Spacing of Scale Circuli versus Growth Rate in Young Coho Salmon

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Abstract.–We compared rate of formation of scale circuli and spacing between circuli with fish growth rate and scale growth rate in three groups of young coho salmon *Oncorhynchus kisutch*): (1) smolts held in saltwater tanks, (2) tagged precocious males (jacks) returning to a release facility after only 3 or 4 months in the ocean in two different years, and (3) tagged juvenile coho salmon caught in the ocean. Rate of formation of scale circuli was significantly and positively correlated with fish growth rate and with scale growth rate in all groups. However, rate of circulus formation at a given growth rate was lower for large jacks than for the smaller and younger fish held in saltwater tanks, suggesting that rate of circulus formation is negatively related to size or age of fish as well as positively related to growth rate. Spacing of circuli was also significantly and positively correlated with fish growth rate in all but one group of returning jacks, and with scale growth rate in all groups. The relationship between circulus spacing and fish growth rate varied among groups, partly because the relationships between scale-radius and fish length and between rate of circulus formation and fish growth rate also varied among groups. Scale circulus spacing could be used to compare growth rates between groups of juvenile coho salmon that are of similar size and age and that have a common relationship between scale radius and fish length.

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Spacing of scale ridges (circuli) is a potentially valuable tool for comparing growth rates of fish where other data are not available. Scale circulus spacing has been found to be positively correlated with fish growth rate in several species of fishes (Doyle et al. 1987; Matricia et al. 1989; Glenn and Mathias 1985; Bhatia 1932; Bilton 1971a, 1975). Use of scales for studying growth has distinct advantages over other methods, such as the spacing of daily rings in otoliths, since scales can be easily obtained without killing the fish and are more quickly prepared and read.

Spacing of scale circuli is determined by both the rate at which circuli are formed and the rate of growth of the scale. Whether scale circulus spacing can be used to estimate fish growth rate depends on whether scale growth and circulus deposition rate are related to fish growth rate in a consistent, predictable manner. To determine the usefulness of circulus spacing for estimating growth rate of juvenile coho salmon, we investigated the relationships between scale radius and fish length, between rate of circulus formation and fish and scale growth rates, and between circulus spacing and fish and scale growth rates in three groups of marked young coho salmon: (1) subyearling (age 0) smolts held in saltwater tanks, (2) yearling (age 1.0)* fish returning as jacks to a coastal hatchery after 3 or 4 months in the ocean in two different years, and (3) marked juvenile coho salmon (age 0.0 and age 1.0) caught in the ocean within 2–4 months of entering the ocean. Our purpose was to develop a method for comparing growth rates of unmarked juvenile coho salmon caught in the ocean in different years (see Fisher and Pearcy 1988).

Methods

Coho smolts held in saltwater tanks

Coho smolts (age 0) were collected from one of the raceways at Oregon Aqua Foods, Inc's. Yaquina Bay, Oregon, release facility and transferred to the Hatfield Marine Science Center in July 1982. About 40 fish were placed in each of seven 1.5-m diameter fiberglass tanks. A constant flow of sea water was maintained to each tank. Daily food rations were varied between tanks from 0.6 to 3.0% of total salmon biomass in order to produce a wide range of fish growth rates. Fish in five tanks were fed Oregon Moist Pellet, while those in two others were fed thawed frozen euphausiids. Water temperature during the experiment was variable, ranging from approximately 11° to 17°C.

During 22–24 July, all the fish were anesthetized with MS-222, measured

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* Age designation follows Koo (1962) and Godfrey et al. (1975), where the number to the left of the decimal indicates the number of winters spent in freshwater, and the number to the right of the decimal the number of winters spent in saltwater.

Table 1

Fork length (FL, mm) vs. scale radius (SR, mm at 88×): Correlation coefficients (r) and geometric mean regressions (GM, Ricker 1973) for age-0 fish held in saltwater tanks (A), for age-1.0 jacks returning to Anadromous, Inc. in 1983 (B) and 1985 (C), and for juvenile coho (ages 0.0 and 1.0) caught in the ocean 1981–84 (D).

Group	n	r	GM regression
A	174	0.96	$FL = 1.69 \cdot (SR) + 18.54$
B	64	0.78	$FL = 1.59 \cdot (SR) + 65.80$
C	99	0.83	$FL = 1.99 \cdot (SR) + 43.05$
D	34	0.96	$FL = 2.13 \cdot (SR) - 20.64$

to the nearest mm fork length (FL), and a scale sample taken from the preferred area (Clutter and Whitesel 1956). Each fish was also marked with a unique combination of color spots above the anal fin by injecting acrylic paint under the surface of the skin (Lotrich and Meridith 1974).

Fish were fed for 63–66 days. At the end of the period fish were again anesthetized, measured and weighed, and new scale samples were taken from the preferred area, although sometimes on the other side of the fish. Good scale samples were obtained from 80 fish at the beginning and end of the experiment. Mean fish lengths at the beginning and end of this 63–66 day period were 135 mm FL (SD 8.7, range 110–155 mm) and 171 mm FL (SD 24.5, range 125–229 mm), respectively. Acetate impressions were made of the scales. All scale measurements were made at a magnification of 88× along the axis 20° ventrad of the posterior-anterior axis of the scale.

Scales from each fish taken at the beginning and end of the experiment were compared to determine the spacing and number of circuli laid down during the intervening growth period. Mean circulus spacing during the growth period was calculated as $(SR_2 - SR_1)/n$, where SR_2 is the radius to last scale circulus, SR_1 is the radius to last circulus before the growth period as determined by comparison with the initial scale sample, and n is the number of new circuli formed during the growth period. Rate of circulus formation for each fish was also determined (n/d, where d is the duration of the experiment in days).

Linear growth rate was calculated for each fish as $(FL_2 - FL_1)/d$, where FL_1 and FL_2 are the lengths (mm) at the beginning and end of the experiment, respectively. Scale growth rate was also calculated as $(SR_{tot} - SR_1)/d$, where SR_{tot} is the total scale radius.

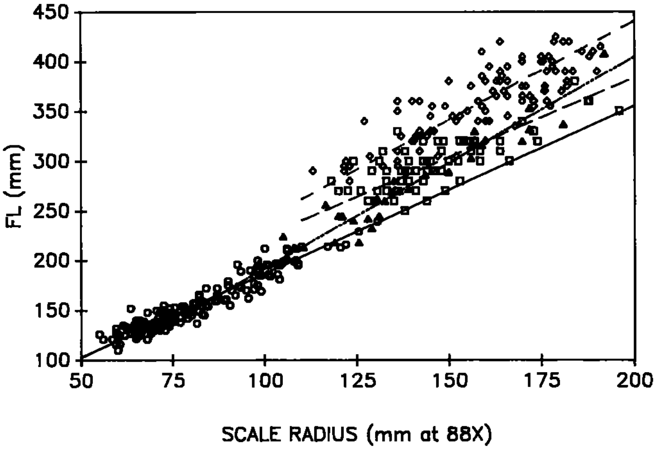

Figure 1

Fork length vs. scale radius scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (○, —), for age-1.0 CWT jacks returning to Coos Bay in 1983 (□, — —) and 1985 (◇, - -), and CWT juvenile fish caught in the ocean (▲, - · · -).

Returning jacks

Fork length was measured and scale samples taken from the preferred area of 64 and 99 coded-wire tagged (CWT) jacks (precocious males) within 2 or 3 days of their return in 1983 and 1985, respectively, to the Anadromous Inc. facility on Coos Bay. Scales had also been taken earlier from a subsample of each release group shortly before their release as smolts. Fork length at time of ocean entrance was backcalculated for each returning jack using the relationship between scale radius and fork length at the time of release for that group and other groups released in the same month. (Tag groups were grouped by month of release to obtain adequate numbers for the prerelease scale radius-fish length relationships). Ocean entrance was detected on the scale as an abrupt change in circulus spacing (see Fisher and Pearcy, 1988). Since these fish were released and returned to a site only 8 km from the ocean, their period of growth in the ocean should be very similar to the time between their release and return. Growth rate of each fish while in the ocean was estimated by $(FL_2 - FL_1)/d$, where FL_2 is length on return to the hatchery, FL_1 is the backcalculated length at time of ocean entry, and d is the days between release and return. Scale growth rate was estimated as $(SR_{tot} - SR_1)/d$, where SR1 is the scale radius to the ocean entrance mark, and SR_{tot} is the total scale radius. Mean circulus spacing during the ocean growth period was calculated as the distance between the first and last ocean circulus divided by $n - 1$, where n = the number of circuli laid down during ocean growth.

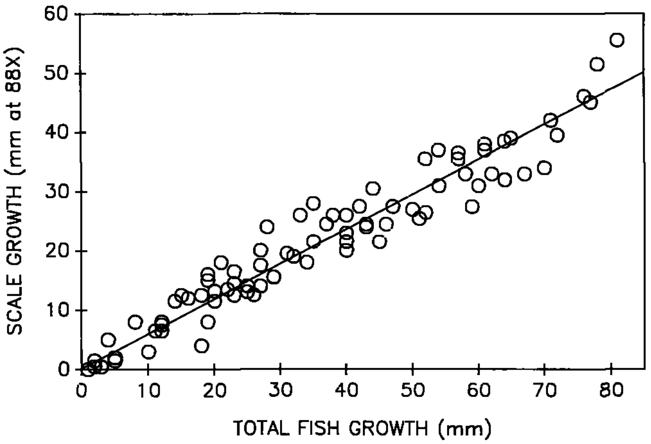

Figure 2

Scale growth vs. fish growth scattergram and GM regression line for individually marked age-0 smolts held in saltwater tanks.

Juvenile coho collected in the ocean

Growth rates in the ocean were estimated for CWT or spray-marked juvenile coho released (a) very near the ocean in Yaquina and Coos Bays and caught 60 or more days later in the ocean in August or September (15 fish), and (b) in the Columbia River (19 fish) and sampled during downstream migration near the ocean (at rkm 75, Dawley et al. 1985) and caught in the ocean 60 days or more after the median fish passed rkm 75, or released below rkm 75 and caught at least 60 days later in the ocean. For fish released in Yaquina or Coos Bays growth rate was estimated by $(FL_2 - FL_1)/d$ where FL_1 is the length at ocean entrance backcalculated from scales using a regression of FL on scale radius from a sample of fish taken at the time of release, FL_2 is length at capture in the ocean, and d is days between release and recapture. For Columbia River fish released in 1981, 1982, 1983, and 1984 length at ocean entrance was backcalculated using a regression of FL on scale radius derived from fish collected at rkm 75 in 1982 and 1983, combined. The number of days in the ocean was estimated from the date the median fish in each group passed rkm 75 and the mean downstream migration rates for each group. Estimated date of ocean entry for each group ranged from 3 to 11 days following passage of the median fish at rkm 75. For CWT Columbia River fish caught in 1984, when no sampling occurred at rkm 75, average downstream migration rates for tag groups from the same hatcheries in 1981–1983 were used in estimating ocean entrance date and days in the ocean (d). Scale growth rate for juvenile coho caught in the ocean was estimated the same way as for jacks.

Table 2

Rate of circulus formation (RCF, circuli per day) vs. fish growth rate (GR, mm/d): Correlation coefficients (*r*), probability that correlation = 0.0 (*p*), and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	*n*	*r*	*p*	GM regression
A	80	0.89	<0.01	RCF = 0.18 · (GR) + 0.03
B	64	0.58	<0.01	RCF = 0.10 · (GR) + 0.03
C	99	0.57	<0.01	RCF = 0.10 · (GR) + 0.00
D	34	0.84	<0.01	RCF = 0.12 · (GR) + 0.02

Results

Fork length was positvely and significantly correlated with scale radius (SR) in all groups (Table 1, Fig. 1). The relationship (geometric mean regression, Ricker 1973) for each group of fish appeared linear. However, SR was smaller relative to FL for jacks returning in 1985 (diamonds in Figure 1) than for jacks returning in 1983 (squares) or for CWT juvenile coho salmon collected in the ocean (solid triangles). In addition, almost all FL–SR data points for returning yearling jacks and juveniles caught in the ocean were above the extrapolated regression line for the smaller subyearling fish held in saltwater tanks (Fig. 1). Thus, the relationships between FL and SR varied between age or size groups (small subyearling fish vs. larger yearling jacks and juveniles caught in the ocean) and between years (1983 vs. 1985 Anadromous Inc. jacks). The relationship between scale growth and fish growth appeared linear for the subyearling coho smolts held in saltwater tanks (Fig. 2).

Rate of circulus formation was positively and significantly ($r = 0.57 - 0.89$, $p < 0.01$) correlated with fish growth rate for all groups (Table 2, Fig. 3). However the slope of the relationship was lower for ocean-caught juveniles and jacks returning in 1983 and 1985 (slopes of GM regression = 0.12, 0.10, 0.10, respectively) than for the subyearling fish held in saltwater tanks (slope = 0.17) At similar fish growth rates, rates of circulus formation were generally higher for the subyearling fish held in saltwater tanks than for juveniles caught in the ocean or for returning jacks (Fig. 3).

The spacing between circuli was positively and significantly correlated with fish growth rate for all groups but jacks returning in 1983 (Table 3). The correlation was strong ($r = 0.80$) for age 0.0 fish held in saltwater tanks, but much weaker for jacks returning in 1985 ($r = 0.24$). However, the relationship between circulus spacing and fish growth rate for subyearling

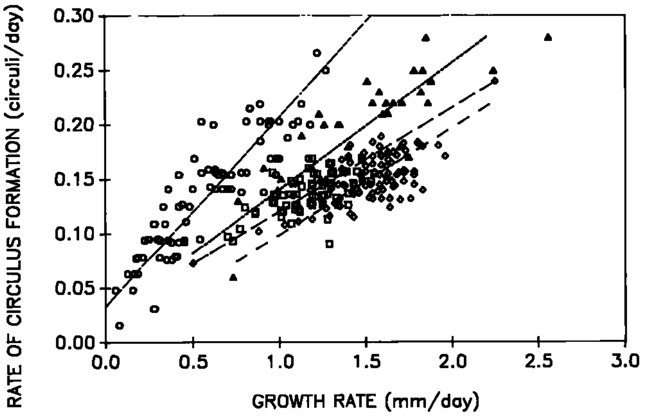

Figure 3
Rate of circulus formation vs. fish growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (O, —), for CWT jacks returning to Coos Bay in 1983 (□, — —) and 1985 (◇, - -), and for CWT juvenile fish caught in the ocean (▲, - · · -).

Table 3
Circulus spacing (CSP, mm at 88×) vs. fish growth rate (GR, mm/d): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both ages 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.80	<0.01	CSP = 1.80 · (GR) + 1.31
B	64	0.08	N.S.	—
C	99	0.24	<0.05	CSP = 2.06 · (GR) + 0.71
D	34	0.52	<0.01	CSP = 1.21 · (GR) + 2.24

* For this group of fish the correlation coefficient for a third-order relationship, CSP = 0.91 + 5.35(GR) − 6.44$(GR)^2$ + 3.04$(GR)^3$, r = 0.83, was higher than for the linear relationship.

fish held in saltwater tanks appeared to be nonlinear (see footnote, Table 3). In general, circulus spacing vs. growth rate values in the three groups that had reared in the ocean were fairly close to the extrapolated linear regression line for the smaller fish held in saltwater tanks, although the variability about this regression line was very large (Fig. 4). Mean growth rates of jacks returning in 1985 and juveniles caught in the ocean (1.49 mm/d and 1.53 mm/d, respectively) were significantly greater (t-tests, $p<0.01$) than the mean growth rate of jacks returning in 1983 (1.17 mm/d). Mean circulus spacings of the two faster growing groups (3.86 and 4.04 mm at 88× for jacks returning in 1985 and for juveniles caught in the ocean, respectively) were also both greater ($p<0.01$) than mean circulus spacing of the slower-growing jacks returning in 1983 (3.61).

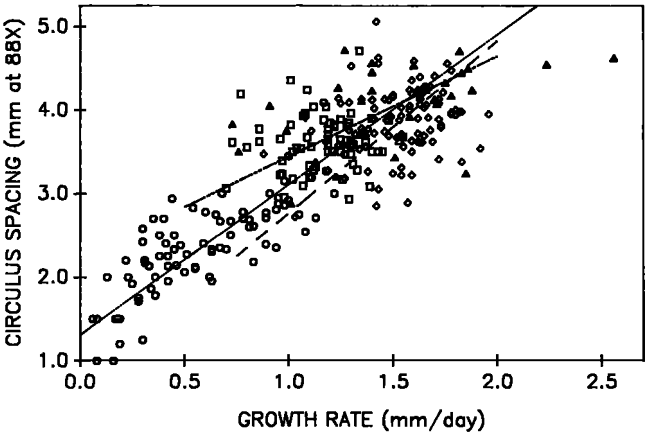

Figure 4
Circulus spacing vs. growth rate scattergrams and GM regression lines for age-0 smolts held in saltwater tanks (O, —), for CWT jacks returning to Coos Bay in 1983 (□, regression n.s.) and 1985 (◇, - -) and for CWT fish caught in the ocean (▲, - · · -).

In each group of fish some of the large variability in the relationship between circulus spacing or circulus deposition rate and fish growth rate was caused by variability in the relationship between fish length and scale radius. To remove this component of variation, we compared circulus spacing and circulus deposition rates with scale growth rates (Tables 4 and 5, respectively). Correlation coefficients for the relationships of circulus spacing and deposition rate with scale growth rate were considerably higher than for the corresponding relationships with fish growth rate, especially for jacks returning to Coos Bay in 1983 and 1985. (Compare Tables 2 with 4, and 3 with 5.) Circulus spacing was positively and significantly correlated with scale growth rate in all groups, whereas the relationship between circulus spacing and fish growth rate was significant for all groups but jacks returning in 1983. Thus, the correlations of circulus spacing or rate of circulus formation with scale growth rate were stronger than the correlations with the underlying fish growth rate.

Discussion

A positive correlation between rate of circulus formation and fish growth rate appears to be a common feature among fishes. We found in young coho salmon that rate of circulus deposition was positively and

Table 4

Rate of circulus formation (RCF, circuli/d) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability that correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A	80	0.94	<0.01	RCF = 0.30(SGR) + 0.03
B	64	0.84	<0.01	RCF = 0.22(SGR) + 0.03
C	99	0.83	<0.01	RCF = 0.20(SGR) + 0.03
D	34	0.90	<0.01	RCF = 0.22(SGR) + 0.02

Table 5

Circulus spacing (CSP, mm at 88×) vs. scale growth rate (SGR, mm/d at 88×): Correlation coefficients (r), probability of correlation coefficient = 0.0 (p) and geometric mean regression (GM) for age-0 fish held in saltwater tanks (A), CWT jacks (age 1.0) returning in 1983 (B) and 1985 (C), and CWT juvenile fish (both age 0.0 and 1.0) caught in the ocean (D).

Group	n	r	p	GM regression
A*	80	0.82	<0.01	CSP = 3.07(SGR) + 1.29
B	64	0.62	<0.01	CSP = 4.22(SGR) + 1.39
C	99	0.59	<0.01	CSP = 4.14(SGR) + 1.56
D	34	0.56	<0.01	CSP = 2.26(SGR) + 2.22

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* For this group of fish the correlation coefficient for a third order relationship, $CSP = 1.02 + 6.92(SGR) - 10.37(SGR)^2 + 6.77(SGR)^3$, $r = 0.84$, was higher than for the linear relationship.

significantly correlated with scale and fish growth rates (Tables 2, 5; Fig. 3). Thus, the faster the fish or scales grew, the more circuli were formed per unit time. Positive correlations between rate of circulus formation and growth rate also have been found for walleye (Glenn and Mathias 1985) and cichlids (Sire 1986). In juvenile walleye, rate of circulus formation ranged from 1.5 circuli/d at high growth rates to 1 circulus every 2–3 weeks at low growth rates. Data presented by Bilton and Robins (1971a) indicated that juvenile sockeye salmon receiving more food, and presumably growing faster, produced more circuli during a given period than those fish that were fed less. Bilton and Robins (1971b) also found that sockeye salmon formed no circuli during periods of starvation. In chum salmon from Olsen Creek, Alaska, the number of circuli and radius to the middle of the first ocean annulus were positively correlated (Helle 1980). Therefore, if time to the middle of the first ocean annulus was constant (which may or may not be true), then fast-growing fish (larger radius) produced more circuli per unit time than slow-growing fish.

Positive correlations between circulus spacing and growth rate also have been reported in other species of fish. Bhatia (1932) found that scales from juvenile rainbow trout fed abundantly and growing rapidly, and scales from those fed sparsely and growing slowly had zones of widely spaced and narrowly spaced circuli, respectively, near the scale margin. Bhatia also was able to produce zones of widely and narrowly spaced circuli by alternately changing feeding level. Doyle et al. (1987) and Matricia et al. (1989) found positive correlations between circulus spacing and fish growth rate in tilapia. Sire (1986) found more widely spaced circuli among faster growing than slower growing cichlids. In juvenile walleye, mean spacing of circuli formed during the period of most rapid growth was found to be greater than mean spacing of circuli formed during periods of slower growth (Glenn and Mathias 1985). Bilton and Robins (1971a) found a significant positive correlation between feeding level and spacing of circuli in sockeye salmon.

Rate of circulus formation and spacing of circuli are probably related to a number of other factors beside growth rate. We found that rate of circulus formation for juvenile coho salmon caught in the ocean and especially for returning jacks were all well below the rates predicted by the regression for the much smaller fish held in saltwater tanks but growing at similar rates (Fig. 3). This suggests that the rate of circulus formation varies with age or size of fish or with environmental conditions, as well as with growth rate. Doyle et al. (1987) found that circuli of tilapia were laid down less frequently as fish grew larger. They also found that the relationship between growth rate and circulus spacing was stronger when a correction was made for the size of fish. Bilton (1975) suggested that rate of circulus deposition was probably a function of a combination of factors such as temperature, food, light, and maternal and inherent characteristics.

Several studies have addressed the possible effects of water temperature on circulus spacing. Generally they suggest that the effect of temperature, by itself, on circulus spacing is relatively small compared with the effect of feeding level or growth rate. By manipulating feeding level, Bhatia (1932) was able to produce zones of widely and narrowly spaced circuli in scales of rainbow trout growing in extremely different water temperatures (4°C and 17°C). Kimura and Sakagawa (1972), working with sardines, found that formation of annuli or checks (bands of narrowly spaced circuli) did not appear to be related to temperature. Barber and Walker (1988) found that in sockeye salmon annulus formation occurred before the coldest months of the year and that during the coldest months widely spaced circuli were formed. Hogman (1968) cited work by Deason and Hile (1947) that indicated that annuli and checks formed in scales of kiyis living at depth in Lake Michigan, despite a very small annual variation in water temperature (2–3°C). Bhatia (1932) cited his earlier work showing that when rainbow trout were fed uniformly throughout the year no periodic zones were formed on their scales and all rings were of nearly the same width despite fluctuations in temperature. However, there is some evidence that in brown trout water temperature during egg and alevin stages prior to scale formation affected subsequent rate of circulus formation (Skurdal and Anderson 1985).

Inherent differences between groups of fish may mask the relationship between circulus spacing and growth rate. For example, for coho jacks returning to the Anadromous Inc. facility in Coos Bay in 1985, scales were generally smaller at a given fish length (Fig. 1), and rate of circulus formation was lower at a given growth rate (Fig. 2), than was the case for CWT juveniles caught in the ocean. This resulted in significantly different mean spacing of circuli in these two groups (3.86 vs. 4.04, t-test, $p<0.05$) despite very similar mean growth rates (1.53 and 1.49 mm/d, t-test, n.s.). Because of differences in the relationships between circulus spacing and growth rate among different groups of juvenile coho salmon, inferences about relative growth rates based on scale circulus spacing are probably only valid when made between groups that are similar in age, size, and morphometric characteristics (i.e., very similar SR–FL relationships).

Data from the group of subyearling fish held in saltwater tanks suggest that the relationship between circulus spacing and growth rate may be complicated. A third-order relationship (see footnote, Table 3) gave a better fit to the data than did a simple linear relationship. In this group of fish there was little change in circulus spacing between growth rates of 0.4 and 0.9 mm/d. More rapid changes in circulus spacing with growth rate occurred both above and below this range (circles, Fig. 4). This result suggests that for coho salmon there may be ranges of growth rates within which circulus spacing is a poor indicator of relative growth rate.

We compared mean circulus spacing in the ocean growth zone of scales for unmarked yearling (age 1.0) juvenile coho caught in the ocean in late summer of 1981, 1982, 1983, and 1984 (Fisher and Pearcy 1988). These fish had very similar SR–FL relationships in all years and were of similar size at time of entry into the ocean (based on backcalculated size at ocean entry). We also estimated growth rates of these unmarked juvenile yearling coho salmon between early and late summer (between June and August or September) from changes in mean lengths with time (see Fisher and Pearcy 1988, their Table 3). Rank order of mean spacing between circuli and growth rates estimated from shifts in mean FL with time are compared in Table 6. Although the rank orders do not agree in detail, they both suggest higher fish growth rates during the summers of 1981 and 1982 than in 1983 and 1984.

Table 6

Rank order of mean scale circulus spacing for unmarked juvenile coho collected in the ocean during the late summer, 1981–84, and growth rates of unmarked juvenile coho estimated from changes in mean length between early and late summer (see Fisher and Pearcy 1988, their Tables 3 and 4).

Year	Mean spacing (mm at 88×)	Rank	Est. growth rate (mm/d)	Rank
1981	4.16	1	1.56	2
1982	4.15	2	1.76	1
1983	3.91	4	1.37	3
1984	3.95	3	1.33	4

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