The Effects of Post-smolt Growth and Thermal Regime on the Marine Survival of Steelhead Trout (*Oncorhynchus mykiss*) From the Keogh River, British Columbia

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Keywords: steelhead trout, post-smolt growth, marine survival, North Pacific, Keogh River

The population of anadromous steelhead trout *Oncorhynchus mykiss* in the Keogh River has been studied intensively in part because of its pattern of declining recruitment attributed to marine survival conditions (Ward 2000). Climate variability has changed the productivity of salmonid species in all regions of the North Pacific (Atcheson et al. 2012), with areas alternately shifting between periods of enhanced and depressed productivity (Irvine and Fukuwaka 2011). An interest in the mechanisms governing marine survival and adult recruitment are central to contemporary concerns related to resource management, but they are also of concern in regard to the long-term prospects of managing biodiversity (Young et al. 2007). As climate change signals superimpose upon climate variation signals, our assessments of population viability are without historical analogy.

Size at ocean entry appeared to affect the recruitment pattern of many salmonid species (Holtby et al. 1990; Henderson and Cass 1991) and was considered to be a main factor in patterning marine survival in Keogh River steelhead (Ward and Slaney 1988). The survival pattern of this population has since changed without a concomitant change in smolt size at ocean entry (Welch et al. 2000), which prompted our consideration of other factors that may be affecting marine survival.

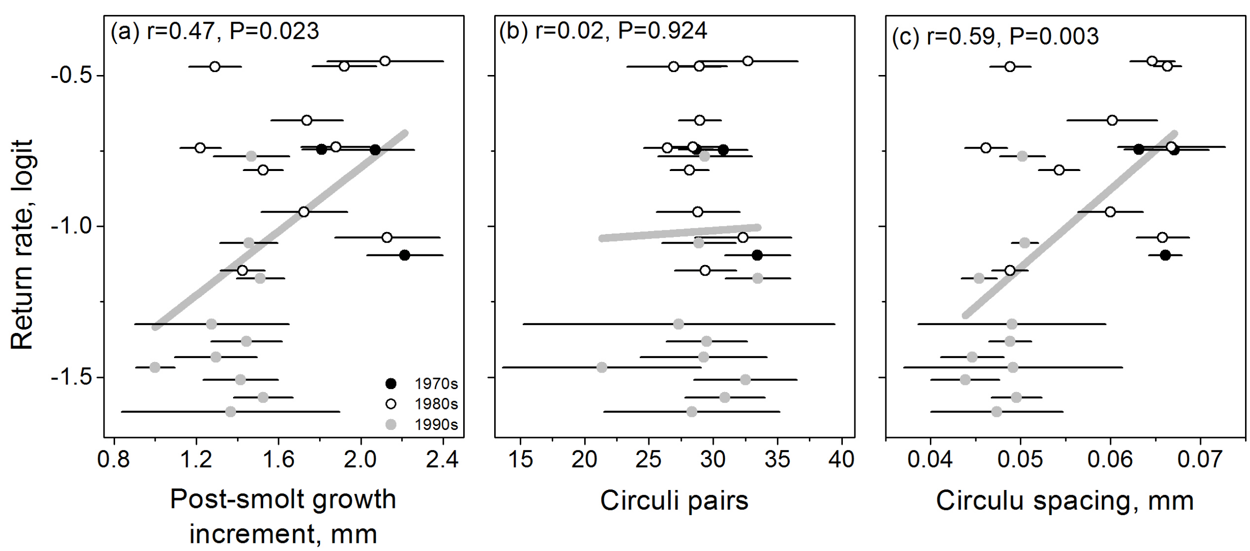

Fig. 1. The relationship between logit transformed return rate of Keogh steelhead and post-smolt growth increment (a), number of circuli pairs in the post-smolt growth increment (b), and average circuli spacing in the post-smolt growth increment (c). Independent variables are plotted with 95% confidence intervals with markers coded to decade of smolt year.

We found that post-smolt growth correlated with the pattern of marine survival of Keogh River steelhead. We measured the circuli spacing of the scales of 425 returning salmon to the Keogh River. Our samples were drawn from both wild (64%) and hatchery (36%) origin fish, which we found provided equivalent estimates of scale growth during the post-smolt phase. We measured the circuli spacing in the post-smolt growth zone, which starts at the end of the freshwater zone and goes to the first winter annulus. We utilized three scale growth parameters from these measurements: post-smolt growth increment, which is the total lineal growth of the scale within the growth zone; the number of circuli pairs deposited in the

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zone; and, the mean spacing of circuli pairs within the zone. Post-smolt growth increment and circuli spacing were found to be correlated with return rate of Keogh River steelhead (Figs. 1a and c, respectively). These data suggest that when post-smolts accumulated higher growth during the post-smolt year, they tended to survive better. Although the sample size used in this study is small, we found that the error structure in the data (plotted as 95% confidence intervals around the growth data) support the contention that the decadal differences in the time series are real. The number of circuli pairs deposited does not correlate with the return rate, suggesting this scale characteristic does not respond to growth variation over the range of growth observed (Fig. 1b). Further, proportional allocation of the scale growth characteristics to month of the post-smolt growth season (June through December of the first year at sea) suggests that the initial growth of the fish when they first go to sea is not as important as the sustained growth experienced during the summer and fall of the post-smolt year.

We think it is important to consider how much time growth-related mortality effects have, and for that matter need, to produce a measurable effect on the annual survival rate of juvenile salmon. Both size at ocean entry and post-smolt growth are taken as indictors of the potential for size-related mortality to shape survival patterns. Size at ocean entry likely affects mortality to some degree, but the rapid growth of post-smolts after entering the ocean may ameliorate any initial size differences among and within smolt classes, making the time window associated with the effect of size of ocean entry quite limited. Unless there an over-riding critical period that exists in the very early life history of the species, post-smolt growth patterns that develop over longer seasonal periods would provide the time for size-related mortalities to accumulate and thus dominate the survival pattern.

The distribution of sea surface temperature (SST) in the ocean thought to provide post-smolt nursery habitat for steelhead show that return rate has been negatively correlated with increasing SST, suggesting that growth is either directly affected by ocean warming or that warming affects the food web steelhead depend upon (Nickelson 1986; Atcheson et al. 2012). Steelhead occupy relatively narrow thermal ranges when at sea (Welch et al. 1998), which have been associated with specific isotherms (Burgner et al. 1992). We correlated the Keogh River return rate to the SST field from the Extended Reconstruction (ERSST) database for the corresponding smolt year. The monthly locations of the 12.5°C isotherm are plotted over the correlation fields to place into context the potential overlap with the assumed distribution of the steelhead post-smolt nursery. There is little correlative density for the first three months at sea, June through August (Figs. 2a-c, respectively). Correlations between SST and return rate develop in September and were highest in October (Figs. 2d and e, respectively), followed by declining correlation in November and December (Figs. 2f and g, respectively). The correlations are negative and the region of highly significant correlation in October is proximate to the 12.5°C isotherm.

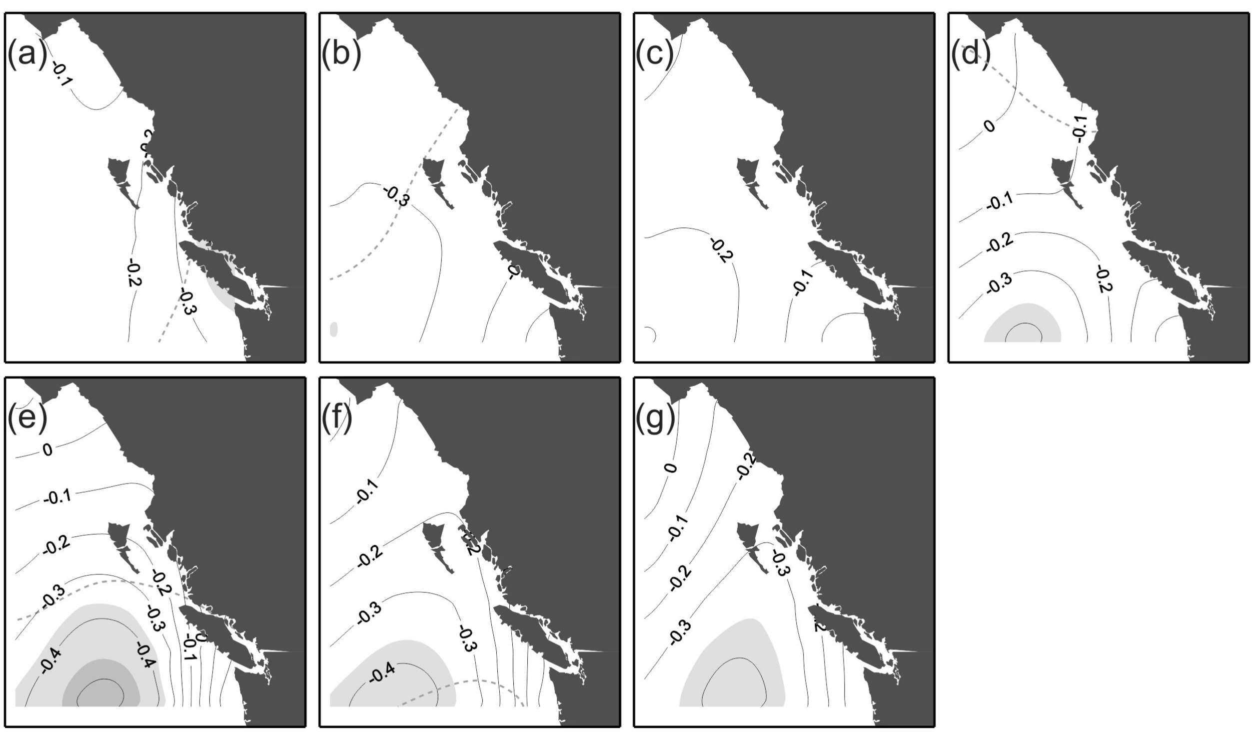

Fig. 2. Contour plots of correlation between the logit transformed return rate of Keogh steelhead and smolt-year sea surface temperatures for the months June through December, panels (a) through (h), respectively. Light grey shading marks approximate regions where correlations are significant at $p = 0.05$, and dark grey shading represents approximate regions significant at $p = 0.01$. Dashed lines mark average position of the 12.5°C isotherm, when present within the map area.

Steelhead appear to be responding to changing climate and growth regimes in the same way as their analog in the North Atlantic, Atlantic salmon *Salmo salar*. Comparative data show that eastern basin populations of Atlantic salmon are also negatively affected by increasing temperature during the post-smolt year (Friedland et al. 2013) and a cause and effect relationship between post-smolt growth and survival has been observed (Friedland et al. 2009). An interesting test would be to see if western Pacific basin steelhead populations also show the same contrasting pattern seen in northwest Atlantic salmon populations of an independence between post-smolt growth and survival and a dependence on thermal regime associated with ocean entry (Friedland et al. 2012).

Acknowledgments—We thank E. Johnson for making scale measurements and N.T. Johnston for providing scale images.

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