeding check, the otolith radius, and individual increment widths of selected samples (total n = 4). Average increment widths were calculated within defined

areas for all samples by dividing the distances (between hatching marks and first feeding marks, between hatching marks and the edge of the otolith, and between the first feeding marks and the edge of the otolith) by the number of increments in those areas. The nucleus length of all otoliths was measured, following the method of Neilson et al. (1985).

Growth rates were calculated from length-at-age data. The average growth rates for both populations were calculated with the formula:

$$GR = (SL_{\text{capture}} - SL_{\text{hatching}}) / \text{age}$$

Size at hatching was taken from the literature to be 17.5 mm (Blackett, 1968; Armstrong and Morrow, 1980). The summer growth rate was calculated from size-at-age data using linear regression methods. Increment-width correlations with season were related by the third-order polynomial equation:

$$y = ax^3 + bx^2 + cx + d$$

where  $y$  is increment width;  $x$  is time in days;  $a$ ,  $b$ , and  $c$  are constants; and  $d$  is the intercept.

## RESULTS

There was no statistically significant difference in age (number of increments) between samples from Alaska and Russia. However, the Alaskan fish were significantly larger and had significantly higher growth rates ( $0.25 \text{ mm}\cdot\text{d}^{-1}$ ) than the fish from Russia ( $0.20 \text{ mm}\cdot\text{d}^{-1}$ ) (two sample t-test, Table 1).

Hatching and first feeding dates were estimated by back-calculation on the basis of daily increment counts (Fig. 2). The differences in hatching and first feeding dates between fish from the two locations were statistically significant (two sample t-test,  $p < 0.01$ ). Both hatching and first feeding took place earlier in Alaska than in Russia, and the time between hatching and first feeding was shorter for fish from Alaska (Table 1).

The length-at-age data for both Alaskan and Russian locations are presented in Figure 3. The growth rates during August and the first half of September were calculated from this data using least-squares linear regression. The Russian population grew faster ( $0.356 \text{ mm}\cdot\text{day}^{-1}$ ) than the Alaskan population ( $0.301 \text{ mm}\cdot\text{day}^{-1}$ ). However, the low correlation coefficients for both regressions, especially for the Russian samples, suggest that these data may represent to a large degree the variation in length for a given age. Thus, the calculated growth rates, even if reasonable, should be taken with caution.

The otolith radius of the Alaskan fish was significantly larger than that of the Russian fish (two-sample t-test, Table 2, Fig. 4). Figure 4 clearly shows the relationship between otolith radius and standard length for samples from both locations. Nevertheless, there was no significant difference in

nucleus length, the distance to the hatching check, or the distance to the first feeding check between the two populations (two-sample t-test, Table 2). The difference in overall otolith radii is attributable to wider increment deposition by fish from Alaska after first feeding (Table 1).

Figure 5 shows the change in increment width with time in two individuals from Alaska (Fig. 5a, b) and two from Russia (Fig. 5c, d). For both groups, the pattern is similar. Increment width began to increase in early June. The widest increments were formed in July, but their width began to decrease in August. The smallest increments were laid down at the beginning of September (Alaska:  $\approx 1 \mu\text{m}$ ; Russia:  $< 1 \mu\text{m}$ ). The difference in increment width between Alaska and Russia is considerable (Fig. 5e, Table 1), Alaskan fish having the wider increments. The maximum increment width among the otoliths we have analyzed was  $5.1 \mu\text{m}$  for Alaskan fish and  $3.8 \mu\text{m}$  for Russian fish. The increase in increment width appears to be associated not only with the time of year, but also with the transition from a yolk-sac phase to external feeding and associated emergence (Fig. 5). Increments deposited before the first feeding check were significantly smaller (two-sample t-test) than those deposited after emergence and the shift to external food sources (Table 1).

## DISCUSSION

In every fish population, the strength of a cohort is defined by the biological and physical factors governing growth and survival (Fogarty et al., 1991; Grosberg and Levitan, 1992). We have concentrated upon growth processes that transpire early in the life history, because cohort numbers are often determined at this time (e.g., Sinclair, 1988) and little is known of the early life history ecology of Dolly Varden.

Abundant literature, especially about salmonids, supports the assumption of daily increment formation (Stevenson and Campana, 1992; Secor et al., 1995). Some species, such as Dolly Varden, thrive at temperatures that would inhibit daily increment deposition in others (Umezawa and Tsukamoto, 1991). For example, Chinook salmon (*Oncorhynchus tshawytscha*) continue daily increment formation at  $4^\circ\text{C}$  (Neilson and Geen, 1982) but with reduced increment width. Similarly, increment deposition in Dolly Varden, which are physiologically adapted to thrive in harsh environmental conditions, is not likely to be inhibited by low temperatures. During the summer months, when larvae and juveniles are developing, the general pattern for arctic rivers is to warm quite rapidly after ice break-up and maintain temperatures above  $5^\circ\text{C}$  until the fall (Power, 1969).

The timing of the deposition of the first otolith increment varies among species (e.g., Wilson and Larkin, 1980; Marshall and Parker, 1982; Radtke and Dean, 1982; Radtke, 1989). Daily otolith increments are deposited at hatching in some salmonids, and these are often used as reference points in increment counts (Marshall and Parker, 1982; Neilson and Geen, 1982; Zhang et al., 1995). In a field study on sockeye salmon (*Oncorhynchus nerka*), Wilson and Larkin (1980)

TABLE 1. Summary of the data on the juvenile Dolly Varden analyzed.

	n		SL <sup>1</sup> (mm)	age (days)	time to ff <sup>2</sup> (days)	increment width (µm)			growth rate (mm·day <sup>-1</sup> )
						all	before ff	after ff	
Alaska	11	average	47.57	147.27	41.6	2.33	1.78	2.65	0.25
Cripple River		SD	3.95	11.54	6.16	0.23	0.35	0.18	0.02
(64°41'N)		min.	40.30	130.00	32	1.98	1.28	2.44	0.23
		max.	53.10	163.00	52	2.67	2.26	2.83	0.27
Russia	30	average	43.20	151.97	52.1	1.93	1.53	2.23	0.20
Cha'atam River		SD	5.68	11.19	5.46	0.20	0.20	0.31	0.03
(64°58'N)		min.	32.30	133.00	42	1.59	1.09	1.61	0.13
		max.	55.30	175.00	64	2.30	1.84	2.83	0.27
t-test	df	39	39	32	32	32	32	32	39
two-sample	t	3.187	2.263	4.440	5.333	2.528	3.700	3.040	3.040
	p	<0.01	<0.05	<0.001	<0.001	<0.01	<0.001	<0.01	<0.01

<sup>1</sup> SL = standard length, nose to caudal peduncle

<sup>2</sup> ff = first feeding

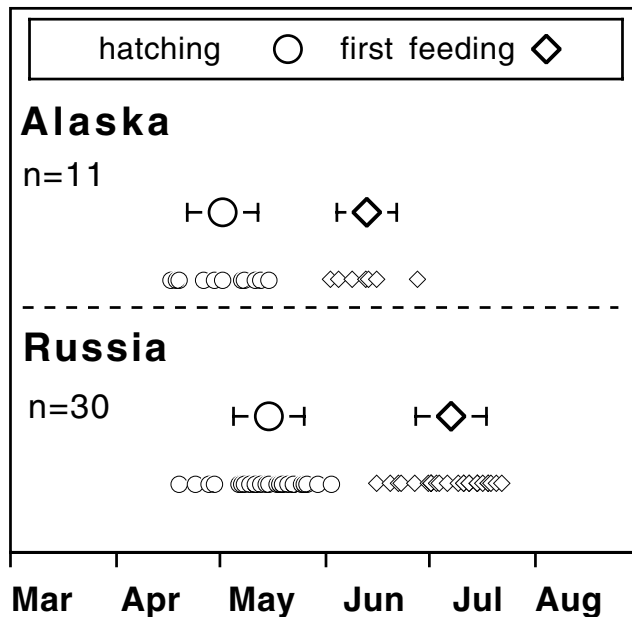


FIG. 2. Calculated hatching and first feeding times of juvenile Dolly Varden from Alaska (Cripple River) and Russia (Cha'atam River). The large symbols represent average dates (± 1 SD); and the small ones show values for individual fish.

concluded that increment deposition begins at emergence from the redd. Differences in the time of first increment deposition may be related to the absence of light in the natural environment, i.e., within the gravel of the redd (Radtke and Dean, 1982). We were able to recognize both hatching and first feeding checks. Our conclusions in this study are based upon the assumption that increments are deposited daily beginning at hatching; thus, increment counts represent the true age of a fish in days.

Hatching in both locations started in the middle of April; however, on average, peak hatching occurred earlier in Alaska (end of April) than in Russia (middle of May). First feeding began significantly earlier in Alaska (June) than in Russia (July), and the time between hatching and first feeding was considerably shorter for fish from Alaska (41.6 vs. 52.1 days). In the rivers of northern Alaska, spawning of Dolly

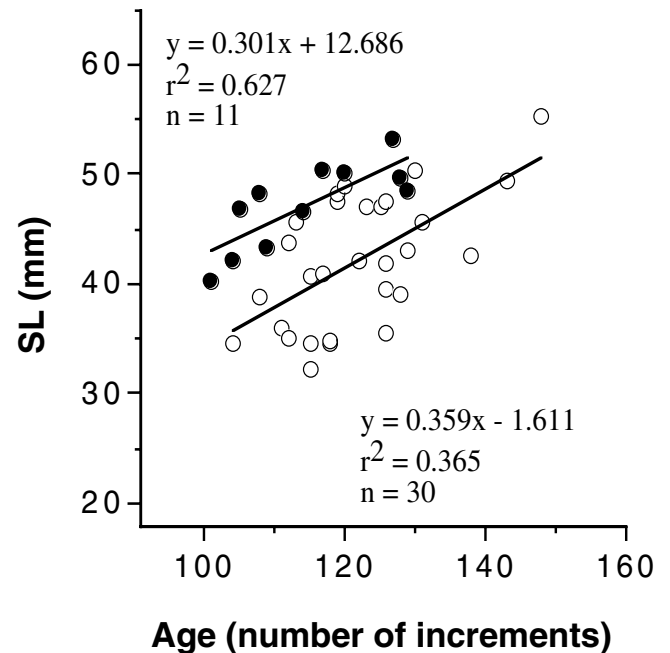


FIG. 3. Least-squares linear regressions of length-at-age data for juvenile Dolly Varden originating from different populations occurring at similar latitudes: Alaskan fish (64°41'N; black circles) and Russian fish (64°58'N; white circles).

TABLE 2. Summary of the data on the juvenile Dolly Varden analyzed in the present study.

	n		hatching check (µm)	first feeding check (µm)	otolith radius (µm)	nucleus length (µm)
Alaska	11	average	60.47	132.91	332.47	211.16
Cripple River		SD	8.91	9.56	20.60	23.93
(64°41'N)		min.	50.15	116.9	299.03	248.30
		max.	73.42	145.6	353.26	183.06
Russia	30	average	58.55	137.82	293.81	206.06
Cha'atam River		SD	4.33	14.28	20.03	19.30
(64°58'N)		min.	49.56	118.11	259.98	182.08
		max.	67.97	160.86	328.14	239.53
t-test	df	32	32	39	39	
two-sample	t	0.824	0.854	5.252	0.572	
	p	0.208	0.200	<0.0001	0.286	

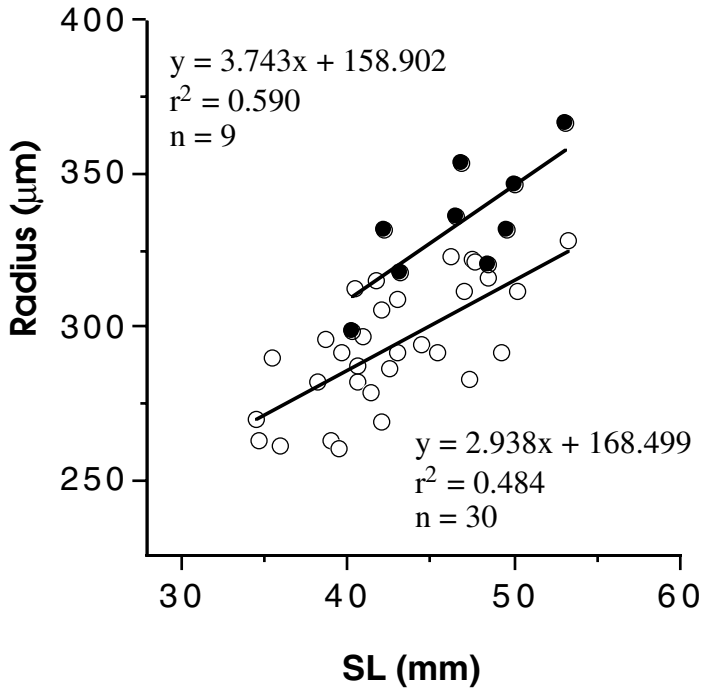


FIG. 4. Differences in the relationship between otolith size (radius) and standard length for Dolly Varden from Alaskan (black circles) and Russian (white circles) populations, analyzed by least-square linear regression.

Varden has been documented to occur between August and November (Armstrong and Morrow, 1980). The development of eggs requires 7–8 months (Yoshihara, 1973a, b); hatching would therefore occur sometime between February and June. McCallum (1972) noticed that the hatching of Arctic charr from Char Lake, Cornwallis Island (72°N) took place in March and early April. Therefore, our estimated hatch dates appear to be realistic, providing indirect confirmation of our increment counts. The time to first feeding back-calculated in our samples is much shorter than that reported by Armstrong and Morrow (1980), who found that emergence and first feeding take place about 60–70 days after hatching.

Knowledge about the early growth history of Dolly Varden can be gleaned from the otolith microstructure. The link between somatic growth and otolith growth has been described for many species, including salmonids (e.g., Bradford and Geen, 1987; Neilson and Geen, 1982; Volk et al., 1984). If we assume that the relationships between otolith dimensions and Dolly Varden body length or weight remain valid from hatching throughout the summer, then reliable back-calculations are feasible.

Assuming a linear or near linear relationship between SL and otolith radius, or between SL and increment width, changes in increment width may provide direct information on changes in growth rate during the first year of an individual Dolly Varden's life. For both groups, Alaskan and Russian, the pattern of change in increment width is similar. The increment widths begin to increase in late spring and become widest in summer (July and August) before narrowing again in the early fall (September). These changes in

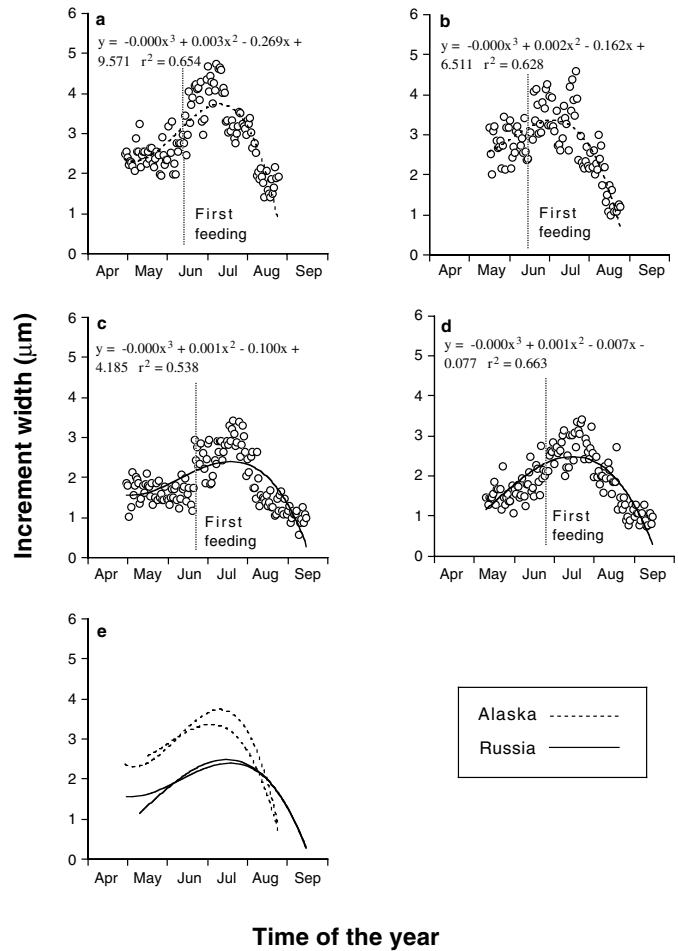


FIG. 5. Measurements of individual increment widths along the otolith radius of two individuals from Russia (a, b) and two from Alaska (c, d). Interpolated curves (derived through the use of the 3rd order polynomial) applied to these data are presented together (e).

increment widths correspond to changes in the growth rate, which is high during summer, low during spring, and likely very low during winter. The changes in increment width seem to be related also to a shift from endogenous to exogenous feeding and therefore to emergence. We found significant differences in the size of increments deposited before and after the first feeding check.

However, back-calculations in field studies should be made with caution (Bradford and Geen, 1987). Error may result from stock and individual differences in the relationship between otolith size and fish size (Mosegaard et al., 1988; Reznick et al., 1989; Secor and Dean, 1989; Secor et al., 1989). Back-calculated weights of sockeye salmon fry based on an otolith radius–fry weight regression were estimated to have an error as high as 15.0% (Wilson and Larkin, 1982). Otolith radius–fish length regressions may, however, be more conservative (Radtke, 1989, 1990). It has also been suggested that otolith growth may be controlled more directly by metabolic rate than by somatic growth (Bradford and Geen, 1992; Wright et al., 1991).

We found that the Alaskan Dolly Varden had larger otoliths than the Russian fish at similar body sizes. This may

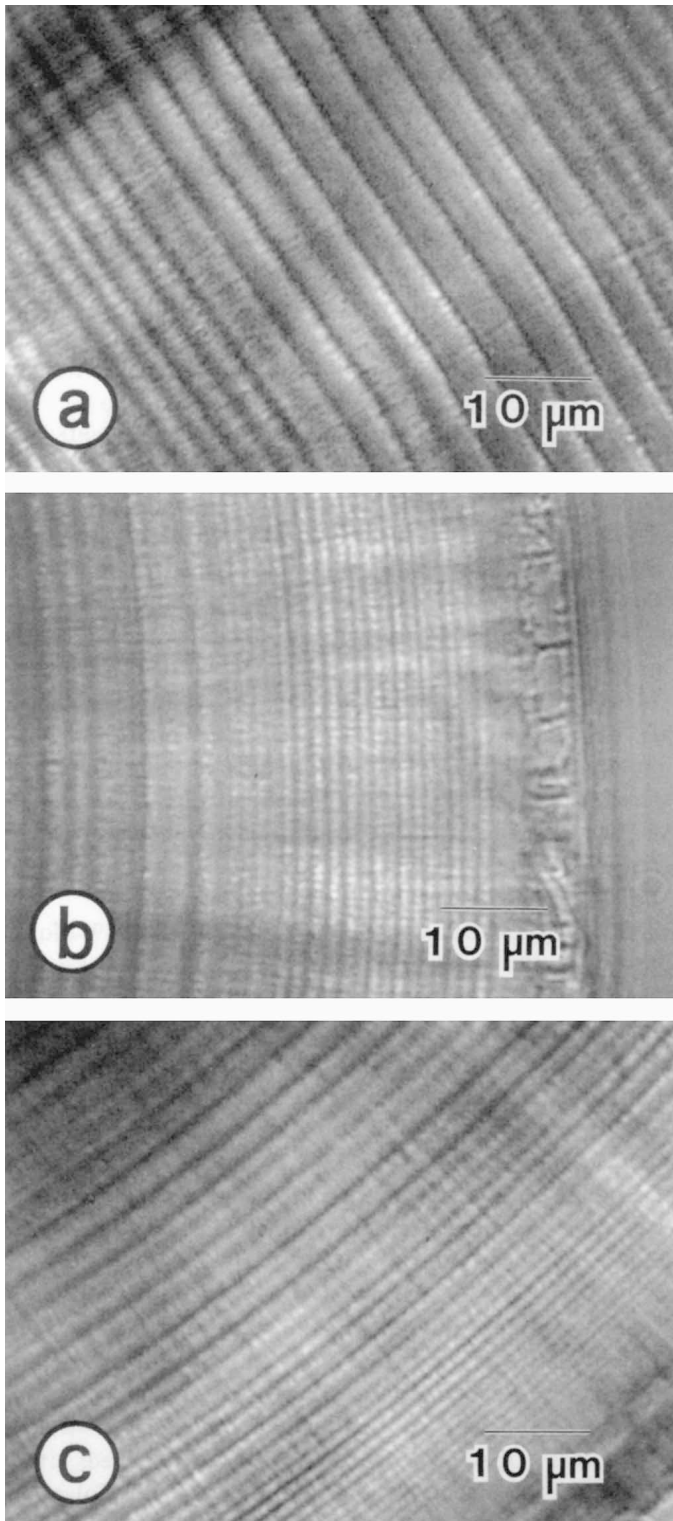


FIG. 6. Light micrographs of increments deposited in the otolith of juvenile Dolly Varden from Alaska: a) the larger summer increments, b) fall increments; and from Russian samples: c) summer and fall increments.

be attributed, at least partially, to differences in growth rate and the deposition of wider increments by faster-growing fish. However, the radii of Dolly Varden otoliths from Alaska were still greater than their Russian counterparts, even when fishes of the same size were compared. This makes impossible the

back-calculation of growth rates of fish from both stocks on the basis of a single fish size–otolith size relationship. It is also possible that the relationship for the full size range of 0-group Dolly Varden (from hatching to one year of age) is not linear; in such a case, the increment width data are useful only if the regression describing the relationship between SL and otolith radius includes the full range of size. Since our data include only fish 32–55 cm (Russia) and 40–53 cm (Alaska), they cannot be used for growth rate back-calculation beyond a general description of the seasonal growth pattern.

Rybock et al. (1975) suggested that nucleus length can be useful for stock identification; however, Neilson et al. (1985) found nucleus lengths to be useless for distinguishing populations of juvenile steelhead and rainbow trout. Since we did not find significant differences in nuclear size or shape between samples from Alaska and Russia, our results suggest that otolith nucleus length may be of little value for stock identification of Dolly Varden.

Armstrong and Morrow (1980) reported that northern Dolly Varden stocks grew from 15–20 mm at hatching to 25 mm at emergence from the redd (a period of  $\approx 65$  days). This amounts to a growth rate of  $\approx 0.12 \text{ mm}\cdot\text{day}^{-1}$  during the first two months of life. This value is much lower than our average growth rate (mm/day) for both Alaska (0.25) and Russia (0.20) as well as the values obtained from the length–age relationship, which represent the maximum summer growth (Alaska: 0.301; Russia: 0.356). Moreover, smaller-sized increments deposited before first feeding marks support the theory of a low growth rate during the first months of life. The emergence and switch to exogenous feeding in connection with the arrival of more favorable summer environmental conditions result in significant increases in growth rate. Water temperatures, which are close to  $0^\circ\text{C}$  during winter, rise quickly to over  $5^\circ\text{C}$  in spring (Power, 1969) and can be as high as  $12\text{--}13^\circ\text{C}$  during summer (Finstad and Heggberget, 1993); they are probably a major factor affecting Dolly Varden growth. Dramatic summer growth ( $\approx 0.3\text{--}0.4 \text{ mm}\cdot\text{day}^{-1}$ ) was also reported by Frost (1965) and Yoshihara (1973a) for Arctic charr, and by Blackett (1968), and Armstrong and Morrow (1980) for Dolly Varden. Thus, almost all growth is accomplished during the summer months.

The present data indicate that analysis of otolith microstructure is of value to early life history studies of Dolly Varden. At times when field sampling is virtually impossible, otolith microstructure analyses can supply information about the timing of morphological and growth events occurring early in life. Otolith microstructure could also furnish information on mortality patterns in early life stages, since changes in the age structure of survivors can be related to dates of emergence, yolk sac absorption, and river conditions.

#### ACKNOWLEDGEMENTS

Special thanks are due to James Ruzicka and Dan Malone for reviewing the manuscript. This study was funded by National Science Foundation grants DPP-9123017, OCE-

9205936 and DEB-9322618. This is the School of Ocean and Earth Science and Technology contribution number 4083 and Hawaii Institute of Geophysics and Technology contribution number 889.

## REFERENCES

- ARMSTRONG, R.H., and MORROW, T.E. 1980. The Dolly Varden charr, *Salvelinus malma*. In: Balon, E.K., ed. Charrs: Salmonid fishes of the genus *Salvelinus*. The Hague: Dr. W. Junk Publishers. 16–98.
- BLACKETT, R.F. 1968. Spawning behavior, fecundity and early life history of anadromous Dolly Varden *Salvelinus malma* (Walbaum) in southeastern Alaska. Alaska Department of Fish and Game, Research Report 6. 85 p.
- BRADFORD, M.J., and GEEN, G.H. 1987. Size and growth of juvenile Chinook salmon back-calculated from otolith growth increments. In: Summerfelt, R.C., and Hall, G.E., eds. The age and growth of fish. Ames, Iowa: The Iowa State University Press. 453–461.
- BRADFORD, M.J., and GEEN, G.H. 1992. Growth estimates from otolith increment widths of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. *Journal of Fish Biology* 41:825–832.
- FINSTAD, B., and HEGGERGET, T.G. 1993. Migration, growth and survival of wild and hatchery-reared anadromous Arctic charr (*Salvelinus alpinus*) in Finnmark, northern Norway. *Journal of Fish Biology* 43:303–312.
- FOGARTY, M.J., SISSEWINE, M.P., and COHEN, E.B. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* 6:241–246.
- FROST, W.E. 1965. Breeding habits of Windermere char, *Salvelinus willughbii* (Günter) and their bearing on speciation of these fish. *Proceedings of the Royal Society of London, Series B* 163:232–284.
- GROSBERG, R.K., and LEVITAN, D.R. 1992. For adults only? Supply-side ecology and the history of larval biology. *Trends in Ecology and Evolution* 7:130–133.
- MARSHALL, S.L., and PARKER, S.S. 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 39:542–547.
- McCALLUM, W. 1972. Arctic char study. In: Rigler, F.H., ed. Char Lake project PF-2 annual report, 1970–1971. Ottawa: Canadian Committee International Biological Program. 67–73.
- MOSEGAARD, H., SVEDANG, H., and TABERMAN, K. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1514–1524.
- NEILSON, J.D., and GEEN, G.H. 1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): Daily growth increments and factors influencing their production. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1340–1347.
- NEILSON, J.D., and GEEN, G.H. 1985. Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Fishery Bulletin* 83:91–100.
- NEILSON, J.D., GEEN, G.H., and CHAN, B. 1985. Variability in dimensions of salmonid otolith nuclei: Implications for stock identification and microstructure interpretation. *Fishery Bulletin* 83:81–89.
- PANNELLA, G. 1971. Fish otoliths: Daily growth layers and periodical patterns. *Science* 173:1124–1127.
- . 1974. Otolith growth patterns: An aid in age determination in temperate and tropical fishes. In: Bagenal, T.B., ed. The Proceeding of an International Symposium on the Aging of Fish. Surrey, England: Unwin Brothers. 28–39.
- POWER, G. 1969. The salmon of Ungava Bay. Technical Reports of the Arctic Institute of North America No. 22. 72 p.
- RADTKE, R.L. 1987. Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. *Coral Reefs* 6:19–25.
- . 1989. Larval fish age, growth and body shrinkage: Information available from otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1884–1894.
- . 1990. Information storage capacity of otoliths: Response to Neilson and Campana. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2463–2467.
- RADTKE, R.L., and DEAN, J.M. 1982. Increment formation in the otoliths of embryos, larvae, and juvenile of the mummichog, *Fundulus heteroclitus*. *Fishery Bulletin* 80:201–215.
- RADTKE, R.L., and FEY, D.P. In press. Environmental affects on daily increment formation in newly hatched charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology*.
- REZNICK, D., LINDBECK, E., and BRYGA, H. 1989. Slower growth results in larger otoliths: An experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:108–112.
- RYBOCK, J.T., HORTON, T.H., and FESSLER, J.L. 1975. Use of otoliths to separate juvenile steelhead trout from juvenile rainbow trout. *Fishery Bulletin* 73:654–659.
- SECOR, D.H., and DEAN, J.M. 1989. Somatic growth effects on the otolith fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* 46:113–121.
- SECOR, D.H., DEAN, J.M., and BALDEVARONA, R.B. 1989. Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. *Rapports et Procès-Verbaux des Réunions. Conseil International pour l'Exploration de la Mer* 191:431–438.
- SECOR, D.H., DEAN, J.M., and CAMPANA, S.E., eds. 1995. Recent developments in fish otolith research. Columbia: University of South Carolina Press.
- SINCLAIR, M. 1988. Marine populations. Seattle: University of Washington Press. 252 p.
- STEVENSON, D.K., and CAMPANA, S.E. 1992. Otolith microstructure examination and analysis. *Canadian Journal of Fisheries and Aquatic Sciences, Special Publication* 177. 126 p.
- SUMMERFELT, R.C., and HALL, G.E., eds. 1987. Age and growth of fish. Ames, Iowa: The Iowa State University Press. 544 p.

- UMEZAWA, A., and TSUKAMOTO, K. 1991. Factors influencing otolith increment formation in Japanese eel, *Anguilla japonica*, Elvers. *Journal of Fish Biology* 39:211–223.
- VOLK, E.C., WISSMAR, R.C., SIMENSTAD, C.A., and EGGERS, D.M. 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. *Canadian Journal of Fisheries and Aquatic Sciences* 41:126–133.
- WILSON, K.H., and LARKIN, P.A. 1980. Daily growth rings in the otoliths of juvenile sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 37:1495–1498.
- WILSON, K.H., and LARKIN, P.A. 1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1335–1339.
- WRIGHT, P.J., METCALFE, N.B., and THORPE, J.E. 1991. Daily growth increments in the otolith of Atlantic salmon parr, *Salmo salar* L., and the influence of environmental factors on their periodicity. *Journal of Fish Biology* 39:103–113.
- YOSHIHARA, H.T. 1973a. Monitoring and evaluation of arctic waters with emphasis on the North Slope drainages. A. Some life history aspects of Arctic char. Alaska Department of Fish and Game, Federal Aid in Fish Restoration. Annual Progress Report, Project F-9-5, Study G-III-A. 14:1–63.
- . 1973b. Life history aspects of anadromous Arctic char (*Salvelinus alpinus*) in the Sagavanirktok River drainage, Alaska. Unpubl. research report. Available at the Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, U.S.A.
- ZHANG, Z., BEAMISH, R.J.B., and RIDDELL, B.E. 1995. Differences in otolith microstructure between hatchery-reared and wild chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:344–352.