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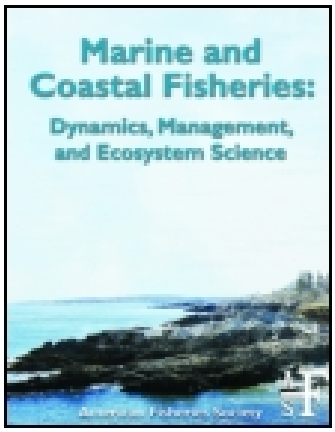

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Postsmolt Growth and Thermal Regime Define the Marine Survival of Steelhead from the Keogh River, British Columbia

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ARTICLE

Postsmolt Growth and Thermal Regime Define the Marine Survival of Steelhead from the Keogh River, British Columbia

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Abstract

The population of anadromous steelhead *Oncorhynchus mykiss* in the Keogh River has been studied intensively, in part because of its pattern of declining recruitment, which is largely attributed to poor marine survival. Climate variability has changed the productivity of salmonid species in all regions of the North Pacific, with areas alternately shifting between periods of enhanced and depressed productivity. The mechanisms governing marine survival and adult recruitment are central to contemporary resource management concerns but are also of concern with regard to the long-term prospects of managing biodiversity. We provide evidence that postsmolt growth contributes to the pattern of marine survival of Keogh River steelhead over the period corresponding to smolt years 1977–1999. Size at ocean entry did not appear to have sufficient contrast to significantly affect survival. However, assessment of scale growth suggested that the fish's initial growth at sea is not as important as the sustained growth conditions during summer and fall of the postsmolt year. The return rate of steelhead was negatively correlated with sea surface temperature in the ocean domains that were assumed to provide postsmolt nursery habitat, suggesting that growth is directly affected by warming conditions or that ocean warming affects the food web upon which steelhead depend. Steelhead appear to respond to changing climate and growth regimes in a manner similar to that of their North Atlantic analog, the Atlantic Salmon *Salmo salar*. Comparative data show that eastern basin Atlantic Salmon populations are negatively affected by a thermal regime of increasing temperature during the postsmolt year, suggesting a relationship between postsmolt growth and survival.

Successful management of anadromous species is challenged by shifting ocean conditions, which have placed many regional populations at risk of extirpation. As oceanic productivity shifts geographically, populations that possess unique traits and adaptations and that reside outside of higher productivity areas must be resilient enough to survive through unfavorable periods and emerge without damage to population genomes (Allendorf et al. 1997). Pacific salmonids are particularly well suited to this challenge at the molecular and behavioral levels (Waples et al. 2008; Healey 2009). However, no one phase of salmonid life history

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can be ignored in the management context (Bisson et al. 2009). This management problem may be more acute for anadromous steelhead *Oncorhynchus mykiss* than for other Pacific salmonids because steelhead life history favors a tradeoff for increased juvenile development in freshwater at the expense of population productivity. Hence, perturbations in survivorship can very quickly place steelhead populations at reduced levels and in danger of experiencing population bottlenecks that sharply reduce genetic diversity. The population of anadromous steelhead in the Keogh River, British Columbia, has been studied intensively, in part because of its pattern of declining recruitment. This pattern of decline has been attributed to marine survival conditions (Ward 2000), making this population an effective index stock for use in understanding the factors that influence the marine phase of steelhead and salmonids in general.

The life history of anadromous steelhead is divided between the freshwater habitats (used for spawning and juvenile rearing) and the oceanic habitats. While in oceanic habitats, individual fish accrue most of their somatic growth in preparation for spawning; however, both sets of environments pose survival challenges. Steelhead utilize a wide range of freshwater rearing habitats, reflecting a highly plastic ability to adapt to local conditions (Sogard et al. 2012). Many impacts on steelhead populations will be local in nature and thus would not be expected to produce coherent recruitment patterns among populations. Populations that are impacted by water use and diversions may respond to differing patterns of dam spillage, which in turn will affect the rate of river and estuarine transit times for migrating juveniles (Haeseker et al. 2012). However, these impacts will be unique to individual river drainages and subsystem drainages. The advent of salmon farming has had a global impact on wild salmon stocks through market forces (Torrissen et al. 2013); however, there is also the more localized concern over the impact of salmon culture on individual populations. Parasitic infections originating from salmon farms in the Northwest Pacific have prompted a number of studies to characterize the possible effects on populations relative to the effects of other stressors (Noakes et al. 2000; Beamish et al. 2005). There are differing views on whether parasites from farms have a localized effect or, for that matter, an impact more severe than that posed by naturally occurring levels of parasites in the region (Frazer 2007; Krkosek et al. 2007; Price et al. 2010; Jones and Beamish 2012).

Some of the stressors associated with freshwater habitats can be attributed to more broadly defined forcing mechanisms. Walters and Ward (1998) posited that broad-scale changes to land use and the concomitant change in insolation of freshwater habitats were increasing the exposure of juvenile salmon to damaging ultraviolet radiation and that this damage was increasing the mortality rate in saltwater. Experimental tests of this theory, however, found no evidence that higher ultraviolet exposure resulted in higher mortality rates in either the freshwater phase or the early marine phase (Melnychuk et al. 2012). Climate helps to define the suitability of freshwater habitats, with limits usually delineated by latitudinal ranges: for example, in the Northern Hemisphere, warming climate conditions will open new habitats at higher latitudes and will make other habitats at lower latitudes unsuitable over time (Rand et al. 2012). However, this aspect of climate forcing does not match the pattern of recruitment coherence seen in Pacific salmon, particularly steelhead, over time (Beamish et al. 2000; Smith et al. 2000; Welch et al. 2000).

Recruitment synchrony appears to be a function of ocean climate variations. The productivity of salmonid species in all regions of the North Pacific has been linked to climate variation (Hare et al. 1999; Atcheson et al. 2012), with regions and their associated stock groupings alternately shifting between periods of enhanced and depressed productivity (Irvine and Fukuwaka 2011). Shifts between production regimes were initially described as a series of reversals between alternative steady states of the North Pacific climate system (Mantua et al. 1997); however, as secular climate change signals begin to superimpose upon climate variation signals, our assessments of population viability may be without a historical analog. The clear change in stock productive potential caused by these climate shifts makes assumptions of time-invariant productivity or carrying capacity parameters obsolete and is a particularly troubling source of added risk in the assessment and management process (Rogers et al. 2013), suggesting that natural shifts in productivity should be incorporated into the management of Pacific salmon stocks (Beamish et al. 2004b). Beyond the descriptive aspect of decadal variation in stock productivity, there is also the prognostic aspect, which depends on a working knowledge of the mechanisms governing marine survival and thus adult recruitment. It is difficult to see how long-term plans to manage fisheries—or, for that matter, biodiversity—can be achieved without the development of a forecast capability built upon a mechanistic understanding of the factors that control the life history of species (Young et al. 2007; Noakes and Beamish 2009).

An approach that has been used to decode the effect of climate on salmonid populations has been the retrospective reconstruction of growth histories by using scale growth patterns as a proxy for somatic growth. Scale growth in salmonids results in circulus spacing patterns that are proportional to somatic growth (Fukuwaka and Kaeriyama 1997), and seasonal differences in growth can be identified with these measurements (Fisher and Pearcy 2005). These features in scales have been used to describe the seasonal contributions of growth in Atlantic Salmon *Salmo salar*—a species with a life history analogous to that of steelhead—during the critical postsmolt year (McCarthy et al. 2008). Steelhead have classic salmonid scales (Maher and Larkin 1955), so scale archives can be analyzed to reconstruct growth histories and test hypotheses relating growth to survival.

The Keogh River steelhead population can serve as an effective index stock, and an archived collection of scales from this population is available for reconstructing variations in somatic growth over time. The goal of our study was to examine the growth history of the Keogh River steelhead population

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and relate this time series to the marine survival rate of the stock. Specifically, the size of migrating smolts and indices of postsmolt growth based upon scale growth proxies were compared with survival rates based on the number of river returns attributed to the enumerated smolt classes. In addition, correlations between monthly fields of sea surface temperature (SST) in the Northeast Pacific and steelhead survival rates were examined to determine whether this environmental variable has co-varied with recruitment.

METHODS

Study system and marine survival index.—The Keogh River is a multibranch river and estuarine system located in western Canada (Figure 1); a counting fence (sited approximately 300 m from the ocean) has been seasonally deployed across the river since 1977. The river supports a wild steelhead population that comprises primarily maiden spawners returning after 2 or 3 years at sea. The marine survival (i.e., return rate) of the population can be calculated from the census of out-migrating smolts and the subsequent return of adults. Adult returns are attributed to specific smolt classes based on age determinations from scales collected from the returning adults. The return rate proportion ([number of returning adults]/[number of migrating smolts]) was used in correlation analyses and is expressed as a percentage for graphic presentation. The annual number of migrating smolts measured at the counting fence has averaged 4,675 fish over the period 1977–2005. The adult return over the same period has averaged 576 fish, with nearly equal numbers of males and females. However, males tend to return at younger ages, with about 60% of the males returning after 2 years at sea and about 38% returning after 3 years. Females, on the other hand, primarily return after 3 years at sea (47% returning after 2 years; 52% returning after 3 years). The return of fish after 1 year at sea (jacks) was very low (<3% of the return). For statistical analysis, the return rate was tested for normality with the Shapiro–Wilk W-statistic, and based on improvement in the W-statistic a logit transformation was selected in preference to other transformations. This approach was also used to evaluate the distributions of the other variables in the study and guided the selection of a transformation method, where appropriate.

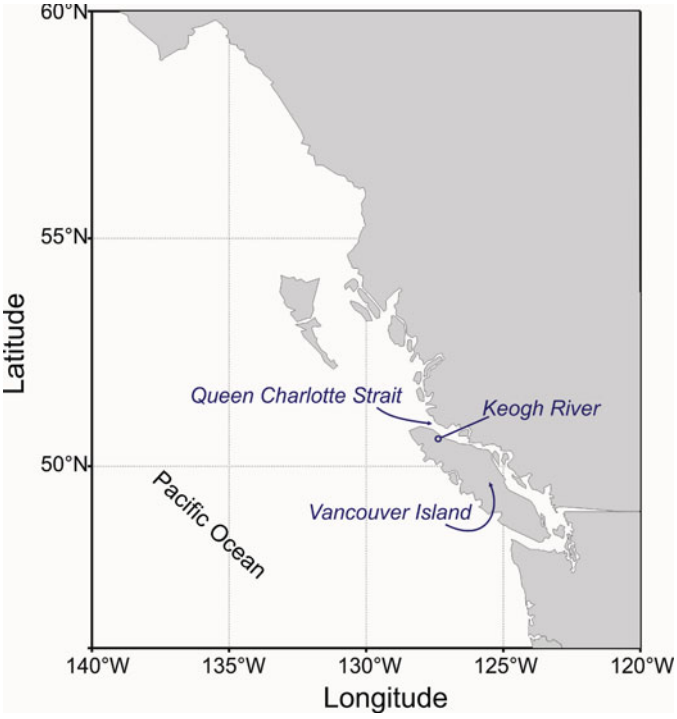

FIGURE 1. Map of western Canada, showing the location of the Keogh River in British Columbia.

Size at ocean entry.—The Keogh River counting fence has permitted virtually complete enumeration of out-migrating smolts during the spring migration. Length measurements (FL) collected on a subset of these smolts provide an index of size at ocean entry, which has previously been compared with marine survival (Ward and Slaney 1988; Welch et al. 2000). In this study, we used the size at ocean entry to assess how well initial size and postsmolt ocean growth were correlated with marine survival (return rate). Smolt length means were not transformed.

Retrospective growth analysis.—Scale samples from steelhead returning to the Keogh River for the smolt years 1977–1999 were obtained from trapping operations conducted by the Province of British Columbia's Fisheries Research group. Scales were removed from the standard area for sampling (left side of the fish; 3–5 scale rows above the lateral line, on a line between the posterior end of the dorsal fin and the anterior end of the anal fin). Scales were dried and stored in paper envelopes prior to being inspected under a dissecting microscope to determine suitability for image analysis. Regenerated scales were rejected unless the regeneration was confined to no more than 50% of the freshwater zone of the scale (Figure 2a); regeneration of scales tended to occur more frequently in hatchery-origin fish than in wild-origin fish (Figure 2c). Suitable scales were rolled using a hydraulic press to form an impression of the scale on an acetate slide. In total, scales from 435 fish of hatchery and wild origin were analyzed for the study (Table 1).

Postsmolt growth increments and estimates of monthly postsmolt growth were obtained from measurements between scale landmarks and circulus spacing in the marine portion of the scale. Using image processing, growth increments and estimates of monthly growth were derived from the spacing between successive pairs of circuli measured along the 360° axis of the scale extending from the first pair of marine circuli to the edge of the scale; thus, all of the circulus spacings in the marine growth zone were measured (Figure 2b). The first pair of marine circuli was identified from the first wide circulus spacing after the relatively tightly spaced circuli of the freshwater zone. The end of the postsmolt growth increment was associated with the first winter growth annulus, which was located by computing five-point running means of circulus spacing and selecting the minimum mean. Averaging with the running mean method

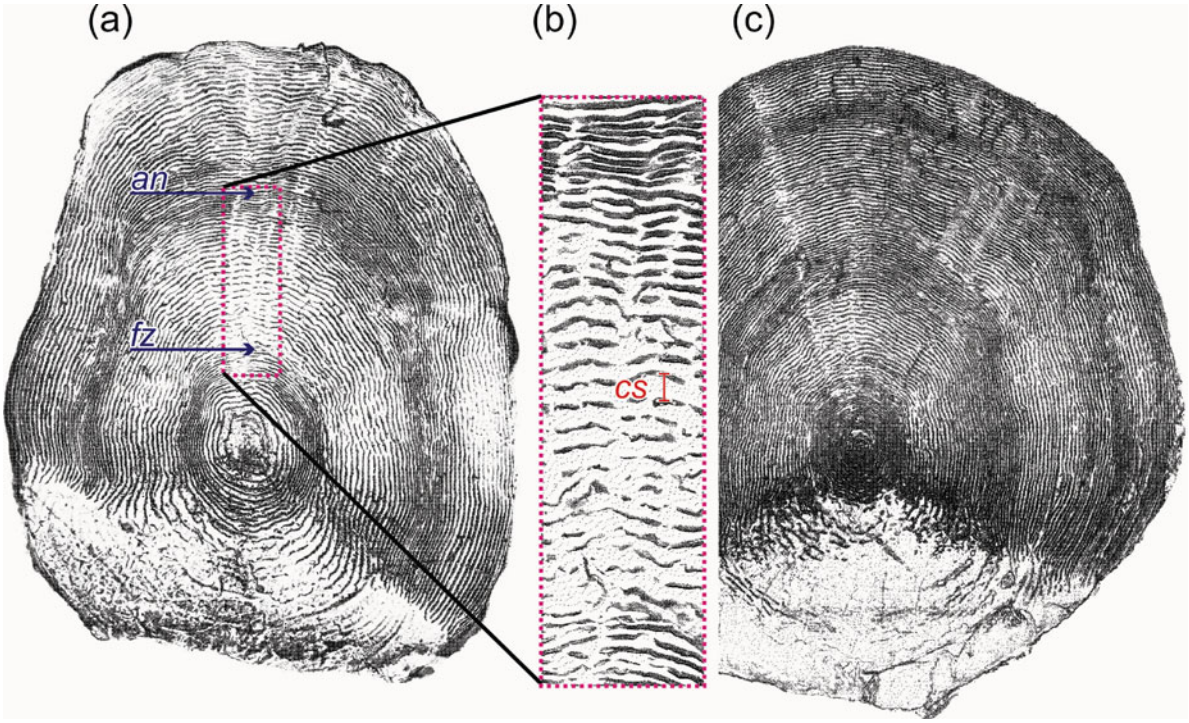

FIGURE 2. **(a)** Micrograph of a scale from a hatchery-origin steelhead, with the freshwater-to-marine transition zone (fz) and first winter annulus (an) marked; **(b)** enlargement of the postsmolt growth zone of the hatchery fish scale from panel a, showing the distance measured to represent intercirculus spacing (cs); and **(c)** micrograph of a scale from a wild steelhead.

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was used to reduce the effect of measurement error on locating the winter annulus. The sum of the circulus spacings from the beginning of the marine zone to the winter annulus was used as the postsmolt growth increment. Three explanatory or independent variables were available from this portion of the analysis, including the postsmolt growth increment, the total number of circulus pairs in the postsmolt growth zone, and the average spacing between circulus pairs in the postsmolt growth zone. These variables were tested for normality, and no transformations were required.

To examine growth more closely during the postsmolt period, the total postsmolt growth increment was partitioned into putative monthly increments. We considered the postsmolt period for the Keogh River stock to last 7 months based on (1) the time when the smolts migrate to sea (May) and (2) the assumption that the winter annulus is formed in December, when the photoperiod is shortest. The total number of circuli present in the postsmolt growth increment for each individual was divided by 7 to determine the number of circulus pairs allocated to each monthly period; thus, the circulus pairs were proportionally allocated to monthly periods. The mean circulus spacing for each month (so calculated) thus provides a more reasonable index for comparing between individuals with varying numbers of circuli deposited in the marine zone. We recognize that the number of circuli actually deposited is unlikely to be the same during each month of the postsmolt period (Bilton 1975), but our approach is an attempt to compare the same portions of scale from different fish. The growth indices for the putative months were tested for normality, and no transformations were indicated.

Sea surface temperature during early marine life.—Trends in SST in the Northwest Pacific were characterized using the Extended Reconstructed SST Data Set (version 3b; monthly data, 2° grid resolution). This time series is based on the SST compilation of the International Comprehensive Ocean-Atmosphere Data Set and represents interpolation procedures that reconstruct SST fields in regions with sparse data (Smith et al. 2008). Using the region bounded by 140–120°W and 51–60°N, we examined correlations between SSTs (June–December) during 1977–2005 and the logit-transformed return rate of Keogh River steelhead. In this paper, the position of the 12.5°C isotherm is plotted with each correlation map as an indication of the potential habitat of steelhead (Welch et al. 1998). Anomalies in SST were also developed by partitioning the data by year and by month. Years in the analysis were sorted and grouped based on return rate: the low-survival year grouping included the years 1978, 1988, 1990–1996, 1999, 2001–2003, and 2005; and the high-survival grouping included the years 1977, 1979, 1981–1987, 1989, 1997, 1998, and 2000. The second partition was based on months of the year, which were divided into an early grouping (June–August) and a late grouping (September–December). For each of the four combinations, SST anomalies were calculated based on the mean of the time series.

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TABLE 1. Sample sizes of hatchery- and wild-origin Keogh River steelhead used in scale analysis.

Smolt year	Hatchery	Wild	Total
1977		10	10
1978		18	18
1979	10	34	44
1980		12	12
1981		22	22
1982	7	3	10
1983	17	10	27
1984	27	24	51
1985		15	15
1986	1	15	16
1987	35	26	61
1988	16	7	23
1989	1	18	19
1990	11	6	17
1991	2	6	8
1992	3	5	8
1993	1	2	3
1994	6	6	12
1995	8	6	14
1996	1	2	3
1997	1	14	15
1998	5	9	14
1999	1	2	3

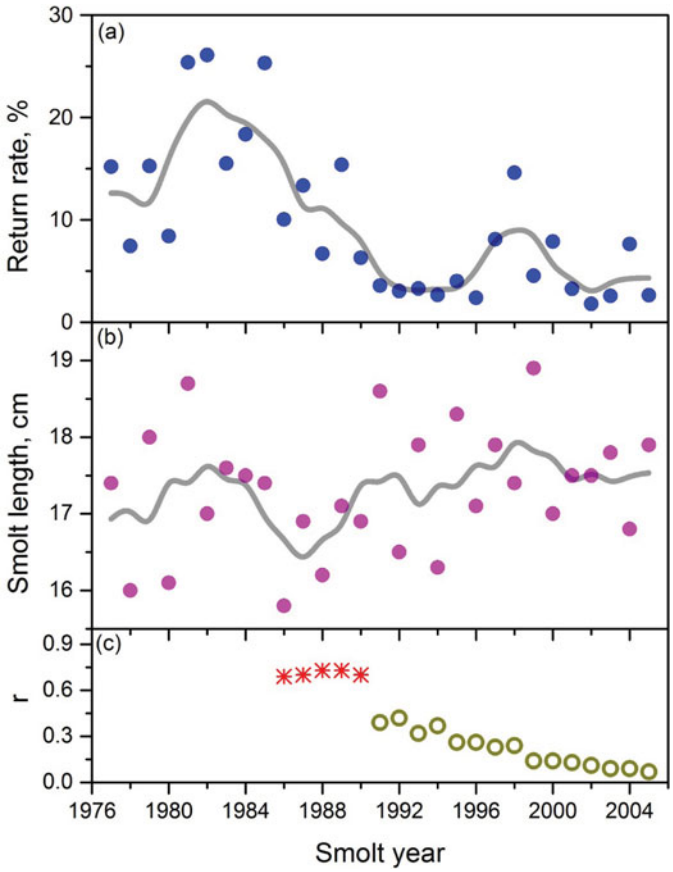

FIGURE 3. Time series of **(a)** the return rate of Keogh River steelhead (100 × [number of returning adults]/[number of migrating smolts]) for the smolt years 1977–2005 and **(b)** the mean length of migrating smolts. Smoothed lines are three-point moving averages (equal weights). **(c)** Correlation coefficients (r) between the logit-transformed return rate and the length of smolts for time series beginning in 1977 and ending in the year given on the x-axis are shown (asterisks = significant correlations at $P = 0.05$; open circles = nonsignificant correlations).

RESULTS

Marine Survival Index and Size at Ocean Entry

The return rate (smolt-to-adult survival) of Keogh River steelhead underwent a multidecadal decline, ranging from 2% to 26% over the period 1977–2005 (Figure 3a). During the first half of the time series, the return rate averaged 14%, whereas during the second half the rate averaged only 5%, representing a threefold decline. Smolt lengths averaged 17 cm over the entire time series, with no evident trend in the size at ocean entry (Figure 3b). Prior to 1990, adult return rates tracked smolt size at ocean entry quite well (Ward et al. 1989), but for later years the correlation failed. We re-examined the correlation between smolt length and return rate by starting with the correlation based on the first 10 years of the time series and then adding each subsequent year until all years in the time series were included (Figure 3c). The time series ending in years 1986–1990 yielded significant correlations between smolt length and return rate; however, for the time series ending in years 1991–2005, correlations were nonsignificant and declined to their lowest observed levels when those data were included. Smolt length was a good predictor of return rate at the beginning of the time series, but as return rates declined it became evident that smolt size at ocean entry was not capturing the variability associated with marine survival.

Retrospective Growth Analysis

There was a pronounced decline in postsmolt growth of Keogh River steelhead during the study period; this decline appears to be related to the decline in marine survival. Because of the small sample size of scale growth data, we first examined the efficacy of combining the data measured for hatchery- and wild-origin fish. Among the 23 years of scale growth data, 12 years had sufficient data to permit comparisons of scale growth characteristics between the two return groups. For the postsmolt growth increment data, only 1 year had an obvious difference between the increments measured in hatchery fish versus wild fish, as indicated by a comparison of the 95% confidence intervals for the two groups (Figure 4a). There appeared to be no systematic bias between the groups, since the number of years in which hatchery fish had the larger increments was nearly equal to the number of years in which wild fish had the larger increments. The circulus pair data did not appear to have any years with statistical differences between hatchery and wild

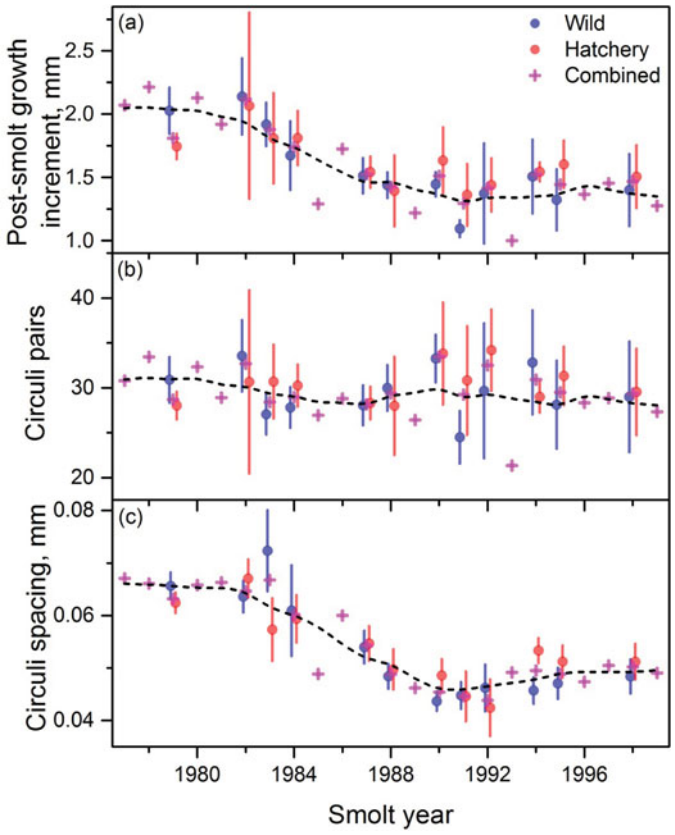

FIGURE 4. Time series of **(a)** postsmolt growth increment, **(b)** number of circulus pairs in the postsmolt growth increment, and **(c)** average circulus spacing in the postsmolt growth increment of scales from hatchery- and wild-origin Keogh River steelhead. Combined data for both groups of steelhead are represented by cross markers, with adjacent average smooths shown as dashed lines. Data specific to hatchery- or wild-origin fish are represented by circles with 95% confidence intervals (for years with sufficient data).

fish, and similar to the increment data, there was no apparent bias between the two groups (Figure 4b). Circulus spacing for hatchery and wild fish was statistically different in 3 years, and there was a bias since 75% of the samples showed higher growth among wild returns (Figure 4c). Overall, this bias represents 3% of the mean circulus spacing for all fish. From this analysis, we concluded that the data from hatchery fish and wild fish could be used as a combined signal.

The postsmolt growth signal associated with the spacing of scale circuli was correlated with the return rate of Keogh River steelhead, whereas the overall deposition of circulus numbers was not. The postsmolt growth increments for all fish combined averaged 1.82 mm for the first half of the time series and declined to 1.37 mm over the second half of the time series, translating to a 25% decrease (Figure 4a). The number of circulus pairs deposited during the postsmolt period changed very little, with an average of 30 pairs for the first half of the time series and 29 pairs for the second half (Figure 4b). Similar to the decline seen in the postsmolt growth increments, circulus spacing during the postsmolt period decreased dramatically from an average of 0.061 mm for the first half of the time series to 0.048 mm for the second half (i.e., a 22% decline; Figure 4c). The postsmolt growth increment for all fish was positively correlated with the return rate (Figure 5a). Data for smolt classes in the 1990s were strongly clustered due to the lower return rates and lower postsmolt growth; growth intervals associated with high return rates seldom overlapped the intervals associated with lower return rates. There was no relationship between the return rate and the number of circulus pairs deposited during the postsmolt period (Figure 5b). Similar to the trend seen in the growth increment data, circulus spacing was also observed to have a strong correlation with return rate (Figure 5c), and the data were clustered by decade.

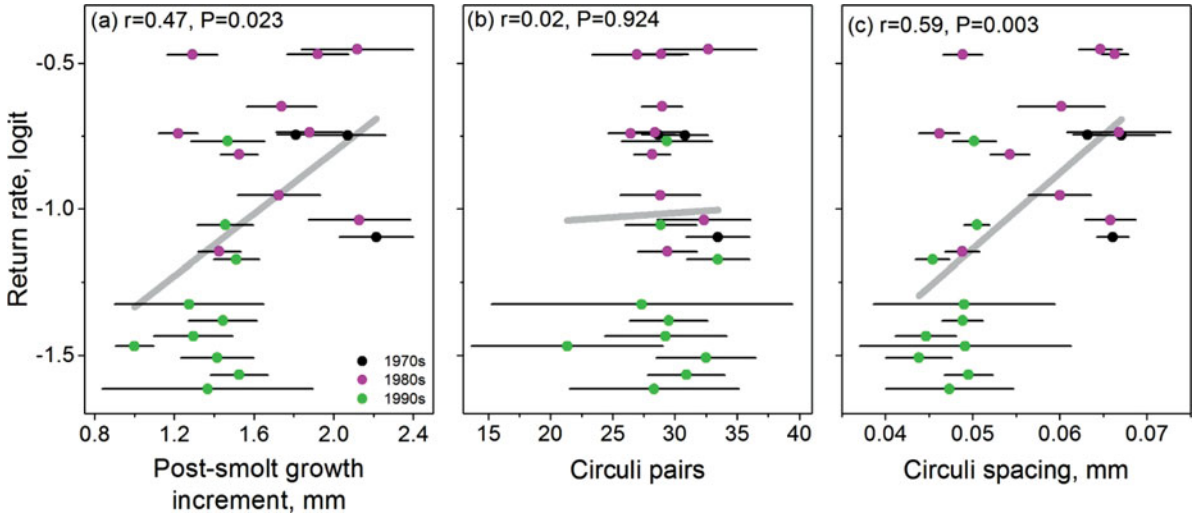

FIGURE 5. Relationship between logit-transformed return rate of Keogh River steelhead and **(a)** postsmolt growth increment, **(b)** number of circulus pairs in the postsmolt growth increment, and **(c)** average circulus spacing in the postsmolt growth increment. Independent variables are plotted with 95% confidence intervals (markers are color coded to represent the decade of the smolt year: 1970s, 1980s, or 1990s).

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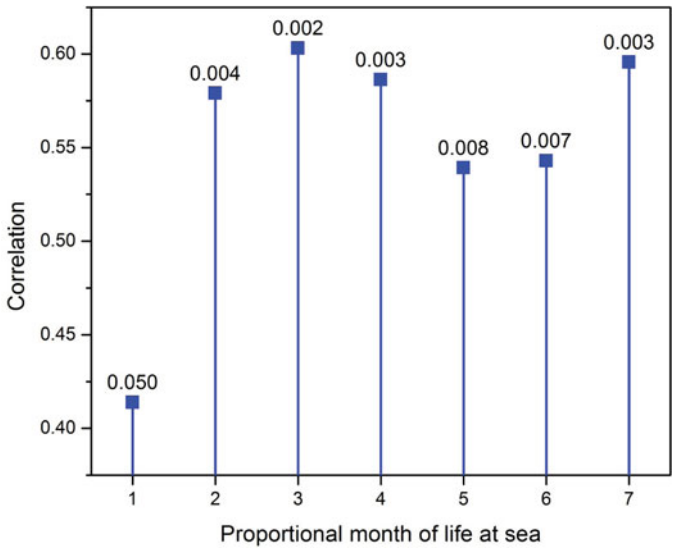

FIGURE 6. Correlation coefficients (r) between the logit-transformed return rate of Keogh River steelhead and proportionally allocated scale growth indices for the first putative month at sea (June) through the seventh month at sea (December). The value above each symbol is the probability associated with the r-value.

Putative monthly postsmolt growth increments associated with summer provided the highest level of correlation with return rate. The correlation between return rate and average circulus spacing during approximately the first month at sea was marginally significant and was the weakest of the monthly correlations (Figure 6). The strongest correlation was associated with the third month; however, all months after the first month had relatively strong correlations.

Sea Surface Temperature during Early Marine Life

Warmer sea conditions in the late-summer and autumn periods appeared to be related to the survival of Keogh River steelhead. The correlation field between SST and the Keogh River steelhead return rate was weakly negative for the first 3 months at sea (Figure 7a–c). During the fourth month at sea (roughly September), a significant negative correlation appeared in the southern end of the likely postsmolt nursery range (Figure 7d). This negative correlation was strongest in the subsequent month (October, Figure 7e) and persisted at a weaker level for the balance of the year (Figure 7f–g). For both the early and late time periods, low-survival years were marked by strong, positive SST anomalies that were especially pronounced in the southern end of the SST field (Figure 8a–b). During the late time period, these anomalies were as high as 0.7°C in the same regions that were shown to have strong correlative relationships with return rate. The SST anomalies in high-survival years were uniformly negative during the early time period (Figure 8c); during the late time period, SST anomalies in high-survival years were distributed in a contrasting pattern to those in low-survival years (Figure 8d).

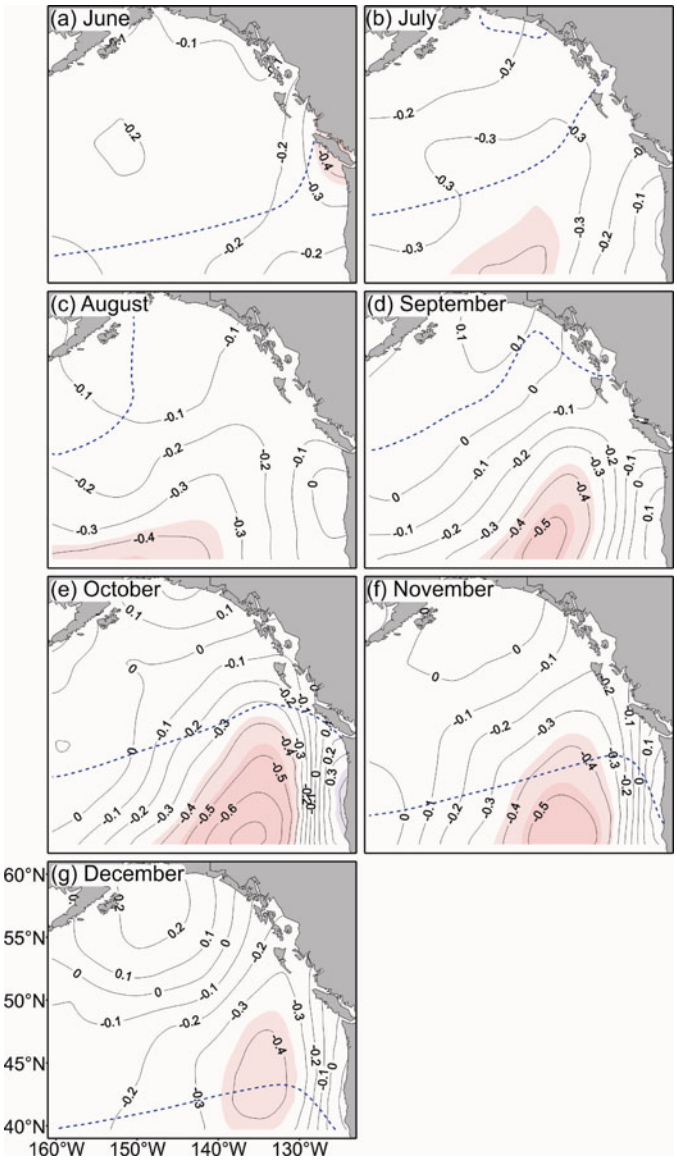

FIGURE 7. **(a)**–**(h)** Contour plots of correlation coefficients between the logit-transformed return rate of Keogh River steelhead and the sea surface temperatures for June–December of the smolt year. Light-red shading marks the approximate regions where negative correlations are significant at a P-value of 0.05; darker tones represent approximate regions where correlations are significant at a P-value of 0.01. Dashed blue lines mark the average position of the 12.5°C isotherm.

DISCUSSION

The main finding of this study was that the marine survival of Keogh River steelhead is related to postsmolt growth, which is consistent with a mechanism wherein size-mediated predation controls survival and thus recruitment. Such a mechanism would basically determine the probability that a postsmolt will be preyed upon as a function of its initial size and growth trajectory, although the exact form of this function remains to be determined (Sogard 1997). Juvenile salmon have extremely high growth rates and would be expected to perhaps outgrow the

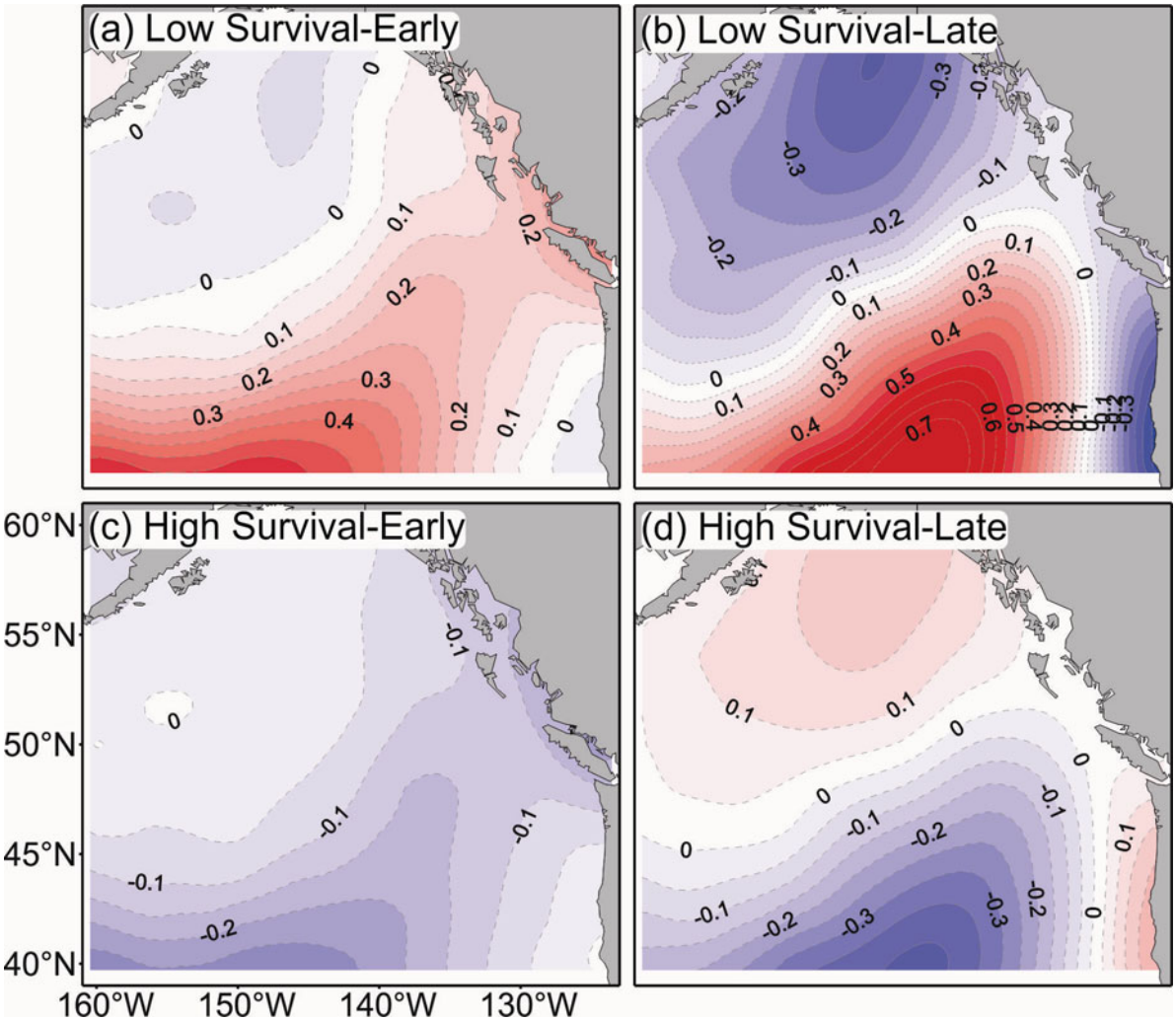

FIGURE 8. Composite sea surface temperature anomalies for year and month groupings based on Keogh River steelhead return rates and segments of the year: **(a)** low-survival years and early segment of the year; **(b)** low-survival years and late segment; **(c)** high-survival years and early segment; and **(d)** high-survival years and late segment. Low-survival years were 1978, 1988, 1990–1996, 1999, 2001–2003, and 2005; high-survival years were 1977, 1979, 1981–1987, 1989, 1997, 1998, and 2000. The early segment of the year is June–August; the late segment is September–December. Anomalies (in °C) were calculated relative to the mean SST for the period 1977–1999.

initially encountered predators soon after ocean entry (Parker 1971); therefore, the rate at which growth occurs during each year will determine how long the smolt class remains vulnerable to early marine-phase predators and how mortality accrues over the whole marine life history period.

The main finding has a number of important extensions that further describe how mortality is patterned over time. The correlation between growth and return rate was highest during late summer and lowest for the first month at sea, suggesting that size-mediated mortality is primarily determined during the multimonth period around August. This agrees with the finding that much of the mortality in juvenile salmon still occurs after the first 1–2 months of life at sea (Welch et al. 2011). Variation in survival is reflected to a greater degree in scale circulus spacing than in the deposition of circulus pairs, suggesting that the latter characteristic does not respond to growth variation over the range of growth observed.

Our results are consistent with other analyses of marine growth and survival in Pacific salmon. Bond et al. (2008) also found that growth registered in the scales of returning steelhead was correlated with survival, but the focus of their study was the growth differential produced by differing postsmolt migration patterns and estuary use. Ruggerone et al. (2007) analyzed scale growth in Bering Sea and Gulf of Alaska Sockeye Salmon *O. nerka* by using measurements of annular distances instead of circulus spacing; those authors found that the accumulated annular growth for the Sockeye Salmon stocks was positively correlated with run size. The collection of additional comparative

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data from stocks within species and between species will undoubtedly provide greater insights on the temporal and spatial nature of recruitment control in Pacific salmonids.

An understanding of when the highest mortality occurs within the first year at sea is critical for any effort to model recruitment. Size at ocean entry appears to affect the recruitment patterns of many salmonid species (Holtby et al. 1990; Henderson and Cass 1991), which would suggest a narrow time window and punctuated mortality during the early spring period. This was previously considered to be a major factor determining marine survival in Keogh River steelhead (Ward and Slaney 1988), but the survival pattern of this population has since changed without a corresponding change in smolt size at ocean entry (Welch et al. 2000), as we have now re-confirmed. In addition, neither growth nor SST correlation results pointed to a short-duration, early spring mortality event. A number of studies have suggested that various portions of the first marine year are most critical for determining overall survival: for example, the spring portion (Holtby et al. 1990; Fisher and Pearcy 2005; Tomaro et al. 2012), spring-into-summer portion (Farley et al. 2011; Beamish et al. 2012), and conditions later in the first marine year (Beamish and Mahnken 2001) may determine subsequent overwintering success (Beamish et al. 2004a). Welch et al. (2011) showed that the majority of survival rate variations occurred after the first 1–2 months of life at sea for both Sockeye Salmon and steelhead. We think it is important to consider the amount of time during which growth-related mortality effects can produce a measurable effect on the annual survival rate of juvenile salmon. Both the size at ocean entry and postsmolt growth are thought to shape survival patterns. Size at ocean entry likely affects mortality to some degree, but the rapid growth of postsmolts after they enter the ocean may ameliorate any initial size differences among and within smolt classes; thus, the time window associated with the effect of size at ocean entry would be quite limited. Unless there is an overriding critical period very early in the species' life history, postsmolt growth patterns that develop over longer seasonal periods would provide the time for size-related mortalities to accumulate and thus to dominate the survival pattern. Finally, the postsmolt period may have a dominant effect on survivorship (although this is conjecture and needs to be objectively established), but we must be vigilant to the possibility that events occurring during the adult migration stage could also play a major role, particularly during extreme environmental conditions such as El Niño–Southern Oscillation events (Johnson 1988).

Time series variation in SSTs within the region that potentially provided postsmolt nursery habitat for Keogh River steelhead was negatively correlated with return rate, suggesting either that growth is directly affected by ocean warming or that warming ocean conditions affect the food web upon which steelhead depend (Nickelson 1986; Atcheson et al. 2012). While at sea, steelhead occupy relatively narrow thermal ranges (Welch et al. 1998) that have been associated with specific isotherms (Burgner et al. 1992). The months for which correlations between SST and return rate were strongest coincided with the period in which return rates and monthly postsmolt growth were most highly correlated, suggesting that SST variation is related to the observed change in growth over time. Thermal properties of the upper water column could impact the productivity of the potential prey species available to steelhead postsmolts; variation in this productivity is thought to affect the survivorship of salmon in general (Duffy et al. 2010). The SST can contribute to water column structure and stratification, which have been associated with survivorship for a number of species. Survival of Coho Salmon *O. kisutch* was favored by shallow mixed layers (Hobday and Boehlert 2001); however, the growth of Coho Salmon varied inversely with mixed-layer depth. In Pink Salmon *O. gorbuscha*, survival was apparently favored by deeper mixed layers (Miller et al. 2012), which were associated with a higher condition factor of individual fish. The variance in these observations suggests that species, and perhaps even stocks, respond differently to increased sea temperatures and that the energetics of juvenile fish are differentially affected by these environmental changes (Martins et al. 2012). Variation in SST may also affect the energetic demands of juvenile migration, which in turn may affect growth during the first year at sea (Abdul-Aziz et al. 2011). These complex interactions will have to be approached in a multidisciplinary (Chittenden et al. 2009) and systematic fashion (Hollowed et al. 2009).

Steelhead appear to be responding to changing climate and growth regimes in a manner similar to that of their North Atlantic analog, the Atlantic Salmon. Comparative data show that eastern basin populations of Atlantic Salmon are also negatively affected by increases in summer temperature during the postsmolt year (Friedland et al., in press), and a cause-and-effect relationship between postsmolt growth and survival has been observed (Friedland et al. 2009). For southern European stocks of Atlantic Salmon, similar to steelhead, summer growth seems to be most critical for the survival patterns. An interesting test would be to determine whether western Pacific basin steelhead populations also show the same contrasting pattern observed in northwest Atlantic Salmon populations—namely, an independence between postsmolt growth and survival and a dependence of survival on the thermal regime associated with ocean entry (Friedland et al. 2012). Atlantic Salmon populations from the northeastern United States and Atlantic Canada appear to be impacted by warming conditions during spring, an effect that has been attributed to a change in predation pressure rather than to size-mediated predation. In both ocean basins, southern-tier stocks of anadromous salmon are under the greatest stress due to their low levels of marine survival, which have prompted action to protect populations and to conduct assessments for determining feasible remedies (Beamish et al. 2010).

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