

Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*)

P.W. Lawson, E.A. Logerwell, N.J. Mantua, R.C. Francis, and V.N. Agostini

Abstract: Climate variability is well known to affect the marine survival of coho salmon (*Oncorhynchus kisutch*) in Oregon and Washington. Marine factors have been used to explain up to 83% of the variability in Oregon coastal natural coho salmon recruitment, yet about half the variability in coho salmon recruitment comes from the freshwater life phase of the life cycle. This seeming paradox could be resolved if freshwater variability were linked to climate and climate factors influencing marine survival were correlated with those affecting freshwater survival. Effects of climate on broad-scale fluctuations in freshwater survival or production are not well known. We examined the influence of seasonal stream flows and air temperature on freshwater survival and production of two stock units: Oregon coastal natural coho salmon and Queets River coho salmon from the Washington Coast. Annual air temperatures and second winter flows correlated strongly with smolt production from both stock units. Additional correlates for the Oregon Coast stocks were the date of first fall freshets and flow during smolt outmigration. Air temperature is correlated with sea surface temperature and timing of the spring transition so that good freshwater conditions are typically associated with good marine conditions.

Résumé : Il est bien connu que la variabilité du climat affecte la survie en mer du saumon coho en Oregon et au Washington. Bien que l'utilisation de facteurs marins ait permis d'expliquer jusqu'à 83 % de la variabilité du recrutement naturel du saumon coho sur la côte d'Oregon, néanmoins, environ la moitié de la variabilité du recrutement du saumon coho provient de la phase de vie en eau douce du cycle biologique. Ce paradoxe apparent pourrait se résoudre si la variabilité en eau douce est reliée au climat et si les facteurs du climat qui influencent la survie en mer sont en corrélation avec ceux qui affectent la survie en eau douce. Les effets du climat sur les fluctuations à grande échelle de la survie ou de la production en eau douce restent mal connus. Nous avons étudié l'influence des débits saisonniers et des températures de l'air sur la survie et la production en eau douce de deux unités de stock de saumons coho, les saumons coho indigènes de la côte de l'Oregon et les saumons de la Queets sur la côte du Washington. Il existe une forte corrélation entre les températures annuelles de l'air et les débits du second hiver de vie des saumons, d'une part, et la production de saumoneaux dans les deux unités de stock, d'autre part. Chez le stock de la côte de l'Oregon, il y a en plus des corrélations avec la date des premières crues d'automne et avec le débit durant l'émigration des saumoneaux vers l'aval. La température de l'air est reliée à la température de surface de la mer et le moment de la transition du printemps, si bien que des conditions favorables en eau douce sont généralement associées à de bonnes conditions en mer.

[Traduit par la Rédaction]

Introduction

Survival rates of coho salmon (*Oncorhynchus kisutch*) smolts in the eastern North Pacific are influenced by broad-scale climate patterns (Coronado and Hilborn 1998). Survival and recruitment of coho salmon in the ocean is correlated with physical environmental factors, including upwelling and sea surface temperature (Nickelson 1986; Cole 2000) operat-

ing across scales of hundreds of kilometers (Mueter et al. 2002). Off the Oregon Coast, a year-long sequence of events beginning in the winter before smolts enter the ocean can explain over 70% of the variability in hatchery smolt survival (Logerwell et al. 2003). Ocean environmental indices explain 75% (Lawson 1997) to 83% (Koslow et al. 2002) of adult recruitment of naturally spawned coho salmon from Oregon. This high fraction of variance is unlikely to be strictly a ma-

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rine effect, given that about half the variability in coho salmon recruitment is thought to be related to the freshwater phase of the life cycle (Bradford 1995; Holtby and Scrivener 1989).

Few studies have examined environmental factors affecting coho salmon production in fresh water. A decline in the coho salmon productivity of Thompson River, B.C., was attributed to agricultural land use, road density, and stream habitat status, but climate effects were considered only in the marine environment (Bradford and Irvine 2000). Holtby (1988) found that water temperatures in Carnation Creek, B.C., increased after logging, causing complex effects on coho salmon smolt production and adult recruitment. Examination of stream flow, temperature, and sediment in three small streams in the Alsea River, Oreg., showed no consistent relationships with smolt production (Knight 1979). In the same streams, timing of fry emergence and probability of smolt migration were related to temperature and flow (Spence 1995). These efforts were focused on reach (1 km) or watershed scale (10–100 km) stock units, while ocean effects operate at regional (100–1000 km) and basin (>1000 km) scales. The mismatch of spatial scales makes it difficult to integrate freshwater and marine studies to examine effects of climate patterns across the coho salmon life cycle.

This paper attempts to examine environmental factors affecting freshwater production of coho salmon across 240 km of the Oregon Coast, matching the scale of variability of marine environmental factors. It is well known that at very local scales physical factors such as stream flow and temperature can affect survival of salmon rearing in streams (Holtby 1988). Climate acts to modulate stream flow and temperature. We hypothesized that interannual variations in climate should result in coherent patterns of freshwater salmon production at a regional scale. We used correlations, generalized additive models (GAMs) and parametric nonlinear regressions in a modeling approach similar to Logerwell et al. (2003) to explore for and describe relationships between environmental factors and freshwater production and survival of Oregon coastal natural (OCN) coho salmon. An independent data set from Queets River coho salmon was used to validate the results of the OCN model.

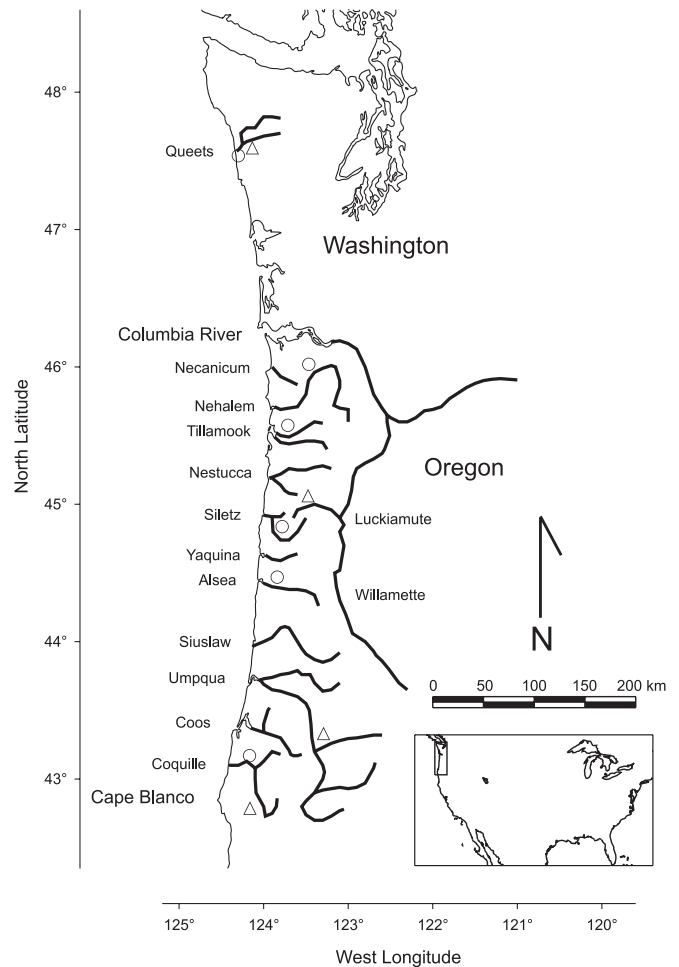
Methods

The stock unit of focus is naturally produced coho salmon from rivers of the northern and central Oregon Coast, referred to as Oregon coastal natural coho salmon. OCN coho are an aggregate of runs from 12 coastal river systems south of the Columbia River from the Necanicum River to the Coquille River (Fig. 1). This stock aggregate and associated hatchery stocks, mostly from the Columbia River, are referred to as Oregon Production Index (OPI) area stocks and are the best documented coho salmon on the West Coast. Three coastal lakes have supported runs of coho salmon totaling from 1500 to 30 000 fish annually since 1960. Population dynamics of the lake runs differ from the OCN river runs, so the lake runs were excluded from this analysis.

Coho salmon life cycle

We summarize the coho salmon life cycle in Fig. 2 and superimpose environmental factors found to be significant in

Fig. 1. Map of the Oregon and Washington coasts showing the 12 coastal river systems with Oregon coastal natural coho salmon (*Oncorhynchus kisutch*). The Queets River and Luckiamute River, tributary to the Willamette, are also shown. Symbols indicate locations of flow (○) and air temperature (△) time series.

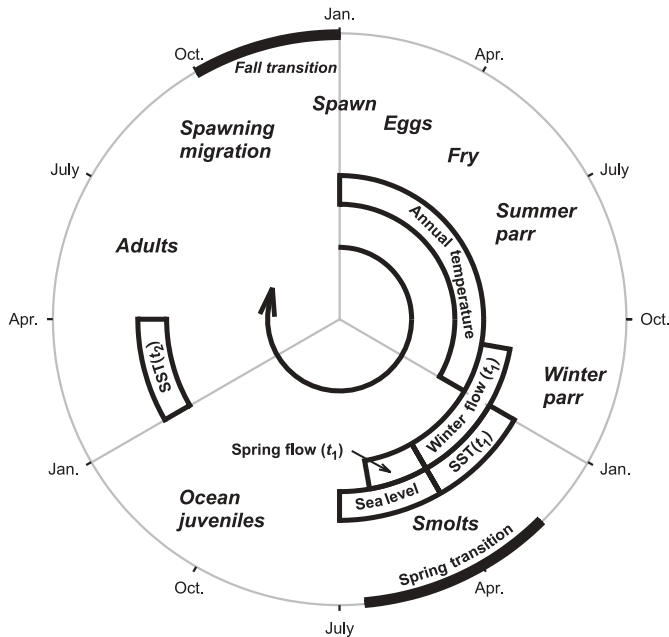


the freshwater (this paper) and marine (Logerwell et al. 2003) phases of the life cycle. Adult coho salmon begin migrating into coastal streams and rivers with the first freshets in the fall. Spawning begins in November, peaks in December or January, and may continue into March. Wild spawners typically migrate and spawn later than hatchery fish in the same area. Eggs hatch in the spring and fry grow rapidly to parr stage by summer or early fall. Parr then seek out areas protected from high flows and spend a second winter in fresh water before migrating to the ocean as smolts in March through June. About 20% of males mature at age 2 and return to fresh water as “jacks” in the same year that they entered the ocean as smolts. The remainder of juveniles rear in the ocean for 18 months and return as 3-year-old adults in the following fall.

Conceptual model

We used an estimate of total smolt numbers to represent annual freshwater production and smolts per parental spawner to represent freshwater survival. Stream flow and air temperature were used as indices of environmental conditions. Stream temperature seemed to be a more direct index of habitat conditions than air temperature, but stream tempera-

Fig. 2. Coho salmon (*Oncorhynchus kisutch*) life cycle. Approximate timing of life history stages are indicated within the 3-year cycle. Environmental variables are mapped onto the life cycle to indicate the relative timing of events. Variables found significant in this study are FallTrans (fall transition), AnnTemp (annual temperature), Flow.NDJFM.t1 (winter flow (t_1)), and Flow.AM.t1 (spring flow (t_1)). Variables from Logerwell et al. (2003) are SST.JFM.t1 (SST(t_1)), TRANS (spring transition), SL.AMJ (sea level), and SST.JFM.t2 (SST(t_2)).



ture time series suitable for this study were unavailable. Air temperature is linked to stream temperature (Mosheni and Stefan 1999), and an adequate time series of air temperature data was available.

We identified stream flow as the physical factor most likely to affect freshwater survival and defined four time periods corresponding to discrete stages of freshwater life history. Flow variable names start with "Flow" followed by the first letters of the months indexed and a year subscript (t_0 or t_1), all separated by periods.

First winter flow, January–March (Flow.JFM. t_0). Eggs are in the gravel and fry emerge. We postulated that intermediate flows would be best. Low flows could lead to dewatering of redds as has happened, for example, in the Columbia River. High flows could cause gravel movement, scouring redds. This has been observed during flood events in Oregon coastal rivers (Koski 1966).

First summer flow, July–September (Flow.JAS. t_0). Juveniles rear during this period. For some Puget Sound streams low summer flows have been associated with reduced coho smolt production (Mathews and Olson 1973). Low flows could reduce or degrade rearing habitat, especially in combination with high temperatures.

Second winter flow, November–March (Flow.NDJFM. t_1). Presmolts overwinter during this period. Nickelson (1998) identified winter rearing habitat as the most important limiting factor in most Oregon coast basins. Coho salmon prefer to overwinter in pools, beaver ponds, and side channels where

there is refuge from high flows and food may be more abundant. Intermediate flows maximize overwintering habitat without washing presmolts out of protected areas.

Second spring flow, April–May (Flow.AM. t_1). Smolts migrate to the ocean during this time period. Higher flows could aid downstream migration by increasing migration speed and reducing vulnerability to predators (e.g., Railsback and Harvey 2001).

We also identified timing of the spawning migration and temperature as potential factors influencing production and survival. We defined two variables to index these factors.

Fall transition (FallTrans). Date of onset of fall freshets (Julian day). Coho salmon from Oregon Coast streams begin their upstream migration with the first freshets from winter storms. Once storms begin flows rarely return to summer levels. We expected that earlier fall transitions would allow spawners to enter rivers earlier and allow access to greater areas of the basin, increasing smolt production.

Air temperature (AnnTemp). Annual average air temperature should correlate with stream water temperatures (O'Neal 2002). Temperature is known to influence development and survival at many stages of fish life history. Sea surface temperature is one of the best predictors of marine survival (Lawson 1997; Cole 2000), although temperature effects on freshwater and marine life history stages of coho salmon are probably very different. There are likely to be seasonal variations in freshwater temperature effects on smolt productivity and survival. However, owing to sparse data we chose to use only an annual temperature index.

Development of data sets

The OCN coho salmon production data are limited to 30 years, so the number of potential explanatory variables had to be kept small to preserve degrees of freedom. Selection of environmental data sets to use in this analysis was influenced by considerations of data relevance and availability, as well as statistical constraints.

Coho salmon production and survival

The Oregon Department of Fish and Wildlife has indexed coho salmon spawner escapements on the Oregon coast since 1948 (Cooney and Jacobs 1995); however, there has been no long-term effort to assess smolt outmigrations (but see Solazzi et al. 2002). Estimates of smolt production, therefore, had to be derived from other data. Nickelson (1986) estimated OCN coho smolt production using estimates from McGie (1984) combined with two methods of estimating harvest rates and scale samples from harvested coho, acknowledging there was no way to independently verify his estimates. Among other problems, these estimates were based on spawner estimates that are now known to be biased high by a factor of three (Jacobs and Cooney 1994). We reconstructed annual smolt production for OCN coho salmon from (i) unbiased spawner escapement data (Steven Jacobs, Oregon Department of Fish and Wildlife, Corvallis Research Laboratory, 28655 Hwy. 34, Corvallis, OR 97333, U.S.A., personal communication), (ii) estimates of marine survival of Columbia River hatchery coho salmon, and (iii) fishery exploitation rates for the OPI area (Pacific Fishery Management Council 2001). There are few direct measures of OCN

marine survival to compare with OPI hatchery marine survival; however, the abundance of OCN ocean recruits from 1970 to 2001 correlates significantly with OPI hatchery survival ($r^2 = 0.68$, $p < 0.0001$). We based our OCN smolt estimates on the assumption that wild and hatchery smolts have similar variation in marine survival (Coronado and Hilborn 1998). Marine survival is indexed as total abundance of adult hatchery coho salmon divided by the number of hatchery smolts released. OCN smolt numbers were estimated by dividing the total number of OCN ocean adults in the following year by the marine survival for the year of ocean entry (smolt year). Freshwater survival, expressed as smolts per spawner, was estimated by dividing the smolt estimate by parental spawner numbers (spawners two years earlier). Estimates in most years ranged from 1.3 million to 6.5 million smolts and 24.8 to 256.2 smolts per spawner. Each spawning female produces approximately 2500 eggs, so 256.2 smolts per spawner represents a 20% egg to smolt survival assuming a 1:1 sex ratio — certainly at the high end of likely survivals. If marine survival of wild fish were double that of hatchery fish, this would represent a 10% egg to smolt survival — still at the high end of expectations. Bradford et al. (2000) examined 14 data sets of spawner abundance and smolt production and found that average freshwater productivity was about 42 smolts per spawner, with a maximum of about 105. In the years 1991–1995 total smolt estimates (6.7 million to 11.2 million) and, especially, smolts per spawner estimates (160.5 to 697.8) were unreasonably or impossibly high. These were years when Columbia River coho salmon marine survival was extremely low (0.46%–1.29%). In these years, we used an alternate estimate of marine survival based on ocean environmental conditions (Logerwell et al. 2003). Even so, the estimate of smolts per spawner in 1992 was 440.1, a number we judged to be out of the realm of possibility. Lacking a third alternative for estimating marine survival in this year, we considered it a bad estimate and omitted it from our model fitting exercises. The year (1980) with 256.2 estimated smolts per spawner was considered as a possible outlier, but no external reason for an inflated estimate could be found, so we retained it in the time series.

In the Queets River, spawning escapements and smolt out-migration numbers were estimated directly from field experiments for the smolt years 1981–2000 (Larry Gilbertson, Quinault Department of Natural Resources, Quinault Indian Nation, P.O. Box 189, Taholah, WA 98587, U.S.A., personal communication).

Flow

Flow data were taken from U.S. Geological Survey (USGS) gauging stations on Oregon coastal river systems with continuous or nearly continuous records from at least 1946 (U.S. Geological Survey, 345 Middlefield Rd., Menlo Park, CA 94025, <http://waterdata.usgs.gov/or/nwis>). The five stations with suitable data were Nehalem, Wilson (Tillamook basin), Siletz, Alsea, and Coquille, providing good geographic coverage (Fig. 1). Flow data from the Queets River USGS gauging station were used for the Queets system. Two statistics were derived from these data: an index of annual flows for seasonal time periods of inter-

est, and an index of the date of onset of winter storms, referred to as fall transition.

Seasonal flows

We used mean monthly flows for time periods deemed potentially important to the salmon freshwater life cycle. Extreme flow events such as winter floods and summer low flows are often cited as controlling events in salmon recruitment (Mathews and Olson 1973; Scarnecchia 1981; Giannico and Healey 1998). We chose not to include extreme events for several reasons. First, they are correlated with the corresponding means flows. Second, including several more explanatory variables would increase the potential for spurious correlations. Third, timing of extreme events relative to the stage of development may be critical at a resolution finer than our time strata. Finally, effects of peak events tend to be localized and vary within and between river systems. In short, the temporal and spatial scales of extreme events are finer than the corresponding strata in our model, and much of the information in the extreme flows is also contained in the mean flow data. Daily flows from each station were averaged to create monthly means. Monthly means were averaged within the four time periods of potential importance to the coho salmon life cycle. Period means for each station were standardized (standard normal) over water years 1947–1999 and the standardized values were averaged across river systems to produce a coastwide flow index for each time period. The time periods were Flow.JFM.t0, Flow.JAS.t0, Flow.NDJFM.t1, and Flow.AM.t1.

Fall transition

Rivers on the Oregon Coast have rainfall-driven hydrographs; snow accumulations are light and have little influence on overall flow patterns. Typically flows are high with numerous storm-related peaks during the winter and early spring, and then taper off through the summer and fall to low base flows. The contrast between monthly mean base and high winter flows is two orders of magnitude. Daily minimum flows and peak flows within a year often differ by three orders of magnitude. The onset of winter storms is reflected in the flow data as an abrupt rise in flows above the base level. Once flows begin to rise above the summer base flow levels, they remain elevated until the following spring. FallTrans was defined as the calendar day when an 11-day unweighted moving average exceeded the September base flow by a factor of three. Examination of the data showed that, once flows reached this level, they usually continued to rise to high levels and rarely receded back to base flows. Annual fall transition dates were calculated for each river system and averaged to obtain a coast wide index. Transitions were generally synchronous across river systems within a year and ranged from day 270 to day 338 (late September to early December), averaging day 295.

Annual temperature

The temperatures of interest were water temperatures in second- to fourth-order streams where coho salmon spawn and rear. Comprehensive time series of water temperature data are not available for the Oregon Coast. Air temperature serves as a surrogate, assuming that both water and air temperature are driven by insolation. This is more true for

Table 1. Pearson's correlation coefficients for the variables considered for modeling.

	Smolt year	FallTrans	Flow. JFM.t0	Flow. JAS.t0	Flow. NDJFM.t1	Flow. AMJ.t1	AnnTemp	Spawners	Recruits	Smolts
Smolt year	1									
FallTrans	0.058	1								
Flow.JFM.t0	-0.149	-0.395	1							
Flow.JAS.t0	-0.183	-0.163	0.008	1						
Flow.NDJFM.t1	-0.054	-0.176	0.201	0.056	1					
Flow.AMJ.t1	0.156	0.016	-0.034	-0.077	<u>0.331</u>	1				
AnnTemp	0.676	0.121	-0.203	-0.398	0.010	<u>0.344</u>	1			
Spawners	-0.278	-0.222	0.385	0.193	-0.065	-0.214	-0.256	1		
Recruits	-0.786	-0.037	0.263	0.072	0.127	-0.154	-0.548	0.268	1	
Smolts	<u>-0.334</u>	0.163	-0.034	0.134	0.192	0.118	<u>-0.314</u>	-0.103	<u>0.332</u>	1
SmperSp	0.018	0.171	-0.228	-0.069	0.013	0.000	0.015	-0.640	-0.018	0.684

Note: Linear correlations >0.349 are significant at $p < 0.05$ and in bold type. Correlations >0.296 are marginally significant, $0.05 < p < 0.10$, and underlined.

inland stations than for stations on the coast, where air temperatures are heavily influenced by sea surface temperatures. Suitable time series of air temperature data from inland stations in the Coast Range are sparse. Three stations with nearly complete time series beginning in 1961 or earlier were located at Falls City, Elkton, and Powers (Western Regional Climate Center, 2215 Raggio Parkway, Reno, NV 89512, U.S.A., wrcc@dri.edu). Elkton, on the Umpqua River, and Powers, on the Coquille River, are near the southern end of the OCN distribution (Fig. 1). Falls City is more centrally located in the Coast Range, even though it sits on the east side of the Coast Divide, on the Luckiamute River, a tributary to the Willamette River. Temperatures at this site reflect conditions in the Coast Range, so it was deemed suitable for indexing North and Central Coast temperatures. Monthly mean air temperature data from these three stations from 1961 to 2000 were standardized and averaged to produce an index of annual air temperature on the Oregon Coast. Air temperature data over an appropriate time period were also available for Clearwater, Wash., on the Queets River approximately 6 km from the ocean.

Model development

The goal of modeling was to find the simplest models using the given set of predictor variables. We used GAM to explore the relationship between freshwater conditions and coho smolt production and survival. Recall that we indexed production as total smolts produced and expressed freshwater survival as smolts per parental spawner. We chose to use GAM because we expected a priori that some relationships would be nonlinear (e.g., Ryding and Skalski 1999). GAMs have flexibility in defining predictor functions. Parametric and nonparametric terms, as well as linear and nonlinear terms, can be combined into a single GAM (Hastie and Tibshirani 1999).

We started with a GAM using all variables, fitted with the "gam" procedure in S-PLUS (Insightful Corp., Seattle, Wash.) and using loess smoothing. Variables with slopes not different from zero, as judged by the plotted confidence limits, were sequentially removed until all remaining variables appeared significant. The resulting GAM was then converted to a parametric nonlinear model. For variables that did not appear to be linearly related to the dependent variable, a *b*-

spline predictor function was chosen because fewer degrees of freedom are used compared with loess. Knots or inflection points were chosen by inspection. In practice, all knots were placed at the means of the standardized variables. The resulting model was then tested for significance using parametric statistics (*F* test). Variables that tested nonsignificant were either simplified by removing the *b*-spline or eliminated. The procedure was repeated until all variables were significant in the regression. The fit of the final models was evaluated with analysis of variance (ANOVA; *F* test) and r^2 , calculated using S-PLUS commands for linear models (Chambers and Hastie 1992).

Additional tests were applied to the OCN models. A GAM was constructed with sequential addition of each variable. Model fit and parsimony were evaluated with approximate *F* tests and the Akaike information criterion (AIC). The *F* test, conducted with each addition of a new variable, indicates whether the model is a significant improvement over the previous version (without the additional variable). The AIC statistic, also estimated with each addition, accounts for degrees of freedom used and the goodness of fit such that more parsimonious models have lower AIC (Chambers and Hastie 1992). The AIC is calculated in S-PLUS as $-2 \log \text{likelihood} + 2n_{\text{par}}$, where n_{par} represents the number of parameters in the fitted model. Residual plots were evaluated for violations of model assumptions.

Given the exploratory manner of model development, we tested for generality by applying the same technique to an independent data set from the Queets River. We explored for relationships in the Queets River using GAMs and, subsequently, fitted parametric nonlinear models as we did with the OCN data.

Results

All Oregon coast variables were tested for linear correlations (Table 1). Only two showed significant time trends over the 30-year period; AnnTemp had a positive trend, while recruits showed a strong negative trend, and recruits were negatively correlated with AnnTemp. Later FallTrans correlated with lower first winter flows (Flow.JFM.t0). First winter flows were positively correlated with spawner numbers. The correlation between FallTrans and spawners was nega-

tive, as expected, but not significant. Summer flows (Flow.JAS.t0) were significantly lower with high AnnTemp. Streamflow and temperature relationships are well known (e.g., Ronan et al. 1998; Constantz 1998). Second winter and second spring flows (Flow.NDJFM.t1 and Flow.AM.t1) showed no correlations with other variables in the data set. Smolt numbers showed no significant correlations with other variables, although a negative correlation with AnnTemp and a positive correlation with recruit numbers were marginally significant. Smolts per spawner (SmperSp) was correlated only with smolt numbers and spawner numbers.

Smolt numbers

A GAM was fitted to smolt numbers using AnnTemp, FallTrans, Flow.JFM.t0, Flow.JAS.t0, Flow.NDJFM.t1, Flow.AM.t1, and spawners. Flow.JFM.t0, Flow.JAS.t0, and spawners showed no functional relationship with smolt numbers. AnnTemp, FallTrans, and Flow.AM.t1 showed linear or nearly linear relationships with smolt numbers (Figs. 3a, 3b, and 3d). Flow.NDJFM.t1 fit with a dome-shaped curve with a peak near the mean (0) (Fig. 3b). The parametric non-linear model showed all variables significant ($p < 0.05$) and had an overall r^2 of 0.52 with $p = 0.0022$ (Table 2). Variables were entered sequentially in the order AnnTemp, Flow.AM.t1, Flow.NDJFM.t1, and FallTrans (Table 3). With each added variable, the AIC declined, indicating increased parsimony, and the model fit improved significantly as indicated by the F statistic.

The time series of observed and predicted OCN smolts (Fig. 4) shows that the model captures the general reduction in smolts after 1985 and much of the interannual variation. The GAM underestimates smolt production from 1980 to 1984. The two years with the lowest estimated smolts (1985, 1990) appear as outliers.

Examination of the time series of residuals suggests that the model underestimated the reduction in smolts after 1985 (Fig. 5). An intervention analysis (Hare 1996) showed a significant shift in the residuals ($p = 0.002$). This suggests either a discontinuity in the data set or an unidentified event that occurred in 1985 and has persisted to the present, generally reducing smolt production.

Smolts per spawner

A GAM of smolts per spawner versus AnnTemp, FallTrans, Flow.JFM.t0, Flow.JAS.t0, Flow.NDJFM.t1, and Flow.AM.t1 suggested that FallTrans, Flow.JAS.t0, and Flow.AM.t1 were the most important factors, with nonlinear fits to all variables. However, the corresponding parametric nonlinear model using these factors was nonsignificant. Reducing the complexity of the model by eliminating the knots did not result in significant fits. A stepwise linear regression selected FallTrans and Flow.NDJFM.t1 with both factors entering significantly into a linear model ($r^2 = 0.25$, $p = 0.0195$) (Table 4). Sequential addition of variables (Table 5) showed FallTrans entering as marginally significant ($p = 0.059$), followed by Flow.NDJFM.t1. The fit of FallTrans in this regression depended on the 1980 estimate of 256.2 smolts per spawner, the highest in the data set. Eliminating this point left only Flow.NDJFM.t1 as a significant predictor, but with $r^2 = 0.1626$ and $p = 0.0301$.

Model validation: Queets coho

Smolt numbers from the Queets River were correlated with annual temperature (Fig. 6a) and second winter flows (Fig. 6b) in the same way that OCN smolts were, including a dome-shaped function in the second winter (Table 6). There was no relationship between smolt numbers and first winter flows, although Seiler et al.'s (2003) smolt production and streamflow data show a strong negative relationship between Queets River daily peak incubation flows and wild coho smolt production on the Clearwater River (the major coho tributary in the Queets system). In contrast to OCN coho smolts, Queets River coho smolts showed no trend with Fall transition or second spring flows. The time series of observed and predicted Queets smolts (Fig. 7) showed that the model does a good job of capturing the interannual variability. Smolts per spawner, as in the OCN analysis, showed weaker relationships with environmental variables. They were related only to annual temperature, and only after the removal of one outlier (Table 7). The Queets data began with the 1981 smolt year, so there was no opportunity to explore for an intervention in 1985.

Discussion

Data examined in this study suggest that, just as in marine environments, interannual environmental variations can affect freshwater production of OCN coho on a regional scale. Cooler temperatures, later fall transitions, intermediate second winter flows, and higher second spring flows all correlated with higher natural smolt production on the Oregon Coast. There was no evidence of a correlation with first winter flows or summer flows. The number of spawners showed no relationship to the number of smolts, even in combination with environmental correlations.

The time series of observed OCN smolts shows a general reduction in smolt production starting in 1985 and continuing to the present. The model shows a similar reduction but underestimates the change, as demonstrated by the intervention analysis. The regime shift in ocean conditions that occurred in 1976 is not apparent in these data. From 1969 to 1979 the pattern of production is well represented by the model, with large interannual variations in 1976–1978 tracked faithfully. From 1980 to 1984 the model predicts lower smolt production than observed, with two years (1981–1982) lying outside the confidence limits of the prediction. The source of this deviation could stem from differences in hatchery and natural smolt survival, or from an incomplete environmental model. If hatchery fish survived more poorly than wild fish during this time period, then wild smolt numbers would be overestimated because wild smolt numbers were reconstructed based on hatchery survivals. Alternatively, if some aspect of the freshwater environment not captured by this model was especially favorable, then smolt production would be underestimated in the model. Smolt production peaked in 1984, followed by a drop in the late 1980s; this is reflected in the model fit except for the extremely low production in 1985. Smolts in 1985 came from the adults that returned at a very small size during the 1983 El Niño. These small size fish had low egg production and relatively small eggs (Johnson 1988), which could have resulted in fewer offspring of lower quality. At the same time, hatchery

Fig. 3. Partial regression plots for the GAM of Oregon coastal natural coho salmon (*Oncorhynchus kisutch*) smolt numbers presented in Tables 2 and 3. Confidence limits (95%, dashed lines) and partial residuals around the fitted lines are shown. The y-axis labels are the expressions used to specify each variable in the GAM formula. bs() indicates a 1-degree *b*-spline smoother with the specified knots. AnnTemp, FallTrans, and Flow.AMJ.t1 were fit using a linear term.

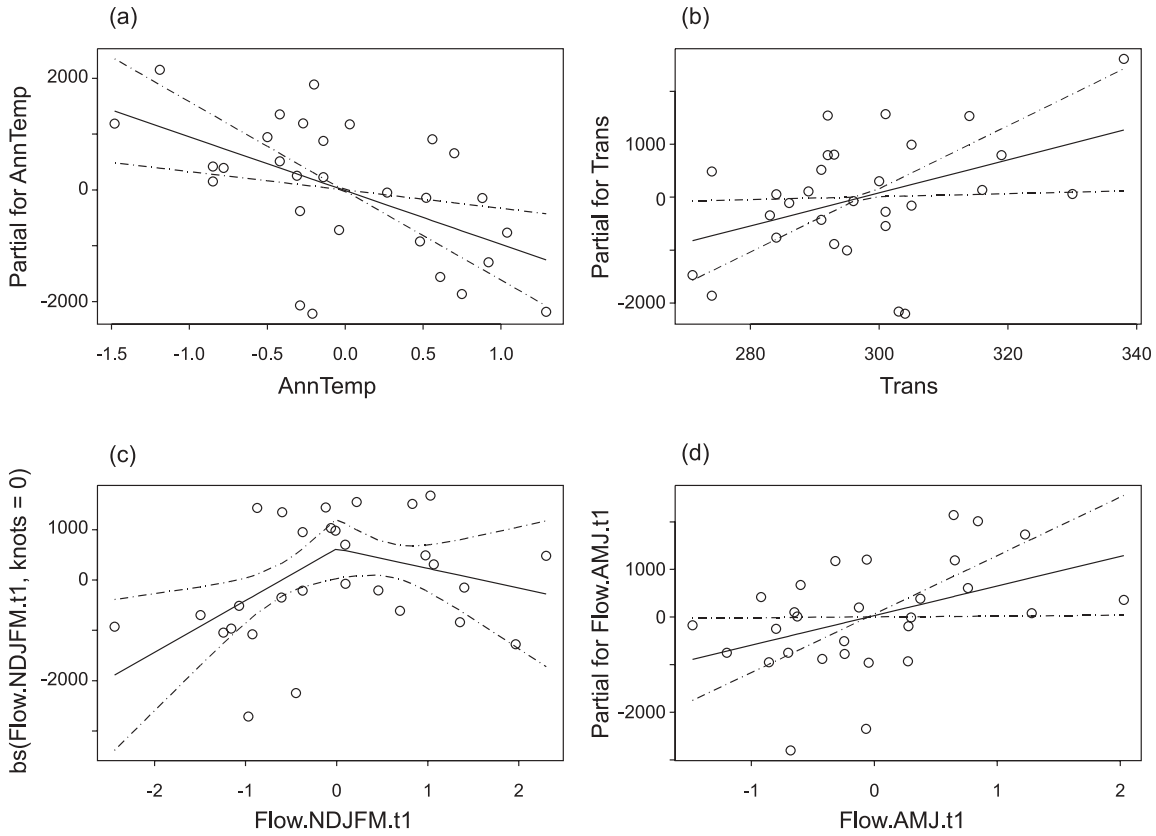


Table 2. Specification of the full model for Oregon coastal natural coho salmon smolt numbers ($F = 5.208$, $r^2 = 0.52$, $p = 0.0022$).

Coefficient	Value	SE	<i>T</i> value	<i>p</i>
Intercept	-6560.3	4081.1	-1.6075	0.1210
AnnTemp	-910.24	270.35	-3.3669	0.0026
Flow.AMJ.t1	558.58	259.18	2.1552	0.0414
Flow.NDJFM.t1,1	2444.5	915.46	2.6703	0.0134
Flow.NDJFM.t1,2	1996.9	923.04	2.1634	0.0407
FallTrans	27.884	13.480	2.0685	0.0495

Note: The two legs of the *b*-spline are designated Flow.NDJFM.t1,1 and Flow.NDJFM.t1,2.

Table 3. Construction of the smolt model for Oregon coastal natural coho salmon.

Terms	Residual df	Residual deviance	r^2	AIC	<i>F</i>	<i>p</i>
AnnTemp	28	1318	0.147	56 525 109	4.83	0.036
AnnTemp + Flow.AMJ.t1	27	1233	0.281	52 816 666	5.03	0.033
AnnTemp + Flow.AMJ.t1 + (Flow.NDJFM.t1,1 and Flow.NDJFM.t1,2)	25	1136	0.435	51 905 070	3.40	0.049
AnnTemp + Flow.AMJ.t1 + (Flow.NDJFM.t1,1 and Flow.NDJFM.t1,2) + FallTrans	24	1068	0.520	50 961 758	4.28	0.050

Note: As each term is added, deviance (and r^2), Akaike Information Criterion (AIC), and the *F* statistic are examined to determine whether the term will be included in the final model. The two legs of the *b*-spline are designated Flow.NDJFM.t1,1 and Flow.NDJFM.t1,2. They are added to the model at the same time, hence the parentheses.

smolt survival was 7.5%, among the highest in this time period. The low observed production in 1990 cannot be explained in the same way. Coho adults in 1988 were near nor-

mal in size (Lawson 1997). Hatchery survival was relatively good at 5.0%, but other years of similar hatchery survival fitted well to the model. Possibly there was a freshwater

Fig. 4. Time series of observed Oregon coastal natural coho salmon (*Oncorhynchus kisutch*) smolts compared with predictions of the generalized additive model. The thick line is the model prediction, dashed lines are 95% confidence limits, and open circles are observations.

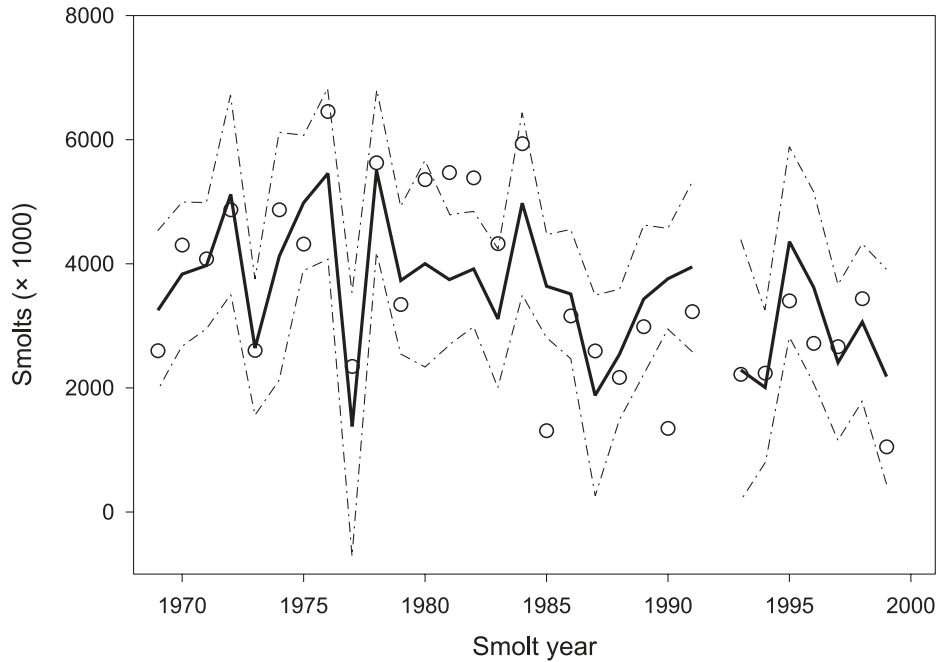


Fig. 5. Intervention analysis of residuals from the generalized additive model for Oregon coastal natural coho salmon (*Oncorhynchus kisutch*) smolts. Thick horizontal lines represent mean residuals for the time periods 1970–1984 and 1985–1999.

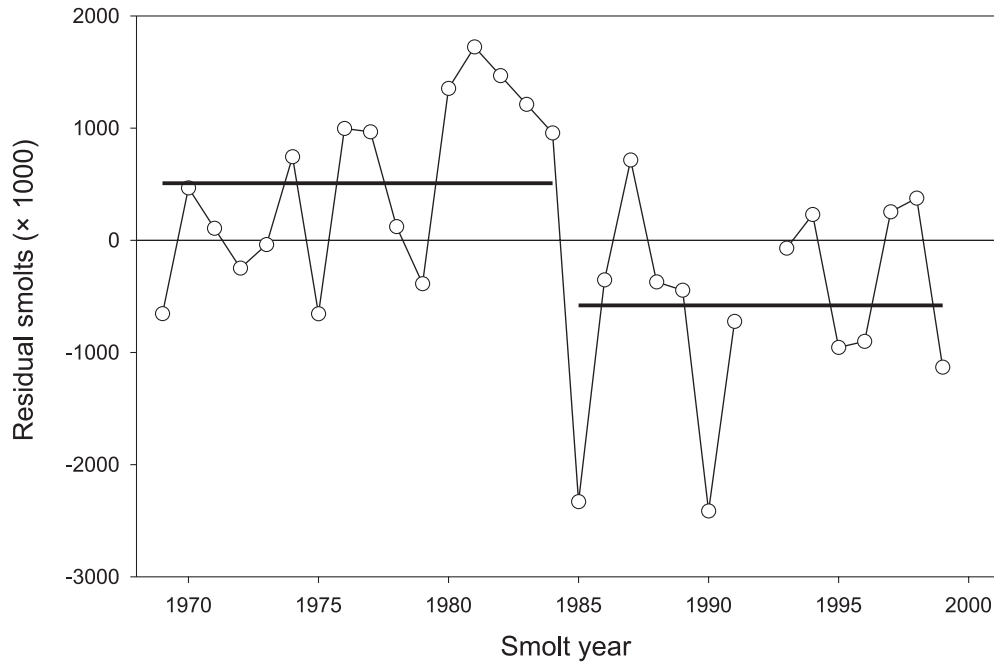


Table 4. Specification of the full model for Oregon coastal natural coho salmon smolts per spawner ($F = 4.574$, $r^2 = 0.25$, $p = 0.0195$).

Coefficient	Value	SE	T value	p
Intercept	-356.46	182.23	-1.9561	0.0609
FallTrans	1.5241	0.6117	2.4917	0.0192
Flow.NDJFM.t1	18.654	8.5698	2.1768	0.0384

event not reflected in our modeling that reduced the 1990 smolt production.

The OCN smolts per spawner model, like the smolts model, suggests that egg to smolt survival is higher with later fall transition but shows a positive linear correlation with second winter flows rather than the dome-shaped fit with smolts. This model explained less of the variability in survival than the smolt model explained for production. One likely reason

Table 5. Construction of the smolts per spawner model.

Terms	Residual df	Residual deviance	r^2	AIC	F	p
FallTrans	28	52.82	0.122	90 403	3.89	0.059
FallTrans + Flow.NDJFM.t1	27	49.62	0.253	84 876	4.74	0.038

Note: As each term is added, deviance (and r^2), Akaike Information Criterion (AIC), and the F statistic are examined to determine whether the term will be included in the final model.

Fig. 6. Partial regression plots for the GAM of Queets smolt numbers. Confidence limits (95%, dashed lines) and partial residuals around the fitted lines are shown. The y-axis label is the expression used to specify each variable in the GAM formula. bs() indicates a 1-degree b -spline smoother with the specified knots. AnnTemp was fit using a linear term.

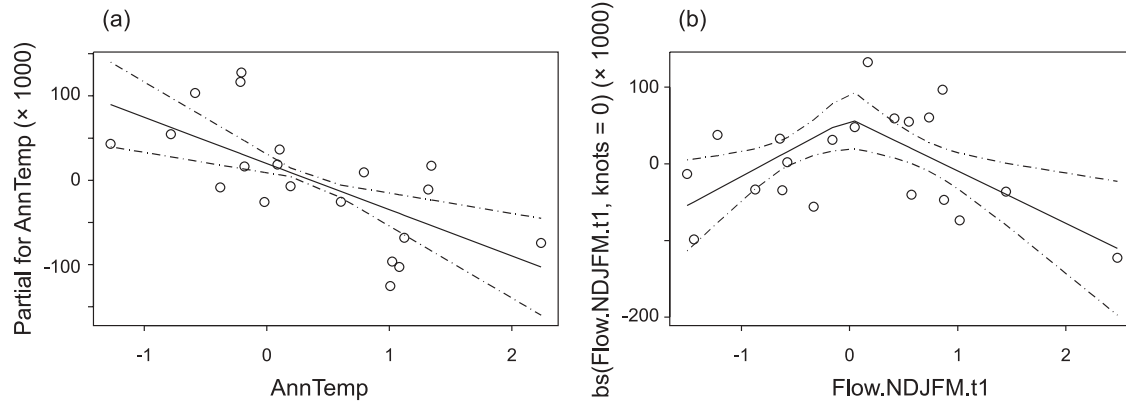


Table 6. Specification of the full model for smolt numbers in the Queets River ($F = 8.886$, $r^2 = 0.62$, $p = 0.0011$).

Coefficient	Value	SE	T value	p
Intercept	177.2	33.4	5.3004	0.0001
AnnTemp	-54.8	15.3	-3.5702	0.0026
Flow.NDJFM.t1,1	113.7	45.2	2.5178	0.0228
Flow.NDJFM.t1,2	-55.8	51.9	-1.0747	0.2985

Note: The two legs of the b -spline are designated Flow.NDJFM.t1,1 and Flow.NDJFM.t1,2.

is the higher uncertainty in the estimates of smolts per spawner compared with smolts. This additional variability is introduced because the divisor, spawners, is estimated with considerable uncertainty, especially prior to 1990. The additional error in estimating the dependent variable makes it more difficult to identify functional relationships with environmental variables. Also, analysis of data from many Pacific Northwest coho salmon populations (Barrowman and Myers 2000; Bradford et al. 2000) suggests that smolt production is relatively independent of spawner abundance above a minimum spawner escapement level. Density-dependent compensatory survival mechanisms in early freshwater stages of the life cycle may reduce the correspondence of smolts per spawner, with environmental factors affecting later life stages. The apparent lack of dependence on spawner numbers may also in part be an artifact of the harvest regime that has been in place since the 1950s. During the past 50 years there has never been an OCN coho escapement much greater than 200 000 spawners, and in recent years we have rarely seen more than 50 000 spawners, with a low in 1997 of 14 100 spawners. In the absence of fishing there would have been close to 1 000 000 spawners in some years of the early 1970s. We cannot evaluate the effects of this 5-

to 50-fold reduction in spawner abundance from either a demographic standpoint or an ecological point of view. Spawner carcasses contribute nutrients to coastal watersheds, increasing primary productivity and improving spawning and rearing habitat (Helfield and Naiman 2001). Reduced nutrient transport over the past 50 years may have fundamentally altered the structure and function of these coastal ecosystems (Cedarholm et al. 1999). Lack of a relationship between spawner abundance and smolt production in this study should not be taken as a rationale for further management reductions in spawner escapements. Rather, we should explore population and ecosystem dynamics at higher escapement levels as improved ocean conditions make this possible.

The Queets River smolts model did a good job of capturing the interannual variation in smolt production. In two of three years when the observed smolts were outside of the 95% confidence limits (1990, 1997), the interannual pattern was preserved. It is interesting that 1990 was the highest year of smolt production in the Queets River and one of the lowest on the Oregon Coast. While our OCN modeling is focused on climatically related regional coherence in freshwater coho production, the contrast between OCN and Queets River coho production in years like 1990 hints at the importance of diverse watershed characteristics and how that diversity translates into variable coho production sensitivities in nearby streams to similar environmental events. Seiler et al. (2003) report on stream-specific coho smolt production data for streams in Puget Sound and on the Washington coast and find different limiting streamflow conditions in different watersheds, with the limiting factors being closely associated with stream morphology. For example, the high gradient Skagit River data show reduced coho smolt production for higher peak incubation flows, while the low-gradient Chehalis River and its tributaries show increased coho smolt production following years with the highest spawning and

Fig. 7. Time series of observed Queets smolts compared with predictions of the GAM. The thick line is model prediction, dashed lines are 95% confidence limits, and open circles are observations.

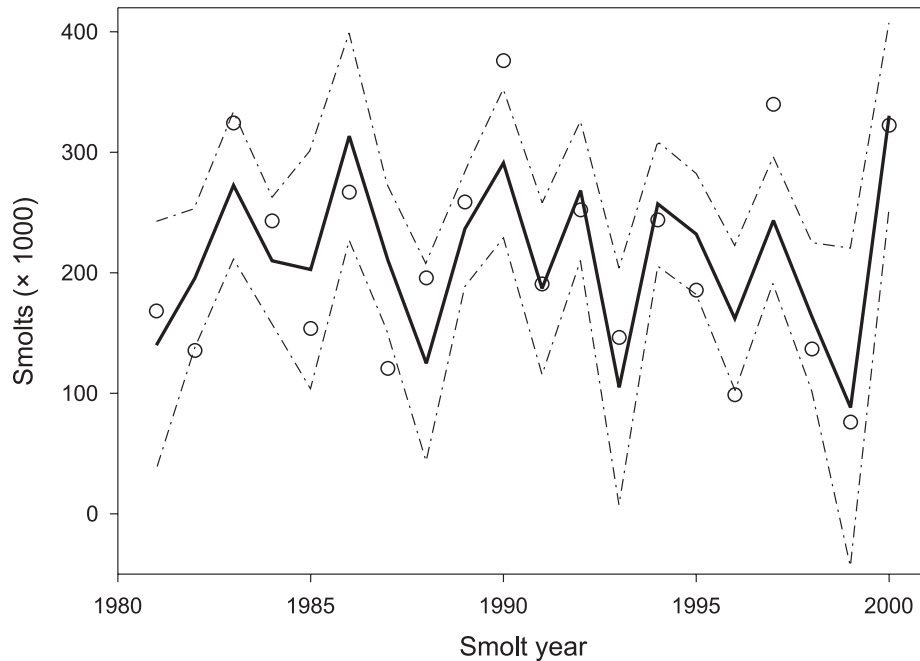


Table 7. Specification of the full model for SmperSp in the Queets River ($F = 8.373$, $r^2 = 0.33$, $p = 0.0101$).

Coefficient	Value	SE	<i>T</i> value	<i>p</i>
Intercept	42.0	3.2	13.2613	0.0000
AnnTemp	-10.1	3.5	-2.8936	0.0101

incubation flows. To the extent that the major OCN production occurs in streams with similar morphology, our use of composite OCN smolt and environmental data are justified.

The strongest and most consistent correlation in three of four models was a negative relationship with annual temperature. The correlation of OCN coho smolts with the AnnTemp time series, by itself, would not be a strong conclusion because the temperature stations are not well distributed within the range of the fish. However, the temperature relationship found for Queets River coho is consistent with the OCN coho models. The Queets temperature data show no time trend, in contrast to the Oregon Coast data, which have a significant increase over the time period. This eliminates the possibility that secular time trends in the two variables are leading to a spurious conclusion. Therefore, the temperature correlation in the Queets adds considerable weight to the general conclusion that temperature is correlated with smolt production in the Pacific Northwest, and the Oregon and Washington coasts in particular.

For salmon stocks in the California Current system, high temperature has long been recognized to be correlated with mortality in marine (Nickelson 1986; Cole 2000) and freshwater (e.g., Udey et al. 1975) environments. Water temperature affects developing salmon by influencing egg development rate (Holtby and Scrivener 1989) and metabolic rate (and hence feeding requirements and growth rates). Holtby (1988) found that emergence timing and fingerling

size of coho salmon in Carnation Creek, B.C., were strongly correlated with late winter stream temperatures. Warmer spring temperatures were associated with earlier smolt migration and reduced marine survival. Water temperature was the principal environmental factor affecting freshwater growth rates of brown trout (*Salmo trutta*) when food was not a limiting factor (Elliott 1988). Coho salmon are not found in waters with temperatures above 23.4 °C (Eaton and Scheller 1996), and juveniles will alter their distribution and behavior to avoid such conditions if possible. High temperatures during summer months are considered to be a problem in Oregon coastal streams, with 46% listed on the United States Environmental Protection Agency's 303(d) list because of high temperatures. The 303(d) standards are based on optimal temperatures, rather than lethal limits, and set a limit of 12.8 °C for salmon bearing streams. Parasites and disease respond directly to changes in temperature (Udey et al. 1975; Marcogliese 2001) and can affect freshwater and marine survival. Interannual variations in temperature could, therefore, be an important factor in the freshwater life history of coho salmon. In the marine environment, high sea surface temperatures are often an indicator for substantial changes in upwelling habitat and many aspects of the predator and prey field (e.g., Emmett and Brodeur 2000; Pearcy 2002; Peterson et al. 2002).

Later fall transitions (FallTrans) correlated with higher smolt output, although the reasons are not immediately clear. We initially expected that earlier transitions would allow spawners into the systems sooner, reducing mortality on the upstream migration and allowing more fish to spawn. Later fall transitions correlate with lower first winter (Flow.JFM.t0) flows and, presumably, less severe floods. FallTrans and Flow.JFM.t0 showed a negative correlation, but Flow.JFM.t0 alone had no explanatory power and no suggestion of a functional relationship with smolt produc-

tion. If spawning timing has been advanced by hatchery brood-stock selection and incubation time has been shortened by warmer temperatures, then fry may be tending to emerge earlier than they did historically. Perhaps the later fall transitions force spawning into a later time period, thereby shifting fry emergence back toward a more optimal schedule.

Low second winter flows (Flow.NDJFM.t1) also limit smolt production, suggesting that overwinter habitat is limiting (Nickelson 1998) and that more habitat is available with higher flows. Although the GAM suggested a dome-shaped second winter response, the right-hand leg of the OCN smolts model did not descend strongly. The fit with Queets River smolts, however, showed a much stronger dome-shaped function, lending support to this feature of the OCN model. During the winter coho salmon need areas of slow-moving water and complex structure such as pools, beaver ponds, and side channels to hold in during high flows. This would suggest that higher flows could flush juveniles out of areas that provide refuge at lower flows (McMahon and Hartman 1989; Shirvell 1990), and the model results indicate that there is a reduction in smolt production and survival at the highest second winter flows. The positive relationship with flows at lower values suggests that some overwinter habitats only become available when flow reaches a certain level. At lower flows juveniles may be displaced from overwintering habitats by competitive interactions with other juveniles, or perhaps predation on these fish is heavier when they are more concentrated.

Higher second spring flows (Flow.AM.t1) could improve survival during smolt outmigration, perhaps by speeding passage and making it easier to avoid predation in this vulnerable life cycle stage. Higher flows during downstream movement and smolt outmigration may reduce the time fish spend in exposed situations. Higher flows are usually associated with higher turbidity that would protect migrants from visual predators (Railsback and Harvey 2001). High spring flows could also increase the complexity of estuarine and nearshore ocean habitats to the advantage of the smolts.

The Queets River system is snow fed, in contrast to the Oregon coastal rivers, which are rain-fed. This could explain the lack of importance to smolt production of the fall transition if flows tend to stay high enough for returning spawners to have access to the river at any time. This may also be true of the spring outmigration flows (Flow.AM.t1). The dependence on temperature is similar in the two systems, as is the dome-shaped dependence on second winter flows. Although smolts per spawner showed different dependencies in the two systems (FallTrans and Flow.NDJFM.t1 for OCN, and AnnTemp for Queets), the relationships are weak.

Freshwater and marine climate links

Habitat for most Oregon coho consists of short coastal streams, small coastal estuaries, and the relatively cool marine waters of the California Current and the subarctic North Pacific (Percy 1992). Marine and freshwater coho habitat varies at seasonal and longer time scales because of regional to basin scale climate variations. During the cool half of the year (October–March), a dominant feature of North Pacific climate is the basin scale Aleutian Low pressure cell. Variability in the intensity and position of the Aleutian Low in-

fluences North Pacific and western North American climate across spatial scales of 1000s of km (Mantua et al. 1997; Mueter et al. 2002). Periods with an intense Aleutian Low favor intense wintertime coastal downwelling off the Oregon Coast, warm coastal ocean and coastal land surface temperatures, reduced precipitation over western Oregon, and reduced runoff in Oregon coho streams. Periods with a weak Aleutian Low favor the opposite conditions. In the springtime, the atmospheric circulation undergoes a spring transition in which the Aleutian Low weakens and migrates to the northwest while a subtropical high pressure area intensifies and migrates to the north, typically influencing west coast climate from the Columbia River mouth to the United States – Mexico border. The spring transition in the atmosphere has a marine counterpart that includes prominent changes in coastal ocean circulation, though the local ocean–atmosphere variations are not always tightly coupled (Thompson and Ware 1996). In summers with an intense subtropical high, coastal Oregon precipitation is below average, coastal Oregon upwelling is above average, and coastal sea levels and sea surface temperatures (SSTs) tend to be below average. Interannual variations in summertime coastal Oregon land and marine climate tend to be more regional than those in the cool half of the year. For instance, in the northeast Pacific the decorrelation scale for both July coastal SST and upwelling winds are ~500 km, while the January decorrelation scale for SST is ~2500 km and for upwelling winds is ~1250 km (Meuter et al. 2002). The bottom line here is that interannual climate variations that include changes in winds, precipitation, river runoff, and upper ocean currents and temperatures covary at spatial scales comparable to the length of the entire Oregon Coast in summer, and at even larger spatial scales in winter.

Logerwell et al. (2003) identified four factors affecting marine survival of OPI area coho salmon. These factors were winter sea surface temperature prior to smolt outmigration (SST.JFM.t1), date of spring transition (TRANS), spring sea level (SL.AMJ), and winter sea surface temperature during ocean residence (SST.JFM.t2). Sea level is lower during periods of strong upwelling. Note that Logerwell et al.'s (t0) is equivalent to the fresh water (t1). Here we have translated the time subscript for consistency. Pearson's correlation coefficients of these four factors and the four factors identified as affecting freshwater production show strong correlations between marine and freshwater conditions (Table 8). AnnTemp, even though it is measured in the year prior, is correlated significantly with all of the marine variables except sea level. Warmer air temperatures are associated with warmer SSTs in the first and second ocean winters and with later spring transitions. Later spring transitions are correlated with higher sea levels. In each case the sign of the correlation is such that good conditions in the marine environment are associated with similar good conditions in fresh water. Cool air temperatures are associated with cool sea surface temperatures and early spring transition. Sea surface temperature in both time periods and AnnTemp exhibit positive time trends; none of the other variables show such trends. Second spring flows are correlated with spring transition and, weakly, with spring sea level. In this case the interpretation of the correlation is opposite, so that good freshwater conditions tend to coincide with poor ocean con-

Table 8. Correlation matrix of marine and freshwater variables affecting production and survival of coho salmon.

	Year	Marine			Fresh water			
		SST.JFM.t1	TRANS	SL.AMJ	SST.JFM.t2	FallTrans	Flow.NDJFM.t1	Flow.AMJ.t1
SST.JFM.t1	0.466	1.000						
TRANS	0.246	0.225	1.000					
SL.AMJ	0.030	0.042	0.719	1.000				
SST.JFM.t2	0.439	0.134	0.261	0.226	1.000			
FallTrans	0.058	-0.019	-0.235	-0.054	0.124	1.000		
Flow.NDJFM.t1	-0.054	-0.125	<u>0.352</u>	0.169	-0.054	-0.176	1.000	
Flow.AMJ.t1	0.156	0.047	0.468	<u>0.319</u>	0.082	0.016	<u>0.331</u>	1.000
AnnTemp	0.676	0.375	0.424	0.278	0.359	0.121	0.010	<u>0.344</u>

Note: Linear correlations >0.3550 are significant at $p < 0.05$ and in bold type. Correlations >0.3010 are marginally significant, $0.05 < p < 0.10$, and underlined.

ditions. Wetter springs are associated with later spring transitions and higher sea levels (less upwelling). This makes sense, because the spring transition is linked to the beginning of upwelling and the end of the winter rain climate pattern. Improved outmigration conditions due to higher spring flows lead to an ocean that has not yet begun the productive upwelling cycle. Three of four pairs of correlated freshwater and marine environmental variables are synchronized in their effects by interannual climate variations, potentially amplifying the climate-related variability in coho salmon recruitment. This may explain the success that several authors have had in correlating OCN coho salmon recruitment or OPI area coho salmon survival with ocean environmental factors. However, the fourth pair of correlates has an opposing effect, so it should be possible to explain additional variability with a linked freshwater–marine model.

The stage is now set to build an integrated model of coho salmon production driven by environmental variability over the entire life cycle. Such a model could be used to link the projections from global climate models to coho production and coho habitat, exploring the implications of various future climate scenarios to the future of coho salmon in the Pacific Northwest. If increasing temperatures are part of future Northwest climate as suggested by climate change assessment models used in Intergovernmental Panel on Climate Change studies (Mote et al. 2003), then prospects for OCN coho salmon in the late 21st century would seem to be poor.

Management implications

It is important to identify the stages in the freshwater life history where temperature has the strongest detrimental effects. Short- and long-term restoration strategies should be focused on efforts to reduce temperatures in the stream areas where the coho reside at such sensitive times. High temperatures could have a direct effect on salmon survival during the summer when flows are low and habitat is limited. Warmer winter temperatures could accelerate egg development and growth, disrupting the adaptive timing of the life history. Temperature shifts have been shown to disrupt the reproductive strategy of some bird and plant species in England and Western Europe (Post et al. 2001; Moller 2002). There is no reason to believe such effects are not operating on salmon and could be exacerbated by human activities such as forestry, agriculture, and urban development that

open the riparian canopy. To a great extent, salmon have shown themselves capable of adapting their life history to anthropogenic changes in their environment. Are they reaching the limits of their ability to respond?

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