Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli

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Abstract—In this study we present new information on seasonal variation in absolute growth rate in length of coho salmon (*Oncorhynchus kisutch*) in the ocean off Oregon and Washington, and relate these changes in growth rate to concurrent changes in the spacing of scale circuli. Average spacing of scale circuli and average rate of circulus formation were significantly and positively correlated with average growth rate among groups of juvenile and maturing coho salmon and thus could provide estimates of growth between age groups and seasons. Regression analyses indicated that the spacing of circuli was proportional to the scale growth rate raised to the 0.4–0.6 power. Seasonal changes in the spacing of scale circuli reflected seasonal changes in apparent growth rates of fish. Spacing of circuli at the scale margin was greatest during the spring and early summer, decreased during the summer, and was lowest in winter or early spring. Changes over time in length of fish caught during research cruises indicated that the average growth rate of juvenile coho salmon between June and September was about 1.3 mm/d and then decreased during the fall and winter to about 0.6 mm/d. Average growth rate of maturing fish was about 2 mm/d between May and June, then decreased to about 1 mm/d between June and September. Average apparent growth rates of groups of maturing coded-wire–tagged coho salmon caught in the ocean hook-and-line fisheries also decreased between June and September. Our results indicate that seasonal change in the spacing of scale circuli is a useful indicator of seasonal change in growth rate of coho salmon in the ocean.

Large interannual and decadal variations occur in the abundance and productivity of North Pacific salmonids. These fluctuations, which affect harvestable biomass, are influenced by survival rates, ages at maturity, and somatic growth (Beamish and Bouillon, 1993; Mantua et al., 1997; Hare et al. 1999; Pyper et al., 1999; Hobday and Boehlert, 2001).

The growth of smolts after ocean entry—growth that is critical to production—is also thought to be an important determinant of their survival. As for juvenile and larval fishes in general, size-selective mortality may occur (Miller et al., 1988; Bailey and Houde, 1989; Litvak and Leggett, 1992; Sogard, 1997) with the result that faster growing salmonids experience less mortality from predators than slower growing salmonids (Parker, 1971; Bax, 1983; Fisher and Pearcy, 1988; Holtby et al., 1990; Jaenicke et al., 1994; Willette, 1996, 2001). This size-selective mortality may explain much of the interannual variability in survival of juvenile salmonids and the subsequent abundance of different year classes. However, other investigators have not found a strong relationship between growth of juvenile salmon and mortality (Fisher and Pearcy, 1988; Mathews and Ishida, 1989; Blackbourn, 1990).

Intercirculus spacing of scales has been used to estimate early ocean growth rate of juvenile salmon and has been linked to differential survival rates. For example, Healey (1982) used the spacing of the first five circuli to demonstrate intensive size-selective mortality in juvenile chum salmon (*Oncorhynchus keta*) as they migrated offshore. Holtby et al. (1990) correlated early ocean growth, based on intercirculus spacing, with marine survival of age 1+ coho (*O. kisutch*) smolts. The spacing of early ocean circuli from the scales of maturing Atlantic salmon (*Salmo salar*) has been used to estimate juvenile growth rates, which are correlated with survival and age at maturity, and to identify stocks (Friedland et al., 1993; Friedland and Haas, 1996; Friedland and Reddin, 2000; Friedland et al., 2000).

Correlation between circulus spacing and growth rate was reported by Fisher and Pearcy (1990) for age 0.0 coho smolts reared for 60 days in salt water tanks. In addition, positive correlations between the spacing of scale circuli and fish growth rate have been observed for rainbow trout (*O. mykiss*) (Bhatia, 1932), and sockeye salmon (*O. nerka*) (Fukuwaka and Kaeriyama, 1997), and between the spacing of circuli and feeding ration and growth for sockeye salmon (Bilton and Robins, 1971; Bilton, 1975). Bigelow and White (1996) were able to manipulate the spacing of scale circuli of cutthroat trout (*O. clarkii*)

Table 1

Main sources of coho salmon data used in this study.

Source	Numbers of fish	Scale samples
CWT maturing fish caught in the Oregon ocean sport and troll fisheries 1982–92 (see Table 2)	687	687
Maturing coho salmon caught in the ocean during research cruises		
1981–85	1391	352
1998–2002	714	236
Juvenile fish caught in the ocean during research cruises		
1981–85		1798
1998–2002	3684	1052
CWT maturing coho salmon caught in the sport and troll ocean fisheries (all catch areas) and released between northern Oregon and northern Washington[1]	149,718	—

[1] FL data in the Pacific States Marine Fisheries Commission, Regional Mark Information System online CWT database http://www.rmis.org/. [Accessed 1 April 2003.]

in the hatchery by varying the feeding levels: the group that was fed the most also grew the most and had the most widely spaced scale circuli. Positive correlations between circulus spacing and growth also have been observed for nonsalmonid fishes including *Tilapia* (Doyle et al., 1987; Matricia et. al., 1989; Talbot and Doyle, 1992), and walleye (*Stizostedion vitreum*) (Glenn and Mathias, 1985).

Circulus spacing is potentially useful for comparing ocean growth rates of salmon in the ocean. Spacing of the first few ocean scale circuli may indicate relative growth rates of juvenile fish immediately after ocean entry. However, in order for spacing of scale circuli to be a practical indicator of fish growth rate, the relationship between the two must be consistent and significant. The relationship between circulus spacing and fish or scale growth rate is determined by the relative rates of growth and circulus formation. If circuli (like tree rings) are formed at a constant rate, then there would be a directly proportional relationship between spacing and growth rate (e.g., a doubling of growth rate would result in a doubling of spacing). Conversely, if the rates at which circuli are formed are directly proportional to growth rates (e.g., a doubling of growth rate would result in a doubling of circulus formation rate), then the spacing of circuli would be constant. Our earlier study of growth rate, circulus formation, and circulus spacing among 82 individually marked juvenile coho salmon growing for a period of 63 days in saltwater tanks indicated that neither of these two extremes is the case, but that both circulus formation rate and circulus spacing are positively correlated with fish growth rate (Fisher and Pearcy, 1990).

Our main objectives in this study are to further assess the reliability of circulus spacing as an indicator of growth rate in FL of coho salmon in the ocean, to investigate how growth of coho salmon changes seasonally, and to compare any seasonal changes in growth rate with seasonal changes in the spacing of scale cir-
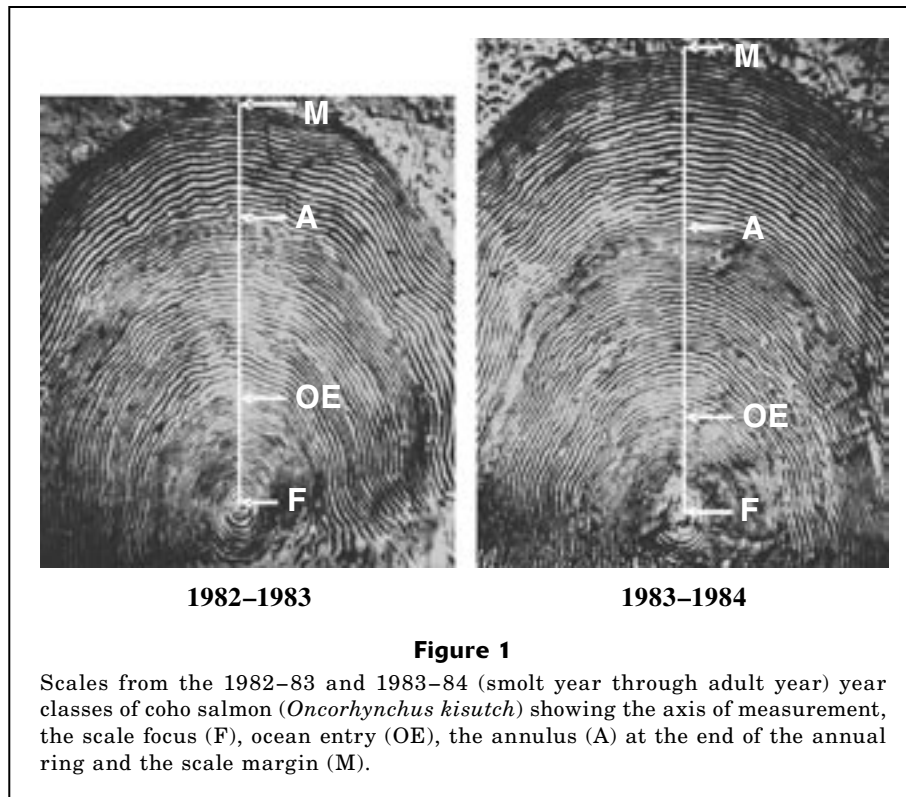
culi. If circulus spacing is a reliable indicator of growth rate, then seasonal changes in growth rate should be tracked by changes in the spacing of circuli laid down at the scale margin. We investigated relationships between scale growth rate, fish growth rate, circulus spacing, and circulus formation rate for coded-wire–tagged (CWT) adult coho salmon collected in the ocean fisheries in years when ocean growth varied widely, including year classes affected by the 1982–83 El Niño, and for juvenile and maturing coho salmon caught in the ocean off Oregon and Washington in research cruises 1981–85 and 1998–2002.

Materials and methods

Scale and FL data

Fish fork length (FL) and scale data from a variety of sources were used in this study (Table 1). During research cruises on the Oregon and Washington coastal shelf we collected juvenile and maturing coho salmon in the upper 20–40 m of the water column with purse seines from 1981–85 (Pearcy and Fisher, 1988, 1990) and with a rope trawl from 1998–2002 (Emmett and Brodeur, 2000). Scales samples were removed from the fish from an area equivalent to area "A" described in Scarnnechia (1979). When scales were not available from area "A," we took scales from between areas "A" and "B" in Scarnnechia (1979). (See also Clutter and Whitesel, 1956). We also examined scales from the same area from 687 maturing CWT Columbia River and northern coastal Oregon coho salmon caught in the Oregon ocean fisheries between 1982 and 1992.

Changes over time in FLs of maturing coho salmon caught in research nets and of CWT hatchery coho salmon originating between northern Oregon and northern Washington and caught in the ocean fisheries be-

Figure 1

Scales from the 1982–83 and 1983–84 (smolt year through adult year) year classes of coho salmon (*Oncorhynchus kisutch*) showing the axis of measurement, the scale focus (F), ocean entry (OE), the annulus (A) at the end of the annual ring and the scale margin (M).

tween 1975 and 2002 were used to estimate growth rates of maturing fish (Table 1).

Scale measurements

We measured the distances (mm) along the anterior–posterior scale axis from the focus (F) to the last circulus of the freshwater zone (ocean entry, OE), to the outside edge of the winter annual ring (the "winter annulus," A) when present, and to the margin (M), and also determined the total numbers and average spacing of circuli in the ocean growth zone (Fig. 1). For certain scale samples we also determined the spacing of every circulus in the ocean growth zone of the scales or of the last few circuli at the scale margin.

Measurements of scales from juvenile fish caught during research cruises 1981–85 were taken from images projected by a microfiche reader at a magnification of about 88× and measurements of scales from all other fish were acquired with image analysis software (Optimas, vers. 5.1, Optimas, Inc., Seattle, WA, and Image-Pro Discovery, vers. 4.5, Media Cybernetics, Silver Spring, MD) by using a CCD camera coupled to a Leica compound microscope. All measurements were calibrated from images of a stage micrometer.

Circulus spacing and formation rate versus growth rate

We used correlation and regression analyses to relate average circulus spacing and formation rate to average

scale and fish growth rate among year classes of juvenile coho salmon during their first four or five months in the ocean and among groups of maturing CWT coho salmon during their entire ocean life (Table 2). We described the relationships between the scale characteristics and growth rate as power functions by using natural log (ln) transformed variables in linear regressions. Geometric mean (GM) regression (Ricker, 1973, 1992; Sokal and Rohlf, 1995) was used to relate the ln-transformed variables because they were subject to both natural variability and measurement error and because our purpose in the present study was to describe the functional relationships between the variables and not to predict one from the other.

For each fish, rates of scale growth, fish growth, and circulus formation in the ocean were estimated as $(SR-SR_{OE})/\Delta d$, $(FL-FL_{OE})/\Delta d$, and $CIRC/\Delta d$, respectively, where SR=scale radius at capture, SR_{OE}= scale radius at ocean entry (F to OE in Fig. 1), FL= fork length at capture, FL_{OE}=estimated fork length at ocean entry, $CIRC$=the total number of circuli in the ocean growth zone of the scale, and Δd = estimated days between ocean entry and capture. Average spacing of circuli was calculated as $(SR_{LAST}-SR_{OE})/CIRC$, where SR_{LAST}=the scale radius to the last circulus before the scale margin.

For juvenile fish, FL_{OE} was estimated by using the Fraser-Lee back-calculation method (Ricker, 1992) and the intercept from the FL–SR regression for ocean-caught juvenile fish (34.16 mm, Fig. 2). However, be-

cause of allometry in the FL-SR relationships of juvenile and maturing fish (Fig. 2), which a ln-ln transformation of the data failed adequately to correct, the Fraser-Lee method was not used to estimate FL_{OE} of the maturing fish caught in the ocean. Instead, FL_{OE} of maturing fish was estimated by direct substitution of (SR_{OE}) into the *GM* regression relationship between *FL* and *SR* for juvenile coho salmon caught in the ocean 1981–85 and 1998–2001 (gray regression line, Fig. 2).

For juvenile fish caught in August or September, Δd was estimated as the capture date minus 25 May, a date near the peak of coho salmon smolt migration in the Columbia River estuary (Dawley et al., 1985a). Because we used a single date of ocean entry for all fish, errors in estimated growth rates of some individual juvenile coho salmon probably were quite large; the timing of ocean entry of fish can vary by as much as two months. However, for the correlation and regression analyses we used growth rates averaged by year class, which were probably quite accurate, if the average date of ocean entry of the fish in the samples is assumed to be similar across years. In the Columbia River, the major source of juvenile coho salmon on the Oregon and Washington coasts, ocean entry was concentrated between late April and early June and the timing of ocean entry varied little between years (Dawley et al., 1985a).

Dates of ocean entry of the maturing CWT Sandy and Cowlitz hatchery coho salmon (Table 2) were estimated from the hatchery release dates and the rates of downstream migrations of these fish observed during extensive sampling of migrating smolts at rkm 75 in the upper Columbia River estuary (Dawley et al., 1985b). To estimate dates of ocean entry of the Fall Creek hatchery fish, for which data on downstream migration were lacking, we assumed that smolts migrated to the ocean from the different release sites at the same average rate of downstream migration as that of Cowlitz Hatchery fish released in late April (5.7 km/d).

Potential errors in estimated growth rates of maturing CWT coho salmon caused by inaccurately estimating size of fish at ocean entry, or date of ocean entry, were proportionally very small when compared to the total amount or duration of ocean growth. At a typical SR_{OE} of around 0.7 mm, the 95% prediction limits for *FL* from the SR-FL regression of juvenile fish (Fig. 2) are about ±31mm. An error in size at OE of 15–30 mm would only be 2–10% of the estimated total growth in *FL* in the ocean of the maturing fish (320 mm–610 mm). Similarly, an error in estimated date of ocean entry of 30 days would equal only about 6–10% of the total time that the fish was in the ocean (336–535 d). Errors for the group-averaged data used in our correlation and regression analyses were probably much lower.

Seasonal changes in spacing of circuli

To investigate whether circulus spacing and growth rate were correlated seasonally, we first described the patterns of seasonally changing circulus spacing of juvenile and maturing coho salmon in the ocean and

Table 2
Nine year classes of juvenile coho salmon caught in research nets in August or September and 17 groups of CWT maturing coho salmon caught in the Oregon ocean fisheries used in the correlation and regression analyses of scale characteristics and growth rate. CWT maturing fish were from three hatcheries (Fall Creek "F" on the northern Oregon coast and Sandy "S" and Cowlitz "C" in the lower Columbia River basin) and were released from hatcheries during three periods.

Capture year	Hatcheries	Numbers of fish
CWT maturing fish released late April or early May (days 119–127)		
1982	F, S	11, 15
1983	F, S, C	34, 17, 51
1984	S, C	52, 35
1985	S, C	12, 26
1986	S	67
1987	S	94
1989	S	57
1990	S	18
CWT maturing fish released in March (days 74–76)		
1984	F	31
1985	F	21
CWT maturing fish released in late May or early June (days 151–157)		
1991	S	30
1992	S	77
Juvenile fish		
1981	—	99
1982	—	95
1983	—	81
1984	—	88
1998	—	13
1999	—	60
2000	—	75
2001	—	67
2002	—	123

then compared these patterns of changing circulus spacing to changing fish growth rates. Because the widths of the pre-annulus and postannulus scale zones and the numbers of circuli in each zone varied greatly among individual fish and among groups of fish, we described circulus spacing in each of 25 equally spaced intervals between *OE* and the annulus and in each of 25 equally spaced intervals between the annulus and the scale margin, rather than on a circulus by circulus basis. Specifically, the pre-annulus and postannulus ocean zones of scales were each divided into 25 equal intervals, and the radial distance from OE to the upper bounds of each of the intervals was determined. Next, the numbers of ocean circuli between OE and the upper bounds of each of the 50 intervals were interpolated. For example, if a boundary fell 25% of the distance
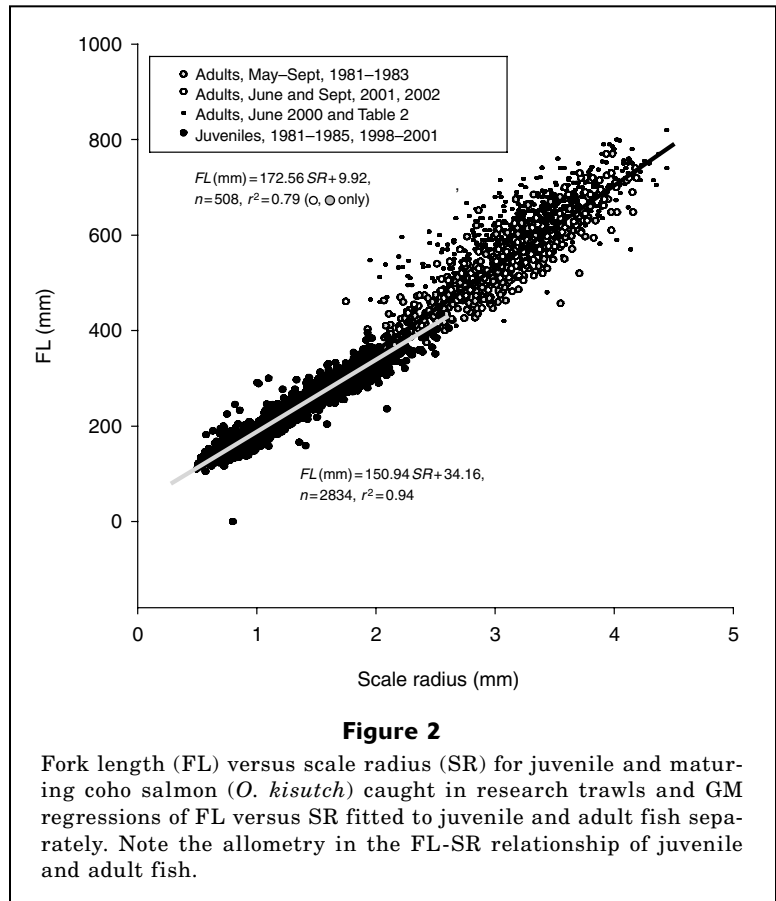
between the 38th and 39th ocean circulus, the circulus number 38.25 was assigned to that boundary. We calculated the circulus spacing in each interval as $\Delta mm/\Delta circ$, where Δmm = the width in mm of the interval, and $\Delta circ$ = the difference between the interpolated circulus numbers at the upper and lower bounds of the interval. The circulus spacing in each of the 50 intervals was averaged across all the scales from the fish in a group. This produced a profile of the average spacing of circuli at 50 different positions in relation to *OE* (lower bound of interval 1), the annulus (upper bound of interval 25) and the scale margin (upper bound of interval 50). Finally, the group-average circulus spacing in each of the 50 intervals was plotted against the group-average radial distance from *OE* to the upper bounds of each of the 50 intervals. For juvenile fish caught in trawls in September 1999–2002, circulus spacing was described at 25 intervals in relation to *OE* (lower bound of interval 1) and the scale margin (upper bound of interval 25).

Seasonal changes in the spacing of circuli at the growing edge of the scale may reflect similar seasonal changes in the growth rate of the juvenile and maturing coho salmon. To investigate this possible correlation, we measured the spacing of the last two circulus pairs at the scale margin of juvenile fish caught in early and late summer in 1982 and 1999 through 2002 and of maturing fish caught in research nets 1981–83 and 2000–2002 and in the ocean fisheries 1982–92 (Table 1). Mean spacing of the last two circulus pairs was summarized by cruise for the fish caught in research nets, and by 10-day catch intervals for the fish caught in the ocean fisheries. The seasonal trends in spacing at the scale margin were then compared with the seasonal trend in apparent growth rates of fish.

Seasonal changes in fish growth rate

Seasonal trends in growth rates of juvenile and maturing coho salmon caught in research cruises 1981–83 and 1998–2002 were estimated from the changes between cruises in average FL. We also estimated average growth rates (pooled across years) of juvenile and adult coho salmon during different seasons by fitting regressions to the FL versus catch date data.

Changing stock composition of the juvenile (Teel et al., 2003) or maturing coho salmon caught in research nets over the course of the summer could potentially have a strong effect, independent of growth, on the size distributions of fish caught at different times. Therefore, changes over time in average FLs of mixed stocks of fish, such as in our research collections, may not accurately indicate actual fish growth rates.

Figure 2

Fork length (FL) versus scale radius (SR) for juvenile and maturing coho salmon (*O. kisutch*) caught in research trawls and GM regressions of FL versus SR fitted to juvenile and adult fish separately. Note the allometry in the FL-SR relationship of juvenile and adult fish.

Because of the potential for error when inferring seasonal changes in growth rate from changes over time in average FLs of mixed stocks of fish, we also examined temporal changes in FL of maturing CWT coho salmon of known origin caught in the ocean hook-and-line fisheries (sport and troll fisheries). Using data available from the Pacific States Marine Fisheries Commission[1] we investigated changes over the summer in FLs of maturing CWT coho salmon originating from six areas (north Oregon coast, lower Columbia River basin–Oregon, lower Columbia River basin–Washington, Willapa Bay basin, Grays Harbor basin, and the northwest Washington coast). Because the date that a smolt is released from a hatchery (e.g., March vs. June) could affect its size the following year, we also grouped the fish by release periods of 25–46 days duration. Data were available on FLs of maturing CWT fish from 1975–2002. For each group in each year we calculated the average FL of CWT fish at 10-day intervals in the hook-and-line fisheries (sport and troll fisheries) pooled for all catch areas between California and Alaska. Data were discarded when there were fewer than 5 fish mea-

1 Regional Mark Information System CWT database (http://www.rmis.org). [Accessed on: 1 April 2003.]

Table 3

Summary statistics of average estimated fish growth rate, average estimated scale growth rate, average estimated rate of circulus formation, and average circulus spacing between ocean entry and late summer for nine year classes of juvenile coho salmon and during the entire ocean growth period for the 17 groups of CWT maturing coho salmon (see Table 2).

Statistic	Average fish growth rate (mm/d)	Average scale growth rate (mm/d)	Average circulus formation rate (circuli/d)	Average circulus spacing (mm)
Juvenile fish, *n*=9				
Grand average	1.33	0.0087	0.188	0.0460
Minimum	1.18	0.0080	0.175	0.0428
Maximum	1.52	0.0101	0.202	0.0494
SD	0.10	0.0007	0.008	0.0023
CV	7.6%	8.3%	4.1%	4.9%
Maturing fish, *n*=17				
Grand average	1.11	0.0060	0.131	0.0463
Minumum	0.94	0.0048	0.110	0.0426
Maximum	1.23	0.0066	0.144	0.0511
SD	0.07	0.0005	0.009	0.0020
CV	6.7%	8.1%	6.8%	4.4%

sured in any 10-day catch period. The average FLs were averaged across all years of data, yielding grand-average FLs for each 10-day catch period. The grand average FL for each 10-day catch interval comprised 1–27 years of data, but those periods with fewer than 5 years of data were discarded. In all, FLs from 149,718 fish were used in the analysis. Grand average FLs and the apparent growth rates in FL between each 10-day catch period were plotted against date and compared with the seasonal changes in circulus spacing at the scale margin of the fish in our scale sample.

Results

Growth and scale statistics for juvenile and maturing fish

Average growth rates and circulus formation rates were greater for juvenile fish during their first ocean summer than for maturing fish during their entire ocean life probably because maturing fish experience slow growth in the winter (Table 3). During their first summer in the ocean, juvenile fish grew an average of 1.33 mm/d and formed circuli at the rate of 0.188/d (one every 5.3 days): whereas, during their entire ocean life maturing fish grew an average of 1.11 mm/d and formed circuli at the rate of 0.131/d (one every 7.6 days). The highest average growth rate (1.52 mm/d) among the eight year classes of juvenile coho salmon was about 28% higher than the lowest average growth rate (1.18 mm/d). The percentage range in growth rate of maturing fish was similar (31%). Average spacing of circuli was similar for both juvenile and maturing coho salmon (0.0460 mm vs. 0.0463 mm), probably because scales from the maturing

fish contained both more narrowly spaced circuli formed during the winter and more widely spaced circuli formed during the second ocean summer (see below). The variation among groups in average circulus spacing (CV=4.9% and 4.4%) was lower than the variation in fish or scale growth rates (CV=6.7% to 8.3%), although estimation error may have increased the coefficients of variation of the growth rates.

Correlations between scale characteristics and growth rate

Circulus spacing was strongly correlated (r=0.89 and 0.82, respectively) with scale and fish growth rates among the nine year classes of juvenile coho salmon (Table 4). Circulus spacing was also significantly correlated with scale and fish growth rates among the 17 groups of maturing fish, but the correlations were weaker (r=0.57 and 0.55, respectively) than those for the juvenile fish. Conversely, correlations between the rate of circulus formation and the scale and fish growth rates were slightly higher for the maturing fish (r=0.85 and 0.75, respectively) than for the juvenile fish (r=0.76 and 0.81, respectively). These results suggest that when growth is averaged over several seasons, during which growth rate varies greatly and may even cease for varying periods of time, differences in growth among year classes or groups may be reflected more clearly by differences in the numbers of circuli laid down on the scale than by differences in the average spacing of circuli.

Although the average spacing of circuli and the average rate at which circuli form were both correlated with scale and fish growth rates, they were not correlated with each other (Table 4). This finding indicates that

circulus spacing and circulus formation rate are inde-
pendent indicators of growth rate—both tending to in-
crease with increasing growth rate but not necessarily
together in the same fish or in the same group or year
class. At least when averaged over periods of months or
more than a year, differences in average growth rate
may be expressed by differences in average spacing of
circuli, differences in average rate of circulus formation,
or differences in both.

Regressions of circulus spacing and formation rate on growth rate

We expressed average spacing of circuli and rates of
circulus formation as power functions of the scale growth
rates, equivalent to linear regressions of ln-ln trans-
formed data. These regressions are shown in Figures
3 and 4 for year classes of juvenile fish and groups
of maturing fish, respectively. Because scale growth
rate and fish growth rate were very strongly corre-
lated (Table 4), we show only the regressions with scale
growth rate.

Change in average spacing of circuli and in average
rate at which circuli form was proportionally smaller
than the change in average scale growth rate. Aver-
age spacing of circuli was proportional to the average
scale growth rate raised to the 0.6 power (juvenile fish,
Fig. 3A) or the 0.5 power (maturing fish, Fig. 4A). If
these relationships hold over a wider range of scale
growth rate and circulus spacing, then a doubling of
scale growth rate would be associated with only a 1.5-
fold ($2^{0.6}$) or 1.4-fold ($2^{0.5}$) increase in circulus spac-
ing. Similarly, average rate of circulus formation was
proportional to the average scale growth rate raised to
the 0.5 power (juvenile fish, Fig. 3B) or the 0.8 power
(maturing fish, Fig. 4B).

Seasonal changes in circulus spacing and fish growth rate

Seasonal changes in average circulus spacing were con-
sistent among the different year classes and release
times of CWT coho salmon (Fig. 5, A–E). During the
first year in the ocean, average spacing of scale circuli
increased rapidly after OE (usually in May) to aver-
age peak values of about 0.050 mm–0.055 mm, then
gradually decreased to average minimum values of
about 0.031 mm–0.040 mm in the annual ring. By late
September 1999–2002, spacing at the margin of scales
from juvenile fish had decreased from peak values (Fig.
5E), indicating that the gradual decrease in spacing of
circuli which forms the annual ring begins as early as
the late summer of the first ocean year. For some year
classes (e.g., 82–83, 85–86, 90–91, 91–92) the annual
ring was a distinct narrow zone of very closely spaced
circuli (Fig. 5, A and C), whereas in other years the
annual ring was broad and subtle, with more widely
spaced circuli (e.g., 83–84, 86–87, and 84–85 for the
March released fish; Fig. 5, A and B).

After the annulus (black dots, Fig. 5), the spacing
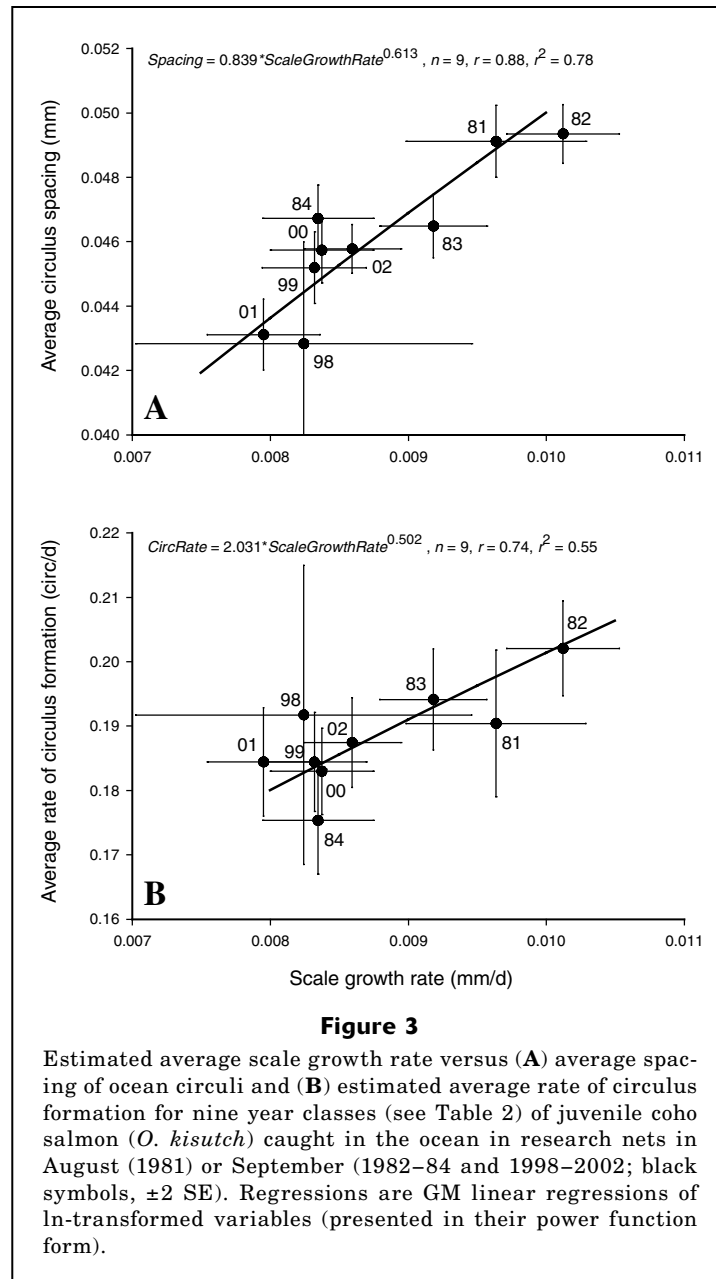of circuli increased sharply to peak values of about

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Table 4

Correlations (r) between average circulus spacing (mm),
average estimated scale growth rate (mm/d), average
estimated fish growth rate (mm/d), and average esti-
mated circulus formation rate (circuli/d) between ocean
entry and late summer for nine year classes of juvenile
coho salmon and during the entire ocean growth period
for 17 groups of CWT maturing coho salmon (see Table
2). All correlations were significant ($P<0.05$), except were
noted ("n.s").

Comparison	Juvenile fish r	Maturing fish r
Circulus spacing vs. scale growth rate	0.89	0.57
Circulus spacing vs. fish growth rate	0.82	0.55
Circulus spacing vs. circulus formation rate	0.38, n.s.	0.05, n.s.
Scale growth rate vs. fish growth rate	0.97	0.91
Scale growth rate vs. circulus formation rate	0.76	0.85
Fish growth rate vs. circulus formation rate	0.81	0.75

0.055 mm–0.060 mm and remained high for a vari-
able distance. Compared to the peak spacing, spacing
of circuli at the scale margin was relatively high for
maturing fish caught in late June or July 1982, 1984,
1985, 1986, 1987, 1991, and 2000, whereas, spacing at
the scale margin was quite low compared to the peak
spacing for fish caught in July 1983, 1989, 1990, and
1992 (Fig. 5, A, C, and D). Spacing at the scale margin
was very low among unmarked maturing fish caught in
late September 2001 (Fig. 5D).

Compared to the large interseasonal variation in
spacing of circuli in the pre- and postannulus zones,
from about 0.03 mm in the annual ring to about 0.06
mm for the most widely spaced circuli, interannual
variation the peak and minimum spacing of circuli was
quite small. The peak spacing of circuli was similar
among year classes, even when total growth differed
greatly (e.g., the 82–83 vs. the 81–82 and 83–84 year
classes, Fig 5A). The unusually small postannulus scale
growth of fish caught during a strong El Niño in July
1983 (Fig. 5A) was characterized by a much narrower
region of widely spaced circuli and more closely spaced
circuli at the scale margin than in other years.

In general, pre-annulus scale growth was greatest for
the fish released in March (Fig. 5B), was slightly less
for the fish released in late April or early May (Fig. 5A),
and was smallest for the fish released in late May or
early June (Fig. 5C). These data indicate that date of
release may strongly affect the amount of growth at-

Figure 3

Estimated average scale growth rate versus (**A**) average spacing of ocean circuli and (**B**) estimated average rate of circulus formation for nine year classes (see Table 2) of juvenile coho salmon (*O. kisutch*) caught in the ocean in research nets in August (1981) or September (1982–84 and 1998–2002; black symbols, ±2 SE). Regressions are GM linear regressions of ln-transformed variables (presented in their power function form).
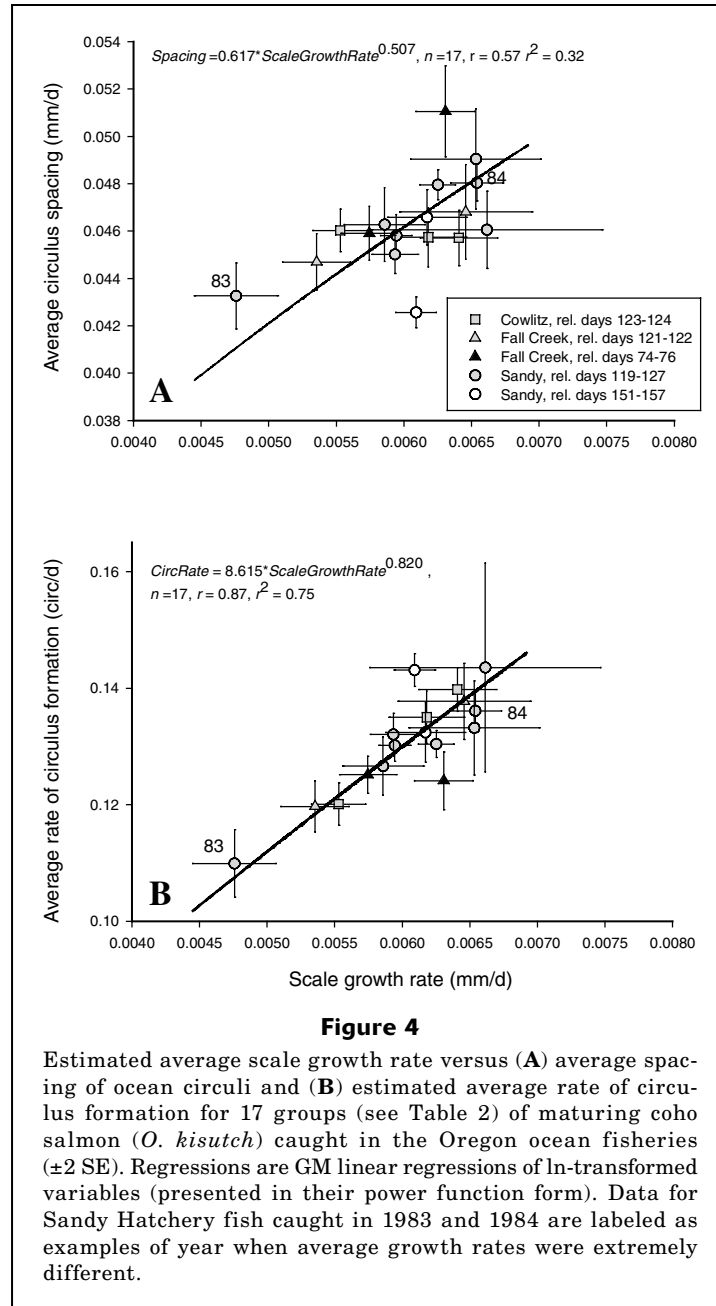
tained by juvenile coho salmon during their first summer, fall, and winter in the ocean.

Do the seasonal changes in circulus spacing in the ocean growth zones of scales coincide with similar seasonal changes in growth rates of juvenile and maturing coho salmon? In Figure 6 we plotted the average lengths of juvenile and maturing coho salmon from all research cruises 1981–2002 and the average apparent growth rates of coho salmon during different seasons (dashed lines). Apparent average growth rate of juvenile coho salmon between June and September was 1.30 mm/d, about twice the apparent growth rate of 0.64 mm/d between September and the following May. Apparent

growth rates of maturing fish between late May and late June was very rapid (2.11 mm/d), about twice as great as the apparent growth rate of maturing fish later between June and September (1.01 mm/d).

In a general sense, this pattern of changing apparent growth rate over time in the ocean corresponds well to the pattern of changing circulus spacing seen in Figure 5, A–E. The rapid growth of juvenile coho salmon between June and September occurs during a period when the spacing of circuli generally is high (Fig. 5E). When maturing fish were caught in the ocean fisheries in late June and in July and August a zone of widely spaced circuli already was present on the scales (Fig. 5,

Figure 4

Estimated average scale growth rate versus (**A**) average spacing of ocean circuli and (**B**) estimated average rate of circulus formation for 17 groups (see Table 2) of maturing coho salmon (*O. kisutch*) caught in the Oregon ocean fisheries (±2 SE). Regressions are GM linear regressions of ln-transformed variables (presented in their power function form). Data for Sandy Hatchery fish caught in 1983 and 1984 are labeled as examples of year when average growth rates were extremely different.

A–C), indicating that these widely spaced circuli were produced earlier during the period of apparently rapid growth in the spring and early summer (Fig. 6). Circulus spacing at the scale margin was already declining in July among maturing fish in some years (Fig. 5A), and was clearly lower among maturing fish caught in August or September (Fig. 5, B and D) indicating that these more narrowly spaced circuli were produced sometime during the apparently slower growth of maturing fish between late June and September (Fig. 6). Finally, the low spacing of circuli in the annual ring occurs sometime between late September of the first year and

mid-May of the second year, which was also the period of lowest apparent growth rate (Fig. 6).

The pattern of changing circulus spacing at the scale margin is most clearly seen when average spacing of the outer two circulus pairs is plotted against the average julian day of capture (Fig. 7, A and B). Among juvenile fish caught in research nets, the average spacing of the circuli at the scale margin was narrower in September than in June (Fig. 7A, see also Fig. 5E). We lack sufficient FL data from mid and late summer to determine whether or not a decrease in the average growth rate of juvenile fish was associated with the observed

Figure 5

Profiles of changing average circulus spacing (±2 SE) versus average scale radius at 50 intervals along the axis of measurement (see "Methods and Materials" section) for maturing coho salmon (*O. kisutch*) caught in the ocean fisheries and (**A**) released as smolts from hatcheries in late April or early May and caught in July, (**B**) released in March, (**C**) released in late May or early June and caught late June to late July, (**D**) unmarked maturing fish caught in research nets in June 2000 and September 2001, and (**E**) juvenile fish caught September 1999–2002. For clarity, error bars for the average scale radius at each interval are not shown.
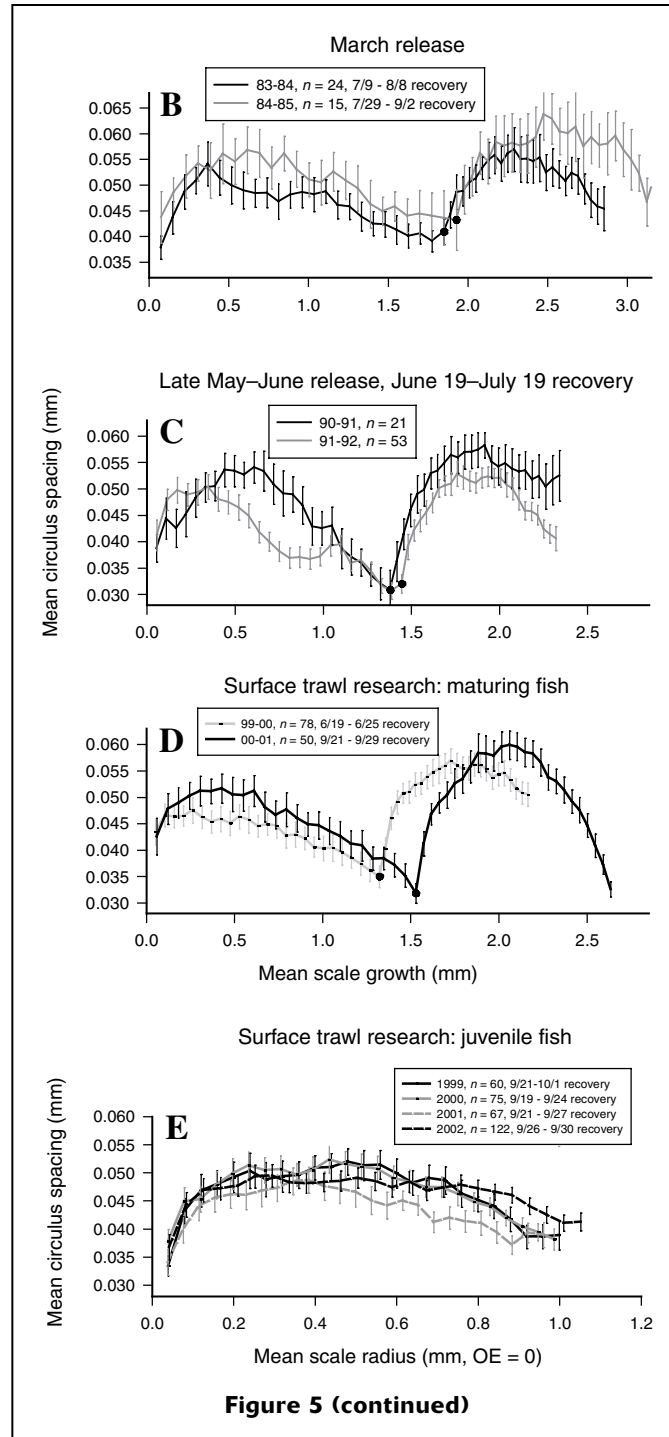
decrease in spacing of circuli at the scale margin in September.

Among maturing fish, average spacing of the last two circulus pairs at the scale margin decreased greatly between the spring through early summer period and early fall (Fig. 7B). The decrease in circulus spacing at the scale margin during the summer occurred for both maturing fish of mixed stocks caught in research nets (gray and white symbols) and for CWT fish of known stocks caught in the ocean sport and troll fisheries (black symbols). The decrease also was very consistent among year classes; 11 of the 12 year-class groups
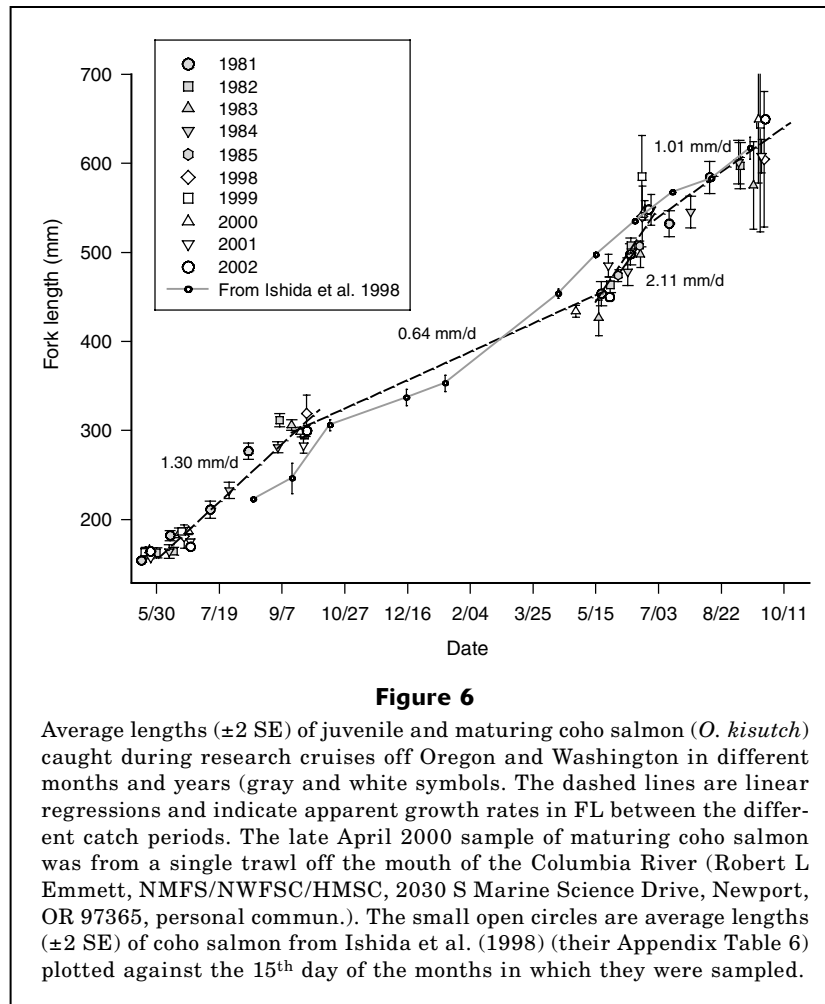
(grouped by release period and pooled across hatcheries) of Table 2 showed significant negative correlations between spacing at the margin and date of capture ($P<0.05$, $r=-0.40$ to -0.59). In September the average circulus spacing at the scale margin was about as low as the average circulus spacing in the annual ring (about 0.035 mm).

The decrease in spacing of circuli at the scale margin over the summer mirrors a similar decrease over the summer in apparent growth rates in FL of maturing fish caught in research nets (Fig. 7C). The apparent growth rates of maturing coho salmon were usually

Figure 5 (continued)

higher between the May and June research cruises (2–3 mm FL/d) than between cruises later in the summer (0.5–1.5 mm FL/d)(Fig. 7C, see also Fig. 6). The concurrent decreases in spacing of circuli at the scale margin and in apparent growth rate of coho salmon in the ocean is consistent with the hypothesis that seasonal changes in scale circulus spacing reflect seasonal changes in fish growth rate.

Additional evidence for decreasing growth rate of maturing coho salmon over the course of the summer comes from FLs of CWT fish in the hook-and-line fisheries (sport and troll fisheries). Generally, apparent growth rates in FL of maturing coho salmon originating from northern coastal Oregon streams and from both the Oregon and Washington sides of the Columbia river basin were highest from late May to mid-June and

Figure 6

Average lengths (±2 SE) of juvenile and maturing coho salmon (*O. kisutch*) caught during research cruises off Oregon and Washington in different months and years (gray and white symbols. The dashed lines are linear regressions and indicate apparent growth rates in FL between the different catch periods. The late April 2000 sample of maturing coho salmon was from a single trawl off the mouth of the Columbia River (Robert L Emmett, NMFS/NWFSC/HMSC, 2030 S Marine Science Drive, Newport, OR 97365, personal commun.). The small open circles are average lengths (±2 SE) of coho salmon from Ishida et al. (1998) (their Appendix Table 6) plotted against the 15th day of the months in which they were sampled.

decreased greatly by mid-August (Fig. 8, A and B). For three periods, 20 May–29 June, 29 June–8 August, and 8 August–27 September, median apparent growth rates were 1.43 mm/d (*n*=19), 0.64 mm/d (*n*=24), and 0.24 mm/d (*n*=27), respectively.
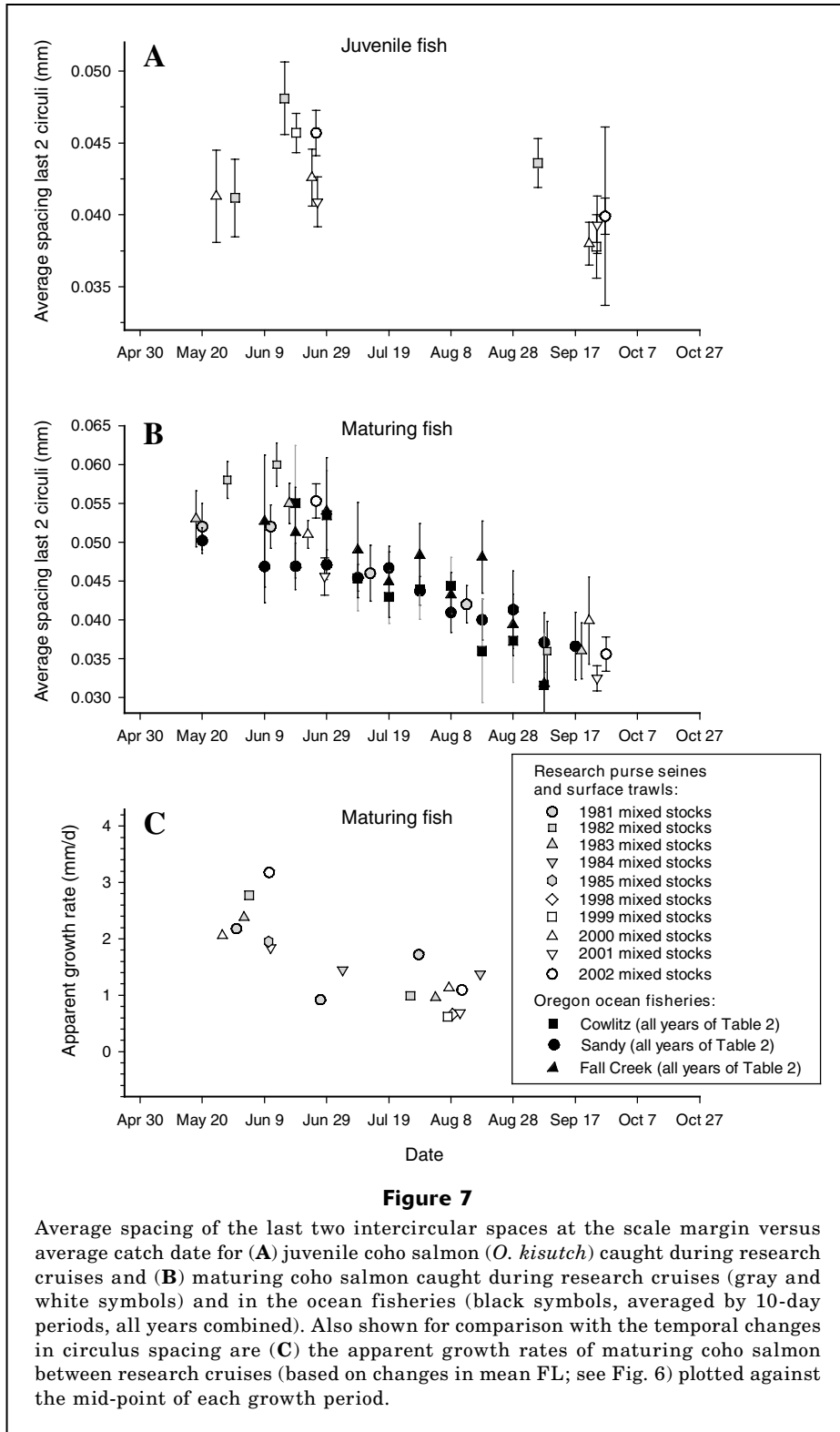
Growth rates of fish from coastal Washington rivers also decreased over the summer, but the decrease was not as great as for the Oregon and Columbia River fish, and the apparent growth rates of the Washington fish were higher at comparable times during the summer (Fig. 9, A and B). The apparent growth rates of Gray Harbor basin fish were over 2 mm/d from late June to mid-July and remained comparatively high (about 1.0 mm/d) into late October (Fig. 9B). Washington fish generally were not caught in the fisheries until mid- or late June, about a month after the first catches of the Oregon and Columbia River fish. For three periods 19 June–29 July, 29 July–7 September, and 7 September–27 October, median apparent growth rates of the coastal Washington fish were 1.23 mm/d (*n*=13), 0.92 mm/d (*n*=16), and 1.06 mm/d (*n*=9), respectively.

The growth data for CWT fish from the sport and troll fisheries, especially those for the coastal Oregon

and Columbia River stocks, were consistent with the growth data from the mixed stock catches of coho salmon in research nets off Oregon and Washington in that both data sets indicated a substantial decrease in growth rate (FL) of maturing coho salmon between the May–June period and the August–September period. The decreases over the summer in circulus spacing at the scale margin (Fig. 7B) and in apparent growth rates of maturing CWT coho salmon of known origin (Fig. 8B) is further evidence that scale circulus spacing and fish growth rate are correlated seasonally.
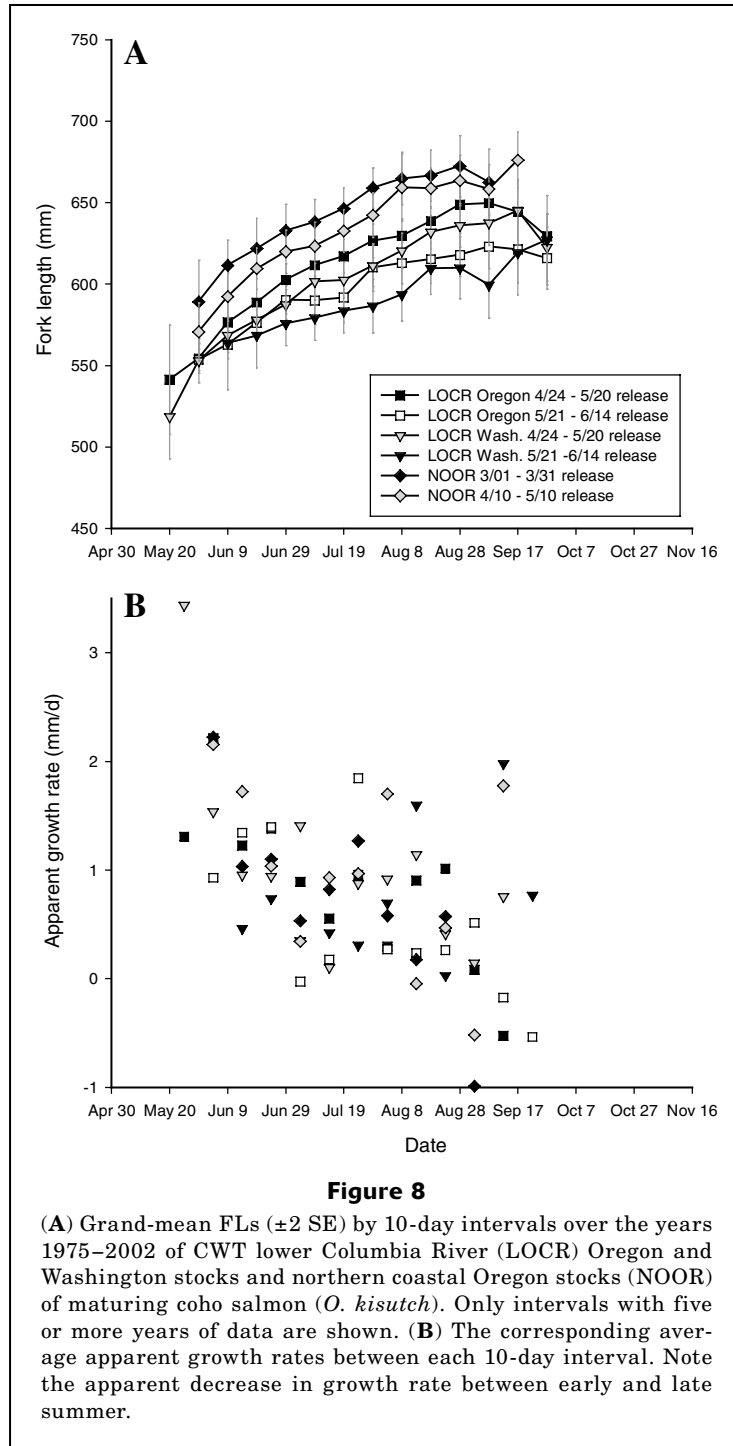
Discussion

Our data indicate that the seasonal cycle of changing ocean circulus spacing on scales of juvenile and adult coho salmon mirrors a similar seasonal cycle in the growth rate of these fish. We lack direct data for coho salmon collected between late September of the first calendar year of ocean residence and mid-May of the second calendar year, but growth rate during part of the fall and winter may be as low as 0.5mm/d

Figure 7

Average spacing of the last two intercircular spaces at the scale margin versus average catch date for (**A**) juvenile coho salmon (*O. kisutch*) caught during research cruises and (**B**) maturing coho salmon caught during research cruises (gray and white symbols) and in the ocean fisheries (black symbols, averaged by 10-day periods, all years combined). Also shown for comparison with the temporal changes in circulus spacing are (**C**) the apparent growth rates of maturing coho salmon between research cruises (based on changes in mean FL; see Fig. 6) plotted against the mid-point of each growth period.

based on data in Ishida et al. (1998). Therefore, the roughly twofold range in spacing of circuli in the ocean growth zone of scales from maturing fish that we found probably represents about a fourfold range in fish growth

rate in the ocean (from about 0.5 mm/d in the winter to 2.1mm/d in the spring and early summer). Thus, changes in the spacing of scale circuli are relatively small when compared to the corresponding changes in fish growth

Figure 8

(**A**) Grand-mean FLs (±2 SE) by 10-day intervals over the years 1975–2002 of CWT lower Columbia River (LOCR) Oregon and Washington stocks and northern coastal Oregon stocks (NOOR) of maturing coho salmon (*O. kisutch*). Only intervals with five or more years of data are shown. (**B**) The corresponding average apparent growth rates between each 10-day interval. Note the apparent decrease in growth rate between early and late summer.

rate. However, the large seasonal changes in growth rate of coho salmon in the ocean are readily detectable from the changes in circulus spacing on the scale.

In June 2001, 2002, and 2003 average spacing of the last two circulus pairs at the scale margin was positively correlated ($P<0.01$) with plasma IGF-I (insulin-like growth factor-I) concentrations from juvenile fish caught in the ocean in research nets (n=119, 163, and 206 and

r=0.52, 0.52, and 0.59 in 2001, 2002, and 2003, respectively) (Beckman[2] and Fisher, unpubl. data). Because plasma IGF-I levels have been shown to be positively
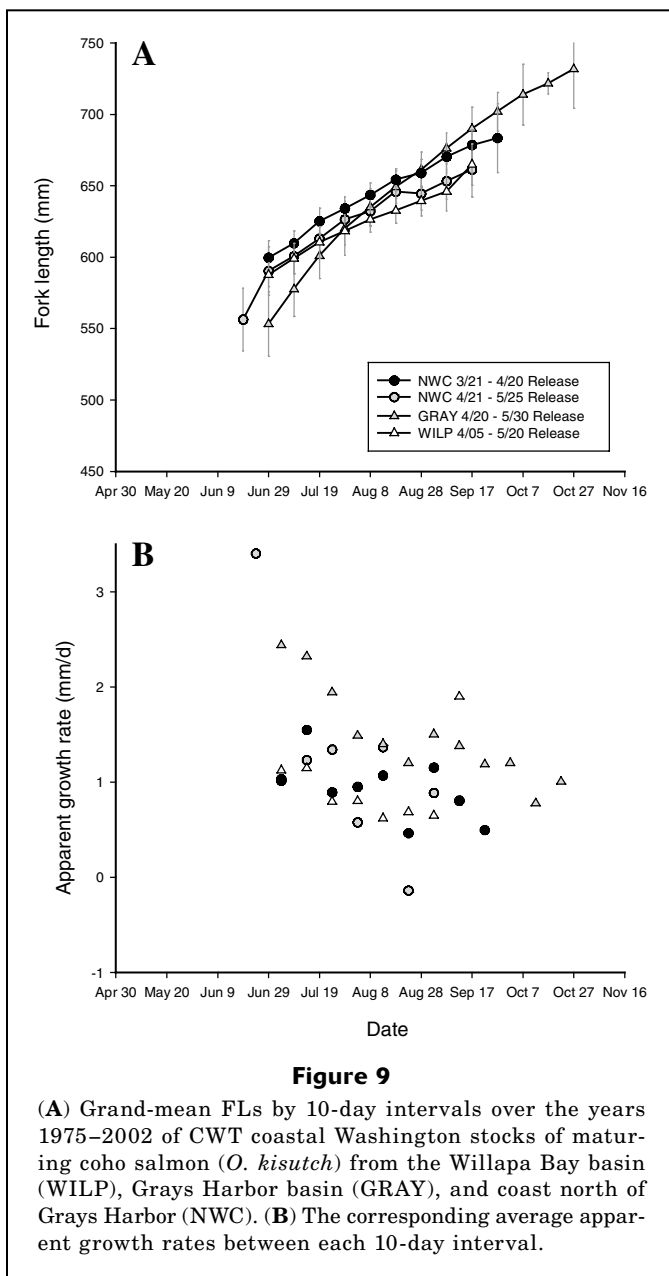
correlated with instantaneous growth rates (in length) of juvenile coho salmon (Beckman et al., 2004), the finding that plasma IGF-I is also correlated with the spacing of circuli at the scale margin of juvenile coho salmon is further evidence that circulus spacing and growth rate are positively related for coho salmon.
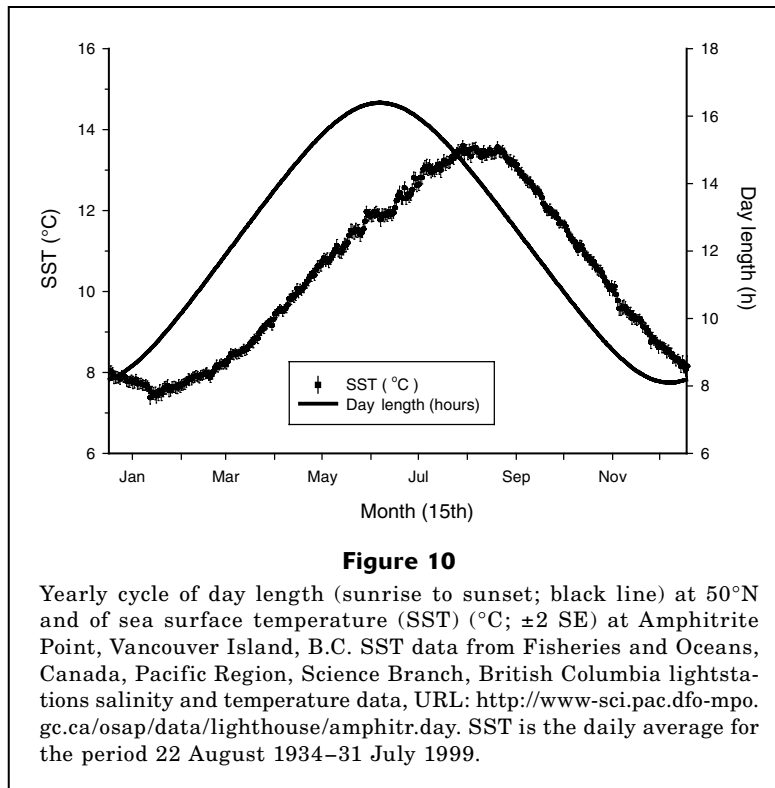
Our data suggest that growth rate in FL of maturing coho salmon is usually highest between early or mid-April and late June. This is a period of increasing photoperiod and often rising sea-surface temperature (SST) at 50°N in the northeastern Pacific Ocean, but is well before the maximum SST in late August (Fig. 10). Both increased day length and temperature stimulate growth in salmonids (Brett, 1979; Björnsson, 1997). The

Figure 9
(**A**) Grand-mean FLs by 10-day intervals over the years 1975–2002 of CWT coastal Washington stocks of maturing coho salmon (*O. kisutch*) from the Willapa Bay basin (WILP), Grays Harbor basin (GRAY), and coast north of Grays Harbor (NWC). (**B**) The corresponding average apparent growth rates between each 10-day interval.

decreases in apparent growth rate in length of maturing coho salmon after the summer solstice could be associated with a number of factors. One possibility is that there is a shift during the summer away from skeletal growth to growth in weight (with a resultant increase in condition) or to gonadal development. Data in Ishida et al. (1998) for coho salmon caught in research nets in the North Pacific tend to support this proposition (their Appendix Table 6). Their data indicate that the rate of growth in FL of maturing coho salmon decreased from 1.45 mm/d between April and May to 0.49 mm/d between July and August. (See also Fig. 6, present study). Over the same time period the condition index (weight $(g) \times (10^7/FL[mm]^3)$) of the fish they sampled increased from 113.3 to 143.8, an increase of 27%. Thus, skeletal growth slowed over the summer, but the condition of the fish increased.

In contrast to growth rates of Columbia River coho salmon, which decreased greatly between early and late summer, and were quite low (≤ 0.5 mm/d) by August and September, the growth rates of fish from the Grays Harbor basin, although also declining during the summer, remained high well into September and early October (~ 0.7–1.4 mm/d), allowing the Grays Harbor fish to attain a significantly larger final average FL. Several factors may result in the differing growth patterns of maturing fish from these two groups. Many of the fish from the Columbia River are early spawners, and peak spawning occurs from late October to early November, whereas the Grays Harbor fish are mainly late spawners, and peak spawning occurs from mid-November to late-December (Weitkamp et al., 1995). Because of their later spawning the Grays Harbor fish may shift from somatic to gonadal growth later in the summer or fall than do the earlier spawners from the Columbia River. Maturing coho salmon from the Grays Harbor drainage also have a much more northerly distribution than do maturing fish from the Columbia River (Weitkamp and Neely, 2002) and, therefore, the two groups encounter very different ocean conditions (e.g., temperature, salinity, prey fields, prey distributions, and potential competitors for food) while feeding in coastal waters. The different environmental conditions experienced by the Columbia River and Grays Harbor fish may also contribute to their differing temporal growth patterns.

Because of the poor conditions for growth of fish associated with the 1983 El Niño, adult coho salmon in 1983 were exceptionally small off Oregon and were in poor condition (Pearcy et al., 1985; Johnson, 1988). Our scale analysis indicates that the small size of fish in 1983 was largely due to a failure of growth of maturing fish after formation of the winter annulus. Although the average scale radius between OE and the winter annulus was slightly smaller for the 1982–83 year class than for other year classes, the average scale radius between the winter annulus and the scale margin, representing the growth of maturing fish in spring and early summer, was

Figure 10

Yearly cycle of day length (sunrise to sunset; black line) at 50°N and of sea surface temperature (SST) (°C; ±2 SE) at Amphitrite Point, Vancouver Island, B.C. SST data from Fisheries and Oceans, Canada, Pacific Region, Science Branch, British Columbia lightstations salinity and temperature data, URL: http://www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/amphitr.day. SST is the daily average for the period 22 August 1934–31 July 1999.

exceptionally low for this year class (Fig. 5A). Circulus spacing revealed two notable trends. First, in 1983 the maximum spacing of circuli following the winter annulus was only very slightly lower than in other years, which indicates that spring growth in FL of maturing fish in 1983 was not unusually low. Perhaps maturing coho salmon continued to grow in length in spring 1983, when photoperiod was increasing rapidly, despite low food availability. Björnsson (1997) found that changes in photoperiod may possibly control the level of pituitary growth hormone (GH), which strongly stimulates skeletal growth in salmonids and that increased levels of GH can induce growth in length even during starvation. Second, the spacing of circuli at the scale margin for fish caught in July 1983 was unusually low, similar to the spacing at the scale margin from fish caught in August of most years. This finding indicates very slow growth rates for maturing fish by July 1983. Length data[1] for maturing CWT coho salmon from the Oregon side of the Columbia River basin caught in the ocean sport and troll fisheries indicated that between June and September 1983 the average length of fish changed very little, which would indicate that somatic growth ceased during the summer.

Our results confirm the utility of circulus spacing as an indicator of growth rate in FL of coho salmon in the ocean. Correlations between average circulus spacing and estimated average growth rates of groups of fish were significant and positive (Table 4), even when growth was measured over long intervals of time (four to five months for juveniles, and over a year for maturing coho salmon), and even when the estimates of growth rate were subject to error In addition, our data indicate large seasonal changes in growth rate in FL of coho salmon in the coastal ocean off Oregon and Washington, a result also suggested by data in Ishida et al. (1998) for coho salmon in the North Pacific (see Fig. 6), and these seasonal changes in growth rate appear to be tracked by seasonal changes in spacing of scale circuli.

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