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Estuarine Influence on Survival Rates of Coho (*Oncorhynchus kisutch*) and Chinook Salmon (*Oncorhynchus tshawytscha*) Released from Hatcheries on the U.S. Pacific Coast

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ABSTRACT: While it has long been known that Pacific salmon use estuarine habitat, it has proven much harder to establish that the loss of estuarine habitat results in reduced survival. We used coded-wire tagging of hatchery fish to estimate the survival from release until maturity and related this survival to several indicators of estuarine condition. We found a significant relationship between the survival of chinook salmon (*Oncorhynchus tshawytscha*) and the percentage of the estuary that is in pristine condition, but no significant relationship for coho salmon (*Oncorhynchus kisutch*). This supports field observations that chinook salmon use estuarine habitat much more than coho salmon and confirms that the loss of estuarine habitat results in lower survival of chinook salmon.

Introduction

One of the most difficult problems in evaluating the impacts of habitat loss on other species is determining if the use of the habitat is necessary or merely convenient. If habitat is lost, will the animals move elsewhere with little consequence, or is the survival of the species reduced? This question arises frequently in debates over the role of estuarine habitat in the life cycle of salmon, and it is unclear whether the general loss of estuarine habitat has played a significant role in the well documented (National Research Council 1996) decline of Pacific salmon in the lower 48 states. The simplest approach is to compare the survival of salmon from pristine and impacted estuaries.

Coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon have been released from hatcheries on the U.S. and Canadian Pacific coast since the late 1800s, but it was not until the 1960s and 1970s that the number of hatcheries and their release output increased dramatically. This was in response to dwindling spawner returns and today more than half of the salmon catches in the Pacific Northwest are of hatchery origin. In Alaska the opposite is true, where most runs consist of wild spawners in pristine watersheds (NRC 1996).

The number of returning spawners, wild and hatchery-reared, fluctuates considerably between years and the dynamics behind those changes are often far from understood. Due to the complex salmon life cycle their survival can be impacted by a multitude of physical and biological factors in local watersheds and the ocean. Survival rate studies are generally based on tag recoveries, either on a local scale in a short-term experiment to estimate the effect of a particular factor such as dam passage or estuarine predation, or on a larger scale based on coded wire tag (CWT) release and recovery data from hatchery operations. In the latter case, tagged individuals are recovered as adults some years after they were released from hatcheries as smolts, so the resulting estimate of smolt-to-adult survival rate is a product of freshwater, estuarine, and marine survival rate.

COHO SMOLTS IN THE ESTUARINE ENVIRONMENT

Hatcheries release coho smolts primarily during the spring and early summer, around 1.5 yr after the time of their parents spawning. Although the duration of estuarine residence depends on the physical and biological characteristics of an estuary (Thorpe 1994), coho smolts generally move directly into neritic waters and pass through the estuary in a week or so (Myers and Horton 1982; Simenstad et al. 1982; Sandercock 1991), although there are examples of smolts residing in estuaries for months (Healey 1982).

Indicative of their large size upon entry into the estuary and occupation of neritic habitats, juvenile coho feed primarily on large planktonic or small nektonic organisms, including decapod larvae, euphausiids, gammarid amphipods, and fish larvae (Simenstad et al. 1982; Bottom and Jones 1990; Miller and Simenstad 1997). Durkin (1982) found little evidence of body growth taking place in the estuary. The smolts are themselves vulnerable to predation by piscivorous fish species, seabirds, and

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marine mammals, but the predator species composition and density varies widely between estuaries (Simenstad et al. 1982; Bayer 1986; Sandercock 1991).

Fall Chinook Smolts in the Estuarine Environment

Subyearling fall chinook smolts are released during the summer and fall, around 0.5–1 yr after the time of their parents spawning. As a rule, they reside in estuaries for a longer period than coho smolts, typically around 1 mo (Healey 1991; Thorpe 1994). In some estuaries the smolts stay for as long as 6 mo, especially in larger systems such as Grays Harbor, Washington (Simenstad et al. 1982). They generally reside longer in coastal Washington and Oregon estuaries than they do in Puget Sound and Georgia Strait, where the coastal habitat is more sheltered (Healey 1982). Nicholas and Hankin (1988) have thoroughly reviewed fall chinook salmon populations in coastal Oregon in terms of distribution, life history, and run sizes.

When the fall chinook smolts enter the estuary they first occupy tidal creeks high in the marsh area and later the outer estuary. Although the estuary appears to be the only habitat suitable for them, many may be swept beyond the river mouth during downstream migration (Healey 1982). The fall chinook diet is more diverse than that of coho, reflecting their extended estuarine residence, diversity of size classes, and different estuarine habitats used. In the inner estuary they feed on emergent insects and epibenthic crustaceans such as amphipods, mysids, and cumaceans, as well as algae, while in the outer estuary they feed on small nekton such as decapod larvae, fish larvae and juveniles, euphausiids, and neustonic drift insects (Healey 1982, 1991; Simenstad et al. 1982; McCabe et al. 1983; Bottom and Jones 1990; Fisher and Pearcy 1996; Miller and Simenstad 1997). Their daily growth rate is on the order of 4% of body weight (Healey 1982, 1991) and Neilson et al. (1985) found evidence of food-limited growth. The predators are much the same species as for coho, but over a longer period of time (Simenstad et al. 1982; Healey 1991; Pearcy 1992). Predation is believed to be a more important cause of smolt mortalities than food shortage (Fisher and Pearcy 1988; Mathews and Ishida 1989; Pearcy 1992).

Estuarine Influence on Smolt Survival

During migrations from freshwater to the open ocean, juvenile salmonids encounter dramatic changes in their environment while undergoing physiological and behavioral changes associated with smolt transformations. Migration of both coho and fall chinook through estuaries is slower than riverine migration, suggesting that a period of estuarine residence may be necessary for them to adjust their osmoregulatory capability, orient for their return migration, feed, or reduce their vulnerability to predators (Simenstad et al. 1982; Macdonald et al. 1988; Moser et al. 1991; Thorpe 1994; Emmett and Schiewe 1997). Quantitative analysis of the relationship between estuarine factors and salmon survival is hardly found in the literature, especially when looking at more than one estuary.

In this study, coho and fall chinook survival rates are analyzed with respect to three estuarine characteristics, to see whether any correspond to the different survival rates in the estuaries. The characteristics are the size of the estuary, the percentage of the estuary that is in natural condition, and the presence of oyster culture in the estuary. These were the only three measures we were able to obtain across a range of estuaries that showed significant contrast between estuaries. We did not have data over time for these factors. We used data from the 1980s, so our analysis is simply cross-sectional. Three characteristics cannot be expected to describe the differences between the estuaries in detail, but they are all the more noteworthy if a pattern can still be discerned.

Methods

Salmon Survival Rate Estimation

Survival rate, defined as the proportion of individuals surviving from smolt release to adulthood, was estimated from CWT release and recovery data (Jefferts et al. 1963; Johnson 1990) obtained from the CWT database of the Pacific States Marine Fisheries Commission (Gladstone, Oregon). The analysis presented here includes 2,666 coho and fall chinook CWT groups, each typically consisting of around 20,000 smolts, tagged and released from 27 coastal hatcheries on the U.S. Pacific Coast (Fig. 1, Table 1). The coho groups were released in 1974–1998 and the fall chinook groups were released in 1972–1996. The most recent year of recovery data for both species is 2000. Survival rates of spring chinook (Magnusson 2002) are not reported here, as relatively few of them are released from coastal hatcheries in Washington, Oregon, and California. Fall chinook and spring chinook are distinguished by the age at release from hatcheries.

A commonly used statistic for analyzing salmon survival rates from CWT data is the Oregon Production Index (OPI). This annual index (McGie 1984) is only provided for coho salmon, and published release and recovery data are pooled within a defined geographical area. The OPI data are not

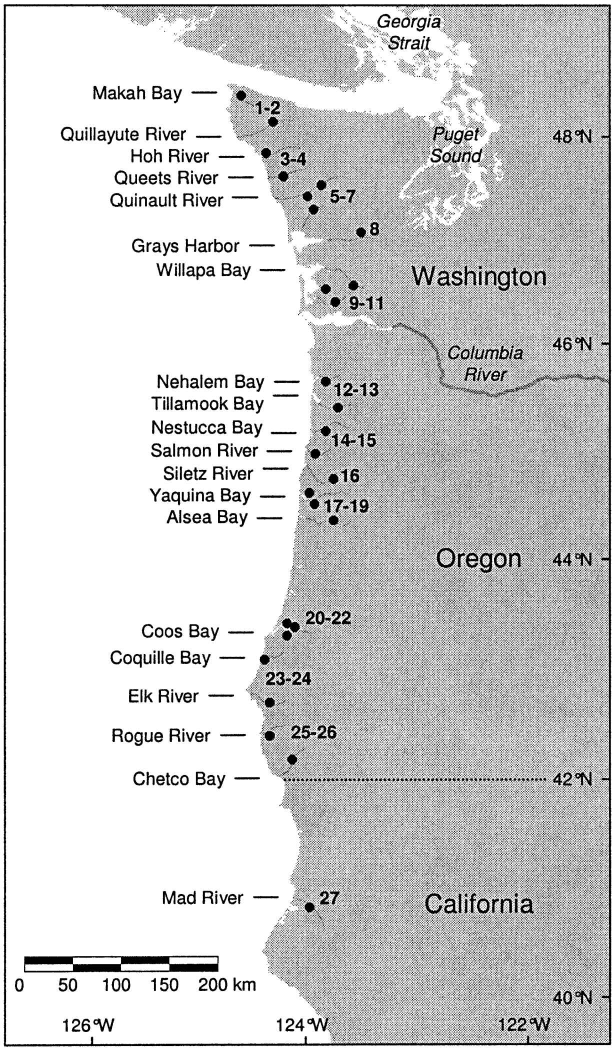

Fig. 1. Map showing the 27 hatcheries releasing coho (*Oncorhynchus kisutch*) and fall chinook (*Oncorhynchus tshawytscha*) salmon in coastal Washington, Oregon, and California. The labels correspond to Table 1 and the Columbia River divides coastal Washington and Oregon.

useful for comparing survival rate trends between estuaries and species, although the overall trend is similar to our data when both are pooled. The way recoveries are standardized to age 3 in our study has little effect on the overall trend. Another alternative way of estimating survival rates is from passive integrated transponder (PIT) tags. These have opened important possibilities in stream survival studies (Prentice et al. 1990), since each fish can be recovered multiple times without physically catching it. The use of PIT tags is still too recent and sporadic for the objectives of our study, compared with the large amount of CWT data available.

The data set for this study was defined using the following criteria: at least 1,000 smolts were tagged in each release group, the hatchery has released at least 10 CWT groups, the hatchery conducts freshwater-estuarine releases within 50 km from the sea, and the hatchery is located in Washington, Oregon, or California, excluding the large systems of Puget Sound, Columbia River, and California south of Cape Mendocino. The first two criteria are sample size thresholds required for the statistical analysis and the last two criteria define the geographical scope; our goal was to include as many estuaries as could be justifiably compared in a simple way. The focus is on salmon released into small to medium sized coastal rivers, and the main exclusions are Puget Sound, Columbia Basin, and Sacramento-San Joaquin Basin. Salmon smolts in those large and complex systems are likely to have different sources of mortalities than those in the smaller coastal rivers, due to growth and acclimatization during their downstream migration, sometimes from deep inland (Healey 1991; Sandercock 1991).

Coho are mainly released at age 2 and fall chinook during the 1st year following their brood year. The age at return varies between regions, but most of the recoveries are 2–3 year-old coho salmon and 3–5 year-old fall chinook salmon. Because of this variation, it was necessary to standardize the number of fish recovered (Coronado and Hilborn 1998) to allow a comparison of survival rates of the same species between regions:

$$N^*_3 = C_2 s_2 + C_3 + \frac{C_4}{s_3} + \frac{C_5}{s_3 s_4} + \frac{C_6}{s_3 s_4 s_5} \quad (1)$$

where N^*_3 is the number of 3-year-olds from a particular release group that would be alive if none were recovered at an age different from age 3, C_a is the number of fish recovered at age a, and s_a is the adult ocean survival rate from age a to a + 1. For coho, $s_a = 0.5$ across all ages, but for chinook $s_2 = 0.6$, $s_3 = 0.7$, $s_4 = 0.8$, and $s_5 = 0.9$ (Argue et al. 1983). This assumed adult ocean survival rate plays a minor role in the computations, and should not be confused with the estimated smolt-to-adult survival rate that depends primarily on the first few months after release, when most of the mortalities occur. Survival rate of each CWT release group was estimated as:

$$\text{survival} = \frac{N^*_3}{\text{number released}} \quad (2)$$

All recoveries are treated the same, be they from ocean catches, freshwater catches, or hatchery escapement, which makes the survival rate a robust statistic under varying fishing intensity. The arithmetic mean and standard error, as well as box plots

TABLE 1. List of the 27 hatcheries releasing coho (*Oncorhynchus kisutch*) and fall chinook (*Oncorhynchus tshawytscha*) salmon in coastal Washington, Oregon, and California. Label refers to map labels in Fig. 1, Grps is the number of CWT groups released, and Surv is the average survival rate.

Label	Hatchery	State	Estuary	Coho Grps	Coho Surv	Chinook Grps	Chinook Surv
1	Makah	WA	Makah Bay	43	3.7%	46	0.3%
2	Solduc	WA	Quillayute River	112	1.2%	25	0.4%
3	Chalaat Creek	WA	Hoh River	13	1.0%		
4	Salmon River (WA)	WA	Queets River	46	1.0%	11	0.7%
5	Quinault	WA	Quinault River	54	1.3%	55	0.8%
6	Quinault Lake	WA	Quinault River	53	1.1%	43	0.5%
7	Humptulips	WA	Grays Harbor	62	2.2%	10	1.2%
8	Bingham Creek	WA	Grays Harbor	59	1.5%	14	0.5%
9	Forks Creek	WA	Willapa Bay	24	3.1%	17	1.1%
10	Nemah	WA	Willapa Bay			18	1.1%
11	Naselle	WA	Willapa Bay	10	6.0%		
12	Nehalem	OR	Nehalem Bay	52	1.3%		
13	Trask	OR	Tillamook Bay	53	1.3%	139	0.7%
14	Cedar Creek	OR	Nestucca Bay			17	0.6%
15	Salmon River (OR)	OR	Salmon River	50	0.8%	59	2.3%
16	Siletz	OR	Siletz River	30	1.3%		
17	Yaquina Bay	OR	Yaquina Bay	628	0.7%	85	1.1%
18	Wright Creek	OR	Yaquina Bay	59	0.4%		
19	Fall Creek	OR	Alsea Bay	122	1.1%	14	0.9%
20	Coos Bay (Anad Inc)	OR	Coos Bay	239	1.9%	135	1.1%
21	Domsea Farms	OR	Coos Bay	13	1.0%	10	0.4%
22	Coos Bay (Oreg Aqua)	OR	Coos Bay	22	0.7%		
23	Bandon	OR	Coquille Bay	12	0.7%	10	0.2%
24	Elk River	OR	Elk River			146	1.8%
25	Indian Creek	OR	Rogue River			14	0.5%
26	Burnt Hill Creek	OR	Chetco Bay			19	0.9%
27	Mad River	CA	Mad River	12	1.1%	11	0.3%

are used to present the distribution of survival rates within strata.

Estuarine Characteristics

The 27 hatcheries release coho and fall chinook salmon into 20 different estuaries (listed in Table 2 along with three characteristics: estuarine area, fraction of estuary in natural condition, and the presence of oyster aquaculture). The total area of each estuary in km^2 is taken from Simenstad (1983), using 1 for all estuaries whose area is less than 1.5 km^2. The estuarine total area is typically measured by planimetry from charts.

The fraction of each estuary in natural condition was only found for Oregon estuaries. It is based on the Oregon Land Conservation and Development Commission (LCDC) classification system where each Oregon estuary is divided into management units, which are discrete geographic areas defined by biological and physical features. There are three types of management units: natural, conservation, and development. Natural management units are the least altered parts of an estuary and include tracts of salt marsh, tide flats, seagrass, and algae beds. The natural area was divided by the total area (both from Cortright et al. 1987) and then rounded to two decimal places. The presence of oyster aquaculture was taken from Parrish et al. (2001).

Regression Analysis

Once the survival rate of each CWT release group had been estimated, an attempt was made to explain the observed variation with estuarine regression terms. This was done by employing a Poisson regression model that belongs to a class of models called generalized linear models (GLM). The application of the Poisson GLM to CWT recovery data was developed by Green and Macdonald (1987), Cormack and Skalski (1992), Pascual (1993), and Coronado and Hilborn (1998). The model has the form:

$$\log \text{Survival}_i = \beta X_i \qquad (3)$$

where Survival_i is the survival rate of CWT release group i, β is the vector of regression parameters, and X is the vector of estuarine regression terms. Each data point is weighted in the regression according to the number of smolts times the recovery sampling fraction. The statistical significance of adding regression terms to this model was evaluated with an F-test: $F_s = \Delta D/(\varphi \times \Delta p)$ where φ is the scale parameter and ΔD is the deviance gained

TABLE 2. A list of the 20 estuaries in coastal Washington, Oregon, and California, their physical characteristics, and salmon survival rates. Area is the total estuarine area, Natural is the fraction of estuary in natural condition, and Oyster is whether oyster aquaculture is present. For the salmon data, Grps is the number of CWT groups released and Surv is the average survival rate.

					Coho		Chinook	
Estuary	State	Area (km²)	Natural	Oyster	Grps	Surv	Grps	Surv
Makah Bay	WA	1		No	43	3.7%	46	0.3%
Quillayute River	WA	1		No	112	1.2%	25	0.4%
Hoh River	WA	1		No	13	1.0%		
Queets River	WA	1		No	46	1.0%	11	0.7%
Quinault River	WA	1		No	107	1.2%	98	0.8%
Grays Harbor	WA	252		Yes	121	1.9%	24	0.8%
Willapa Bay	WA	347		Yes	34	3.9%	35	1.1%
Nehalem Bay	OR	9	0.59	Yes	52	1.3%		
Tillamook Bay	OR	36	0.52	Yes	53	1.3%	139	0.7%
Nestucca Bay	OR	4	0.70	No			17	0.6%
Salmon River	OR	1	1.00	No	50	0.8%	59	2.3%
Siletz River	OR	5	0.76	No	30	1.3%		
Yaquina Bay	OR	17	0.47	Yes	687	0.7%	85	1.1%
Alsea Bay	OR	9	0.73	No	122	1.1%	14	0.9%
Coos Bay	OR	50	0.62	Yes	274	1.8%	145	1.0%
Coquille Bay	OR	3	0.49	No	12	0.7%	10	0.2%
Elk River	OR	1	1.00	No			14	1.8%
Rogue River	OR	3	0.13	No			14	0.5%
Chetco Bay	OR	1	0.03	No			19	0.9%
Mad River	CA	1		No	12	1.1%	11	0.3%

by incorporating Δp more parameters (Venables and Ripley 2002, p. 187). The degrees of freedom for the test are Δp and $n - p_1$, where n is the total number of data points and p_1 is the number of parameters in the model being tested.

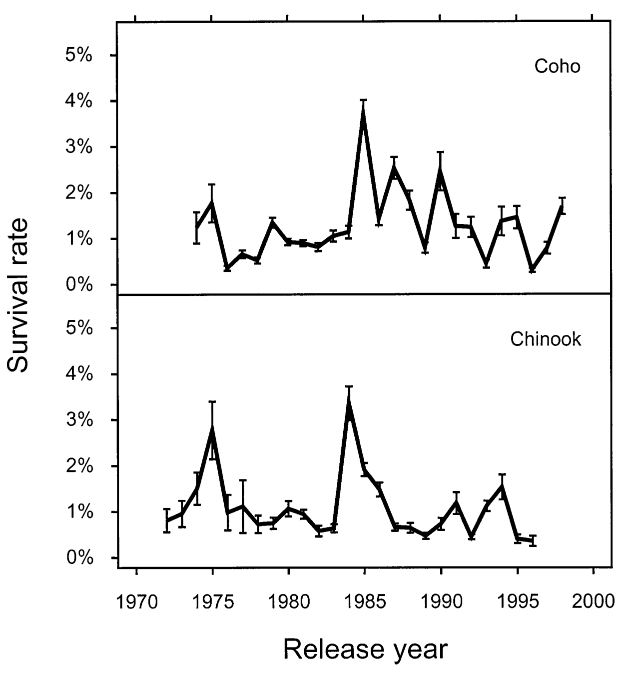

Fig. 2. Average survival rate of coho (*Oncorhynchus kisutch*) and fall chinook (*Oncorhynchus tshawytscha*) salmon in coastal Washington, Oregon, and California. The error bars show the standard error of the mean.

Results

Coho Survival Rates

The average survival rate of all 1,768 coho CWT groups was 1.2%, ranging from 0.4% to 6.0% by hatchery (Table 1), and the average survival rate in coastal Washington was 1.8%, somewhat higher than 1.0% in Oregon. Grouped by estuary, the survival rates were highest in Willapa Bay and Makah Bay, and lowest in Yaquina Bay and Coquille Bay (Table 2). More than two thirds of the coho CWT groups were released in coastal Oregon, 687 into Yaquina Bay alone and 274 into Coos Bay. The average survival rate by release year has ranged from 0.3% to 3.7% and the time series does not show a steady long-term trend (Fig. 2), but the highest survival rates are from the mid and late 1980s.

Chinook Survival Rates

The average survival rate of all 898 fall chinook CWT groups was 1.1%, ranging from 0.2% to 2.3% by hatchery (Table 1), and the average survival rate in coastal Washington was 0.7%, somewhat lower than 1.2% in Oregon. Grouped by estuary, the survival rates are highest in Salmon River and Elk River, and lowest in Coquille Bay, Mad River, and Makah Bay (Table 2). More than two thirds of all fall chinook CWT groups were released in coastal Oregon, primarily into Elk River, Coos Bay, and Tillamook Bay. The average survival rate by release year ranged from 0.4% to 3.4%, with the time series showing no long-term trend (Fig. 2), but no-

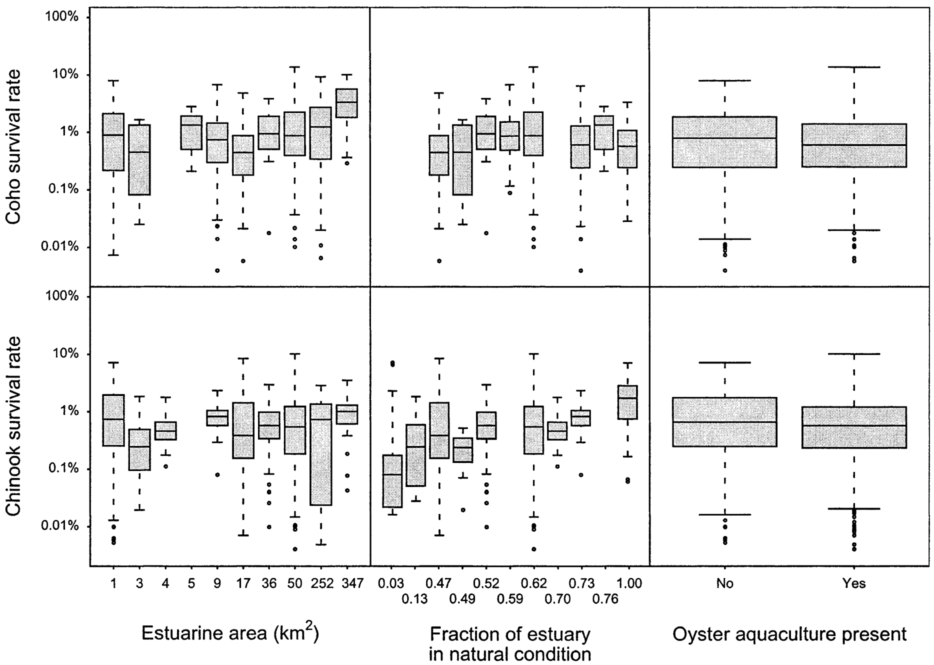

Fig. 3. Box plots showing the relationship between each estuarine regression term and survival rate of coho (*Oncorhynchus kisutch*) and fall chinook (*Oncorhynchus tshawytscha*) salmon. The data sets for estuarine area and oyster aquaculture include Washington, Oregon, and California, but the data set for estuarine condition is only available for Oregon.

tably high survival rates around the mid 1970s and the mid 1980s.

Estuarine Characteristics and Salmon Survival Rates

The relationship between the observed survival rates and each of the three estuarine regression terms is presented in Fig. 3. The analysis that shows the most convincing linear effect is between fall chinook salmon survival rate and the fraction of estuary in natural condition (abbreviated Natural). This relationship is described in more detail in Fig. 4, showing Natural on a linear scale and the Poisson GLM fit superposed on the data scatter. The best model fit is log $\text{Survival}_i = -5.342 + 1.310 \times \text{Natural}_i$, which translates into an intercept at Survival = 0.50% and exponential growth towards Survival = 1.77% where Natural = 1.0. The analysis of deviance (Table 3) shows that adding Natural to the null model is highly significant: $F_s = 45.74 > 3.86 = F_{0.05[1, 646]}$. The analysis also shows that when release year is included in the model as a covariate, the addition of Natural to the model becomes even more significant: $F_s = 143.04 > 3.86 = F_{0.05[1, 625]}$.

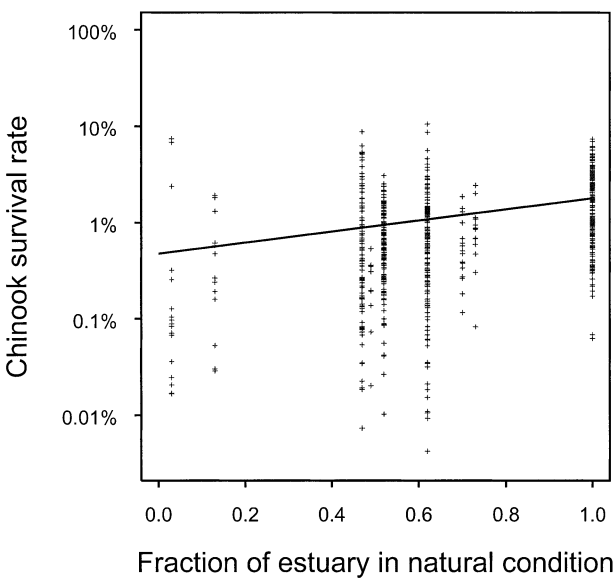

Fig. 4. Poisson regression fit to fall chinook salmon (*Oncorhynchus tshawytscha*) survival rates in coastal Oregon, using the fraction of estuary in natural as the only regression term.

TABLE 3. Analysis of deviance from the Poisson regression model for fall Chinook salmon (*Oncorhynchus tshawytscha*). D is deviance, df are degrees of freedom, and F_s is the significance test statistic. ΔD shows how much deviance is explained by the regression terms when incorporated in different order.

	df	D	Δdf	ΔD	F_s	p
Null	674	74,724	1			
+Natural	646	67,278	1	7,446	45.7	<0.001***
+Year	625	34,240	21	33,038	25.3	<0.001***
Null	647	74,724	1			
+Year	626	43,134	21	31,590	20.6	<0.001***
+Natural	625	34,240	1	8,894	143.0	<0.001***

The relationship between coho salmon survival rates and Natural was not significant, with $F_s = 0.39 < 3.85 = F_{0.05[1,1\ 278]}$. On the other hand, the relationship between coho salmon and estuarine area was significant, the best model fit being log $\text{Survival}_i = -4.572 + 0.07853 \times \log \text{Area}_i$, with $F_s = 26.29 > 3.85 = F_{0.05[1,\ 1766]}$. This translates into an intercept at Survival = 1.03% and power growth towards Survival = 1.64% where Area = 347 km^2.

Discussion

This study demonstrates for the first time a direct link between estuarine condition and survival of salmon through their entire life history, suggesting that subyearling chinook salmon are dependent on estuarine habitat for growth and transition from fresh to salt water. This result will surprise no one familiar with chinook salmon biology, but adds considerable strength to the arguments for preservation and restoration of estuarine habitat as a component of salmon recovery plans by showing that pristine estuaries have much higher chinook salmon survivals than degraded estuaries. The fact that coho salmon do not show a similar relationship with estuarine condition adds further support; they use estuaries much less intensively so we would expect to see much less of a relationship.

The magnitude of the impact of estuarine condition on salmon life history is considerable. The regression shown in Fig. 4 shows that with zero habitat left pristine, the estimated average survival rate is 0.50%, while the estimated survival in total pristine estuaries is more than three times higher, 1.77%. From these estimates the benefits, in terms of added number of fish surviving, could be estimated for habitat preservation or restoration actions.

Although the relationship between estuarine area and coho salmon survival is significant, we believe that this statistical relationship is less useful for interpretation. Ecologically sound hypotheses have been put forward about the importance of natural estuarine habitat for fall chinook smolts (Simenstad et al. 1982; Healey 1991; Moser et al. 1991; Thorpe 1994; Emmett and Schiewe 1997), but a causal linkage between coho survival and estuarine area is less clear.

Our analysis has a number of weaknesses associated with cross-sectional studies. We have only shown that estuaries in Oregon that have more pristine habitat have higher chinook salmon survival rates. This result could be due to a direct effect on mortalities, such as plants providing shelter from predation, or an unexamined co-variate that is correlated with the presence of lost habitat and human disturbance, including everything from reduced water quality to exotic species. We were unable to find any other quantitative factors to include in our database that differed significantly across estuaries, but we do not preclude the possibility that data on such factors can be assembled and the results we explain by percentage of pristine habitat is in fact due to another factor.

Smolt-to-adult survival rate of salmon is a complex function of physical and biological effects during their life in freshwater, estuarine, and marine environment. Scarnecchia (1981) and Skalski (1996) describe a positive relationship between salmon survival rate and river flow, while Holtby (1988) and Baker et al. (1995) report a negative relationship between survival rate and river temperatures. The mortality rate of smolts crossing large dams in the Columbia Basin has been estimated around 5–10% per dam, depending on the dam in question (Mathur et al. 1996; Skalski et al. 1998). In his analysis of declining survival rate with distance upstream, Newman (1997) relates those increased mortalities primarily to dams in the study area.

Salmon smolts are subject to considerable mortalities in estuaries and in the ocean just outside the estuaries (Mathews and Buckley 1976; Macdonald et al. 1988) where predation appears to be the dominating factor, as opposed to food shortage (Fisher and Pearcy 1988; Mathews and Ishida 1989; Pearcy 1992). Density-dependence during the smolt and ocean phases, meaning lower survival rates when abundance is high, is likely to differ between watersheds and seems to play a greater role in years when survival rates are low in general (Emlen et al. 1990; Levin et al. 2001).

Many oceanographic variables in the North Pacific are correlated with each other, for example strong upwelling causes lower sea surface temperature (SST) and this combination is in turn correlated with high survival rates of salmon (Scarnecchia 1981; Nickelson 1986; Emlen et al. 1990). These and other oceanographic variables are related to a low atmospheric pressure system termed the Aleutian Low, which is known to shift on a decadal scale and markedly alter marine ecosystems in the North Pacific, a phenomenon that was last known to occur during the winter of 1976–1977 (Beamish and Bouillon 1993; Francis and Hare 1994). These studies have shown that the consequences of such shifts for salmon survival rates are the opposite in Alaska compared with the Pacific Northwest. Recent results (Cole 2000; Hobday and Boehlert 2001; Koslow et al. 2002; Magnusson 2002; Logerwell et al. In press) indicate that large-scale changes in climate or ocean conditions can explain the dramatic differences in survival trends between Washington, Oregon, British Columbia, and Alaska. Other studies in this volume (Hickey and Banas 2003; Roegner et al. 2003; Swartzman and Hickey 2003) iterate the importance of climate on estuarine and marine productivity.

The above studies show a clear synchrony between Washington and Oregon salmon survival trends, and it is this synchrony that enables us to statistically distinguish the treatment effect of each estuary. The relative importance of climate variability and estuarine degradation for salmon survival is bound to vary between regions. In northern British Columbia and Alaska, where estuaries are virtually untouched by human activities, the fluctuations of survival rates are likely to be determined primarily by annual climate conditions, operating across the freshwater, estuarine, and marine habitat. Conversely, the data presented here show clearly that fall chinook residing in severely altered estuaries in northern California, Oregon, and Washington have significantly lower survival rates than those residing in estuaries where the habitat is more or less natural.

Still, in the San Francisco estuary, the southern end of their distribution, MacFarlane and Norton (2002) report that juvenile fall chinook salmon show less estuarine dependency than populations in the Pacific Northwest. The authors note that this may not have been the case when the estuary was less degraded. These results highlight the need for better data on estuarine conditions that could be used in future analysis such as those presented in this paper. Our ability to evaluate estuarine conditions was limited by the number of estuaries for which data were available, and by the range of indicators available for these estuaries.

Further studies could include a longer-term historical analysis of different estuaries, looking at changes in salmon abundance by estuary as pristine habitat was lost. Such studies would well predate the availability of CWT data and would presumably need to rely largely on catch and escapement records.

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