

THE RELATIONSHIPS BETWEEN PREDATORY FISH, FORAGE FISHES, AND JUVENILE SALMONID MARINE SURVIVAL OFF THE COLUMBIA RIVER: A SIMPLE TROPHIC MODEL ANALYSIS

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ABSTRACT

A trophic model that simulates interactions between a predatory fish (Pacific hake, *Merluccius productus*), forage fish, and juvenile salmon off the Columbia River was constructed to identify if trophic interactions could account for marine mortality of Columbia River juvenile salmon. The model estimates the number of juvenile salmon that are eaten annually by Pacific hake off the Columbia River for a given hake and forage fish population. Model results indicate that the presence of high numbers of Pacific hake could account for high mortality of some juvenile salmonid species/stocks leaving the Columbia River, and that this mortality would be much reduced when forage fish are abundant. Estimates of hake and forage fish abundance, based on field data collected from 1998–2005, were used in the model to derive annual estimates of the number of salmon possibly eaten by hake. A multiple regression analysis using the output from the trophic model and average May/June Columbia River flows accounted for much of the annual variation in Columbia River fall Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon marine survival ($p < 0.05$, $R^2 > 60\%$), but not spring or summer Chinook salmon. For these two stocks, average May/June sea-surface temperature was the best predictor of marine survival. Results support the hypothesis that for some Columbia River salmon species/stocks, marine survival is predation-driven and affected by the interaction between the abundance of Pacific hake, forage fish, Columbia River flows, and possibly ocean turbidity. Future modeling work should include predation estimates of other large fishes, marine mammals, and sea birds.

INTRODUCTION

Pacific salmon run sizes are determined by mortality in fresh and marine waters, with both habitats being equally important (Bradford 1997; Lawson et al. 2004). While causes of juvenile salmon mortality in fresh water have been extensively studied, the causes of mortality in the marine environment remains one of the least resolved questions in Pacific salmon biology (Groot and Margolis 1991; Pearcy 1992; Beamish and Mahnken

2001; Logerwell et al. 2003; Beamish et al. 2004). To address this question, we initiated a pelagic fish ecosystem study off the Columbia River in 1998. The primary objective of this study was to identify the abundance and feeding habits of potential predators of juvenile salmonids (Emmett and Krutzikowsky, in press), and how fluctuations in physical and biological oceanographic conditions affected the distribution and abundance of predatory and forage fishes (Emmett et al. 2006).

We now have seven years of information on the physical oceanographic conditions, temporal distribution and abundance of fishes, and the feeding habits of predatory fishes offshore of the Columbia River. We have observed that Pacific hake (*Merluccius productus*), a limited salmonid predator (Emmett and Krutzikowsky, in press), is at times very abundant in this region, and hypothesize that it may be responsible for the death of many juvenile salmonids (Emmett et al. 2006). We also observed wide fluctuations in the abundance of forage fishes, which predators can consume as “alternative prey” instead of salmonids (Fisher and Pearcy 1988; Pearcy 1992; Svenning et al. 2005). The alternative-prey hypothesis proposes that when forage fishes are abundant, predators will eat forage fishes instead of salmonids because predators would rarely encounter juvenile salmonids relative to forage fishes. This appears to be particularly true for the California Current System, where forage fish are at least two orders of magnitude more abundant than juvenile salmon, versus the Alaska Coastal Current, which has relatively low forage fish abundance (Orsi et al. 2009).

Columbia River salmon runs showed large annual fluctuations from 1998–2005, which appeared to reflect changing ocean conditions (ocean temperatures, upwelling, primary production, fish production, etc.) (Williams et al. 2005). These observations suggest that marine survival of salmon off the Columbia River, and perhaps the Pacific Northwest, may be influenced by interactions between forage and predatory fish populations. As such, we hypothesize that marine survival of juvenile Columbia River salmon is largely controlled by marine predation, but when forage fish populations are high, large predatory fishes should consume primarily forage fishes instead of juvenile salmonids (fig. 1). The

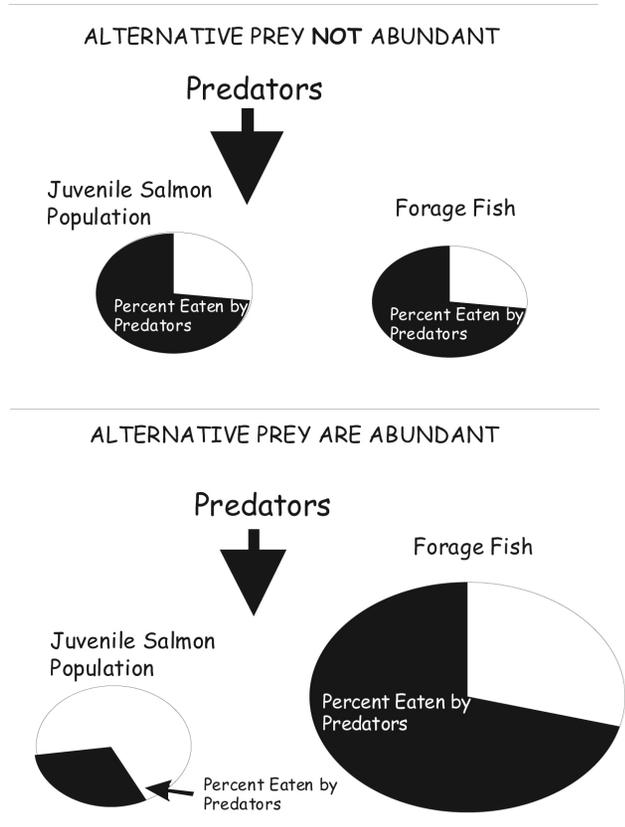


Figure 1. Diagram of the hypothesized role that alternative prey (forage fishes) play in reducing predation on juvenile salmonids in the marine environment.

purpose of our research was to explore this hypothesis by using a dynamic trophic model in conjunction with pelagic fish data collected off the Columbia River.

Predation can play an important role in structuring marine ecosystems (Estes and Palmisano 1974; Bogstad and Mehl 1997; Ware and McFarlane 1995; Bax 1998; Estes et al. 1998; Livingston and Jurado-Molina 2000). However, documenting predator effects (e.g., distinguishing relative importance of top-down processes versus bottom-up processes) in the marine environment has been difficult (Walters et al. 1978; Worm and Myers 2003). Studies of marine bird (Collis et al. 2002) and marine mammal (Riemer and Brown 1997) feeding in the Northwest indicate they can be important predators of juvenile salmonids at specific locations, but they do not appear to account for a significant proportion of the juvenile salmon marine mortality in the Pacific Northwest. There have been few actual observations of predation on juvenile salmon by large marine fishes in the Pacific Northwest (Brodeur et al. 1987; Beamish et al. 1992; Beamish and Neville 1995, 2001; Percy 1992; Emmett and Krutzikowsky, in press). For example, from 1998–2004 only seven juvenile salmonids were identified from 7,402 predator fish stomachs collected off the

Columbia River (Emmett and Krutzkowsky, in press). Nevertheless, the negative correlation between marine predator fish abundance and salmon marine survival in the Pacific Northwest provides correlative evidence that fish predation may be important (Emmett and Brodeur 2000; Emmett et al. 2006).

Ecosystem and population models provide one method to investigate how environmental factors might control juvenile salmon marine survival. The juvenile salmon marine survival model of Gertseva et al.¹ found that salmon growth, migration, and mortality were important parameters affecting survival. They concluded that salmon marine survival was determined primarily by top-down mechanisms (predation). Field (2004) developed an ecosystem-based model of the northern California Current using a mass-balance modeling approach (Ecopath/Ecosim) (Christensen and Pauley 1992). Field et al. (2006) evaluated the effect of changing hake distributions and abundance on hake prey resources by running model simulations, and concluded that hake can affect the abundance of forage fish resources, especially if climate effects are included.

Our research considers three questions. First, can Pacific hake, the most abundant fish predator in the California Current ecosystem, be responsible for a large percentage of the marine mortality of Columbia River juvenile salmonids? Second, can the abundance of forage fish alter hake predation rates on juvenile salmonids? Finally, do Columbia River plume conditions affect these predation interactions? We explored these questions by building a dynamic trophic model containing interactions between Pacific hake, forage fish, and juvenile salmon. The model is limited to the area around the Columbia River (fig. 2) and the April–July 120-day period. During this initial ocean entry period, juvenile salmon are similar in size to forage fish and thought to be most vulnerable to predation (Percy 1992; Weitkamp 2004; Emmett and Krutzikowsky, in press). While the model provides a simplistic view of a complex ecosystem, it presents what are believed to be the major pathways and begins to identify general properties of the pelagic ecosystem off Oregon and Washington.

METHODS

To develop a model of predator fish/prey fish interactions off the Columbia River, it was necessary to obtain fish abundance estimates and food habit information. Predator and forage fish population estimates were acquired by conducting regular night-time surface trawling and determining predator feeding habits by taking

¹ Gertseva, V. V., T. C. Wainwright, and V. I. Gertsev. 2004. Juvenile salmon survival in the Northeast Pacific Ocean: top-down or bottom-up control? Unpublished manuscript. NOAA Fisheries, Newport, Oregon.

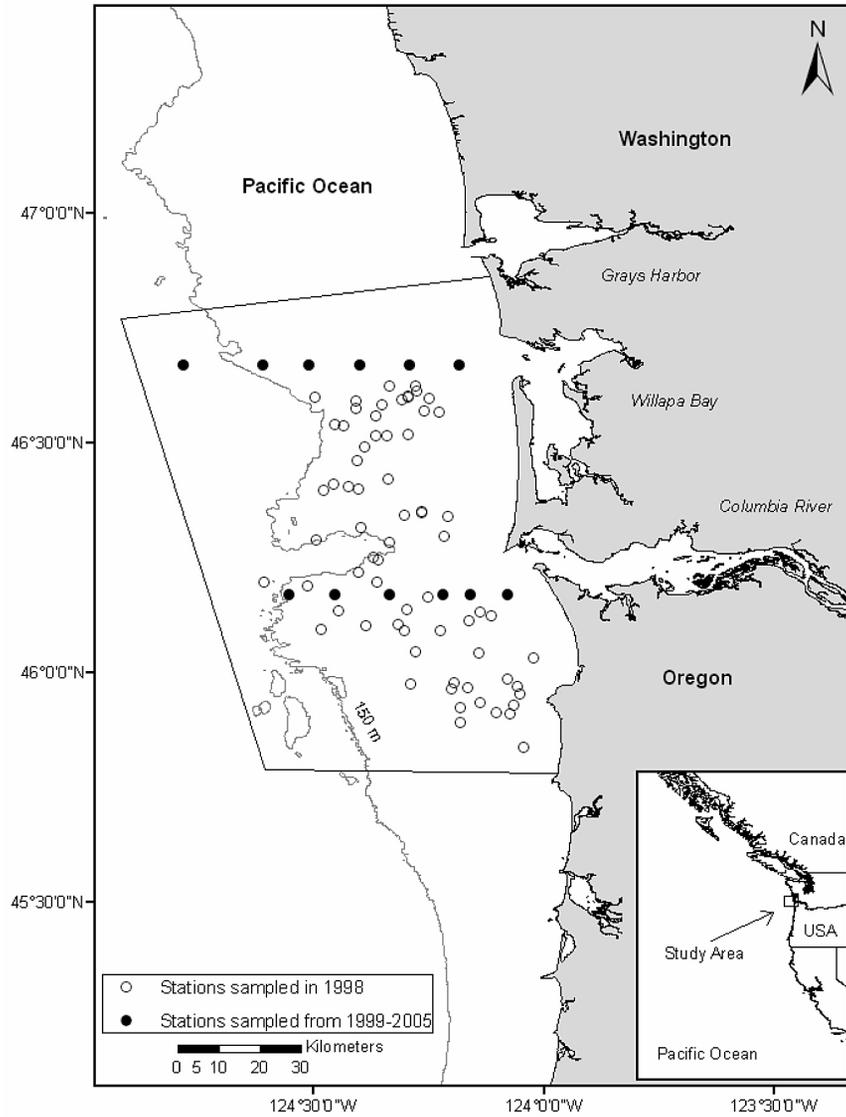


Figure 2. Location of stations off the Columbia River region sampled by surface trawl at night during spring/summer 1998–2005. Also shown is the estimated total coastal area represented by the trawl data and the 150 m depth contour.

fish stomachs from late April–July 1998–2005. These efforts provided seasonal density estimates for forage fishes, Pacific hake, and other predatory fishes. Juvenile salmon densities were not determined from fishing data, but extrapolated from estimates of Columbia River natural production, hatchery releases, migration timing, and freshwater survival.

Study area

Much of the marine mortality of juvenile salmon is thought to occur during the first days or months that smolts enter the ocean (Percy 1992; Beamish and Mahnken 2001; Weitkamp 2004). Thus, we located our study site off the Columbia River (fig. 2), a river basin with relatively large salmon runs. We also conducted our

field collections during spring/early summer, the time when most coho and Chinook salmon smolts emigrate from the Columbia River (Dawley et al. 1986). The study site is situated in the northern portion of the California Current ecosystem, and has seasonally variable winds and currents: in the summer, winds come from the northwest, currents move southerly, and upwelling occurs; in the winter, winds come from the south, currents move northerly, and downwelling occurs (Hickey 1989; Hickey and Banas 2003). The low-salinity Columbia River plume is a dominant feature of the study area, and is typically located on the continental shelf off Washington during winter and beyond the shelf off Oregon during summer (Hickey and Banas 2003). Columbia River flows are generally highest in

May/June and lowest in August/September. Flows are presently highly regulated (by dams) and high flows are now much lower than historical levels (Sherwood et al. 1990).

Fish collections

During 1999–2005, we collected forage and predatory fishes at fixed stations along two transect lines, one just south of the Columbia River and the second approximately 80 km north (fig. 2). Six stations were sampled along each transect, with the first station as close to shore as possible (30 m deep), and the farthest station approximately 55.6 km from shore. In 1998, the first year of our study, we sampled at a variety of stations along a broad arc from Willapa Bay, Washington, to Tillamook Head, Oregon. During this year, part of our research was to identify the appropriate trawl equipment and station locations for collecting predator and forage fishes. We tried a variety of trawls before choosing a 264-rope trawl. Only data collected by rope trawl are reported. All sampling was conducted at night, dusk to dawn, approximately every 10 days from mid-April through July/early-August, for a total of 20 sampling days, for a maximum of 10 sampling cruises per year. Sampling was conducted at night because hake, clupeids, and other forage fishes make diel migrations from depth to surface waters (Blaxter and Holliday 1963; Averson and Larkins 1969).

All samples were collected by surface trawling with a chartered commercial trawler. The trawl equipment was a NET System 264-rope trawl with 3 m foam-filled Lite doors. This gear has also been used to capture juvenile salmonids and associated fishes off southeast Alaska (Murphy et al. 1999) and California (MacFarlane and Norton 2002). The trawl is 100 m long with a fishing mouth area 28 m wide and 12 m deep. The effective mouth area (336 m²) was measured in earlier work using a backward-looking net sounder (Emmett et al. 2004). The net was fished close to the surface, but the head rope depth was usually 1–1.5 m deep (Krutzikowsky and Emmett 2005). Mesh size ranges from 126.2 cm in the throat of the net near the jib lines to 8.9 cm in the cod end. A 6.1 m long, 0.8 cm stretch knotless web liner was sewn into the cod end to capture small fishes and invertebrates. The 264-rope trawl was fished by towing it 137 m (75 fathoms) behind the vessel, which traveled at approximately 2.9 knots (1.5 m/s) for 30 minutes. However, starting in 2001, haul times were shortened to 15 minutes because longer tows resulted in very large catches of forage fishes. Large catches increased our fish processing time and reduced our ability to trawl at every sampling site before daylight.

From each haul, all fish species were identified and enumerated, and 30 random fish of each species were

measured. However, when haul catches were large ($\sim >200$), a random sample of 30 individual fish from each species was measured, and a subsample of each species (approximately 5–30 kg, depending on fish size) was counted and weighed, and then the remaining fish of that species were weighed. The total numbers of each species captured for that haul were determined by adding the number counted to the estimated number that was weighed (i.e., mass weight divided by the average weight/individual).

Fish abundance estimates

Fish densities for each haul were calculated by dividing the number of fish captured by the water volume of each haul. Volume of each haul was calculated by multiplying the distance fished by the effective mouth area. The distance each haul fished was identified by the geographic positioning system. We assumed a net efficiency of 1.0 (i.e., all fish at the mouth of the net were captured). Because the fish catch data were highly skewed, average monthly densities of forage and predator fishes were calculated using the delta-distribution method (Pennington 1996). This method uses a lognormal model to first calculate the mean and variance of the non-zero catch data (i.e. hauls where the fish catch was not zero) and then adjusts these values using the proportion of non-zero hauls. Because we sampled approximately every 10 days, monthly densities were calculated using data from two or three cruises (24 or 36 hauls). Estimates of total fish abundance in the study area were calculated by multiplying the average May/June densities by the total volume of the study area. Total water volume of the study area (1.56×10^{11} m³) was calculated by multiplying the study area (1.3×10^{10} m²) (fig. 2) by an assumed surface-trawl sampling depth of 12 m.

Forage fish migration into the study area begins in early May and peaks in late May (Emmett et al. 2006). The model incorporates these fluctuations by gradually increasing forage fish numbers until the end of May (fig. 3), after which forage fish immigration is discontinued. Recruitment, the addition of 0-age juveniles, to forage fish populations occurs in the fall after our study period (Emmett et al. 2005; Emmett, unpubl. data), so the model assumes no recruitment of forage fish during the model period.

Juvenile salmonid abundance estimates

Surface trawling at night does not collect juvenile salmonids effectively (Krutzikowsky and Emmett 2005), so surface trawl catches of juvenile salmonids were not used to estimate their abundance. Total counts or estimates of juvenile salmonids, hatchery releases plus wild production, leaving the Columbia River are not available. However, in 2004 an estimated 157 million hatch-

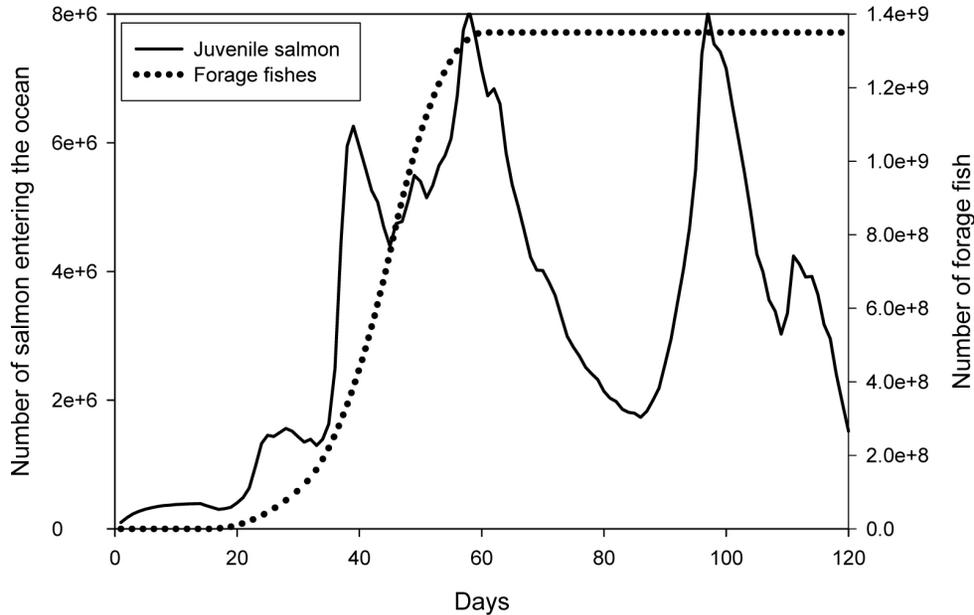


Figure 3. Graphic representation of how the trophic model populated the study area off the Columbia River with number of juvenile salmon entering per day and number of forage fish off the Columbia River. Zero on the x axis corresponds to 1 April.

ery salmon smolts were released in the Columbia River (NPCC 2004). Approximately 75% of juvenile salmonids in the Columbia River are of hatchery origin, thus ~50 million (25%) are wild smolts (Memo. from J. Ferguson, NOAA/NMFS, Seattle, Washington, to J. Lecky, NOAA/NMFS, Portland, Oregon, 25 August 2005). This provides a total estimate of 200 million smolts entering the Columbia River annually. However, approximately half of all smolts die before they reach the ocean (Douglas Marsh, NOAA/NMFS, Seattle, Washington, pers. comm.), so we estimated that about 100 million smolts entered the ocean from the Columbia River in 2004, and we assumed that smolt numbers were similar in other years. Columbia River hatchery and wild production, along with riverine survival of juvenile salmon, does vary annually, but specific estimates of the number of smolts entering the ocean each year are presently unavailable.

The annual smolt (juvenile salmon) migration through the Columbia River estuary is well documented. Yearling (coho and spring Chinook salmon) and older (steelhead, *O. mykiss*) smolts begin migrating in April, with peak migration in May, and decline through June (Dawley et al. 1986). Subyearling Chinook salmon smolts migrate primarily from June through September, with a peak in July (Dawley et al. 1986). The number of smolts that migrate into the ocean each day (fig. 3) was calculated by multiplying 100 million times the percent of Columbia River juvenile salmon that migrate each day. The percent of the juvenile salmon that migrate each day was modeled using the percent of the salmon-smolt run passing Bonneville Dam each day in 2002, and assumed to

be similar each year. These data were obtained from the Fish Passage Center, Portland, OR (<http://www.fpc.org/>). It takes approximately three days for juvenile salmon to travel from Bonneville Dam to the ocean, so the ocean entry date was adjusted accordingly.

Juvenile salmon are known to migrate out of the study area and generally move directly offshore (steelhead), or move north (Percy and Fisher 1988; Fisher and Percy 1995) after spending time in the Columbia River plume, or move south for a short period. Unfortunately, no empirical data are available on the residence time of individual smolts in the study area. We assumed that 25% of the juvenile salmon leave the study area (fig. 2) per day, implying that only 13.3% of the juvenile salmon will be left in the study area after one week, assuming no predation. We believe this estimate of percent migration/day may be high. Decreasing the migration rate would increase predation rates on juvenile salmon in the study area. By using 25% we are making a conservative estimate of residence time.

Large fish consumption rates

Pacific hake consumption rates were obtained from the literature (Francis 1983; Rexstad and Pikitch 1986), but modified by our own stomach analysis findings. For example, the literature indicated that Pacific hake consume ~1.0–2.5% of their body weight/day. For the average Pacific hake that we captured, which weighed ~500 g, this consumption rate implies that they ate only 5–10 g/day, but our stomach analysis showed that Pacific hake could consume a least 5.0% of their body weight

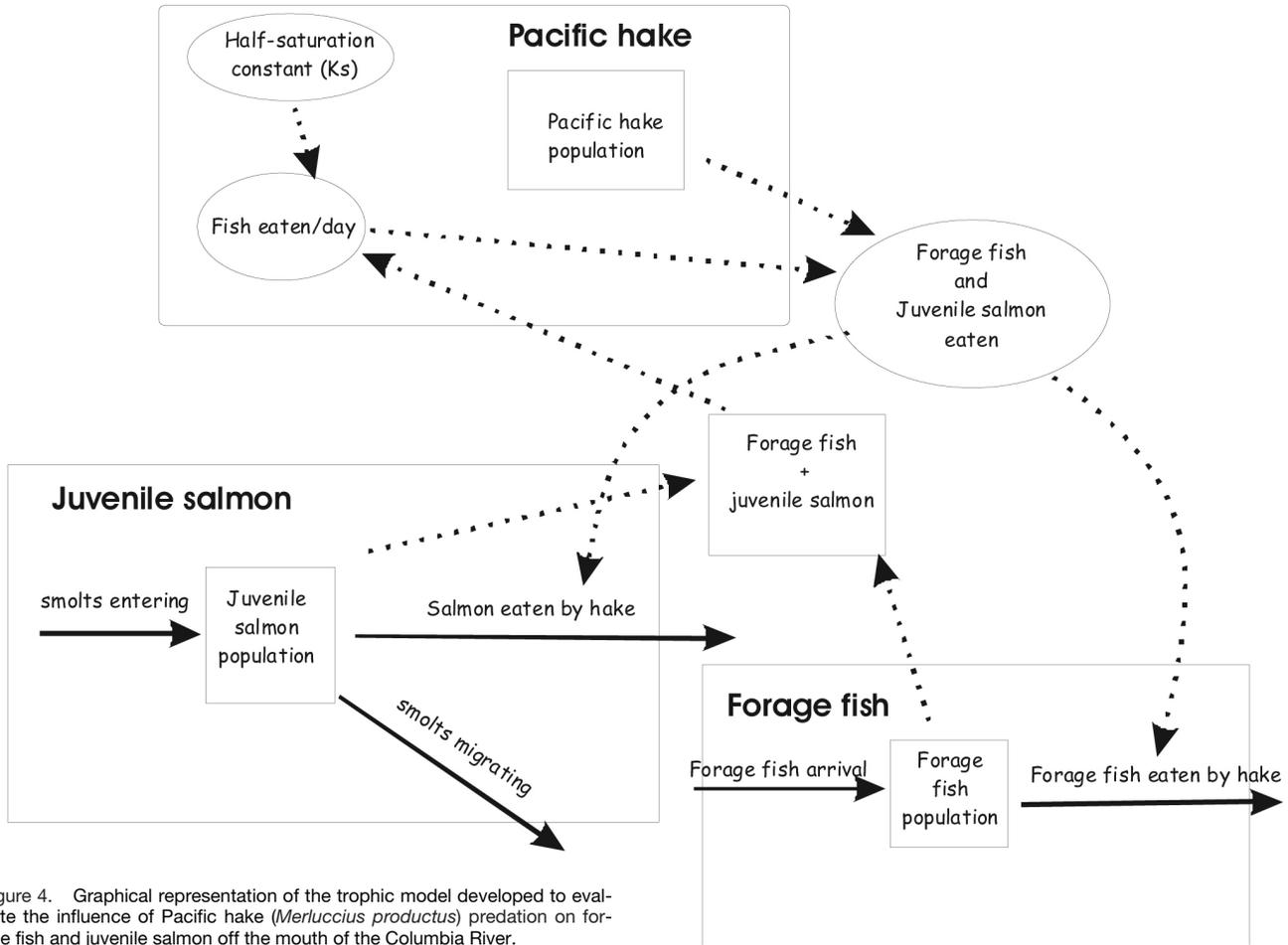


Figure 4. Graphical representation of the trophic model developed to evaluate the influence of Pacific hake (*Merluccius productus*) predation on forage fish and juvenile salmon off the mouth of the Columbia River.

during one meal. Cartes et al. (2004) reported that European hake (*Merluccius merluccius*) ate 1.01–5.51% of their body weight/day. As such, we estimated that our average Pacific hake had a maximum daily consumption rate of approximately 25 g/day, similar to the value in Field (2004). Since the average northern anchovy (*Engraulis mordax*), a primary prey of Pacific hake (Emmett and Krutzikowsky, in press), was approximately 25 g (our unpublished data), we estimated that Pacific hake had a maximum consumption rate of one forage fish per day.

Model overview

All model development and mathematical calculations were conducted using the STELLA software package (High Performance Systems 1997). The model describes the pelagic food web off the mouth of the Columbia River for 120 days (April through July), the period when most Columbia River juvenile salmonids first enter the ocean (Dawley et al. 1986) and when mortality is thought to be high (Percy 1992). The model has one major predator (*Hake*) and two prey groups, *Salmon* and *Forage Fish (FF)* (fig. 4). Pseudo-code for the STELLA mathematical model is available by contacting the first author.

Predatory fishes have been shown to be primarily selective for prey size, not species (Ursin 1973; Sogard 1997), so juvenile salmon were considered a member of the forage fish, or prey, community. As such, we grouped forage fish (*FF*) and juvenile salmonid (*Salmon*) populations into one prey population variable (*FFSalmon*). Hake were allowed to prey on this mixed population, and the number of juvenile salmonids eaten by hake (*FFSalmon_Eaten*) was derived by multiplying the number of fish eaten (*FFSalmon_Eaten*) by the proportion of *FFSalmon* composed of juvenile salmon:

$$\text{Salmon_Eaten} = \text{FFSalmon_Eaten} * (\text{Salmon}/\text{FFsalmon}) \quad (1)$$

The total number of forage fish and salmon eaten per day (*FFSalmon_Eaten*) can be calculated by multiplying the number of hake in the study area (*Hake*) by feeding rate (*FR*):

$$\text{FFSalmon_Eaten} = \text{Hake} * \text{FR} \quad (2)$$

Feeding Rate (*FR*) changed as prey (*FFSalmon*) abundance changed. This was accounted for by using a (Michaelis-Menton) function:

$$\text{FR} = \text{MaxFF} * \text{FFSalmon}/(\text{Ks} + \text{FFSalmon}) \quad (3)$$

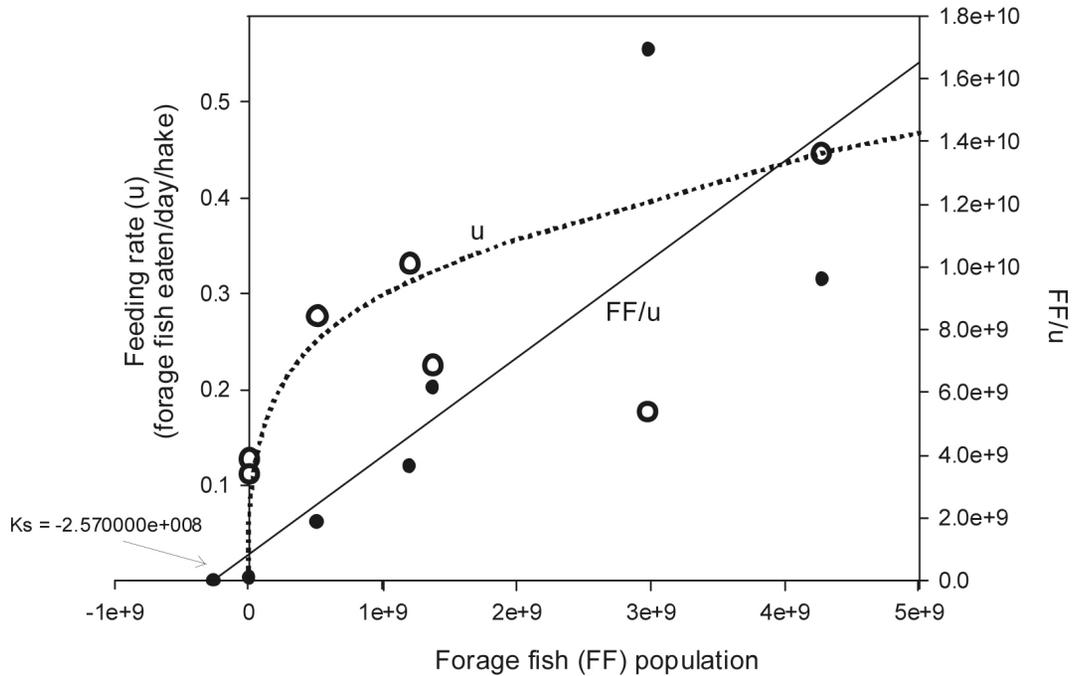


Figure 5. The relationship between the relative number of Pacific hake (*Merluccius productus*) feeding on fishes (○) (estimated hake fish feeding rate) at various forage fish population abundances. The straight line is the regression of the forage fish population/hake fish feeding rate ratio versus forage fish population abundance (●) from which the Michaelis-Menton K_s (half-saturation feeding constant) was estimated.

Since the maximum feeding rate ($MaxFF$) was estimated to be equal to one forage fish/day, it can be ignored in the equation. The half-saturation feeding constant, K_s , was estimated by subtracting the intercept from a linear regression of the observed annual average percent of hake with fish in their stomachs (i.e., an estimate of hake fish-feeding rate) regressed against the observed ratios of the number of forage fish plus juvenile salmon (FF_{salmon}) over the hake fish-feeding rate (Eppley and Thomas 1969) (fig. 5). At very high forage fish and juvenile salmon densities, FR approaches 1. At low prey densities, FR approaches 0 and the number of forage fish and juvenile salmon consumed also approaches 0.

The total number of juvenile salmon ($Salmon$) in the study area on any day (t) was calculated as:

$$Salmon(t) = Salmon(t - 1) + Salmon_{Entering}(t) - Salmon_{Eaten}(t) - Salmon_{Migrating}(t) \quad (4)$$

for $t = 1$ to 120.

The total number of forage fish (FF) in the study area was calculated as:

$$FF(t) = FF(t - 1) + Forage_Fish_arriving(t) - Forage_Fish_eaten(t) \quad (5)$$

A list of parameter and constant values is provided in Table 1.

Model evaluation

Calibration/Confirmation. This model serves as an initial “framework” to evaluate if a dynamic trophic model, describing the relationships between hake and forage fish, could account for annual fluctuations in marine mortality of Columbia River juvenile salmon. The model predicts how many smolts would be eaten by hake under different levels of abundance for hake and forage fish populations. We used linear regression to compare the annual number of salmon eaten as predicted by the model, the independent variable, with four observed measures of salmon marine survival: the Oregon Production Index Area (OPI) of hatchery coho salmon (*Oncorhynchus kisutch*) marine survival (PFMC 2005), and spring, summer, and fall Chinook (*O. tshawytscha*) salmon jack counts at Bonneville Dam. Since annual production of smolts in the Columbia River is approximately constant (Douglas Marsh, NOAA/NMFS, Seattle, Washington, pers. comm.), jack counts, which

TABLE 1
 Constants and parameters for model simulations.

Parameter or constant	Description	Value
K_s	Half-saturation feeding constant	2.3×10^9
Percent Migration	Percent of smolts migrating from the study area per day	25%
$Max\ FF/day$	Maximum number of forage fish eaten by the average hake per day	1

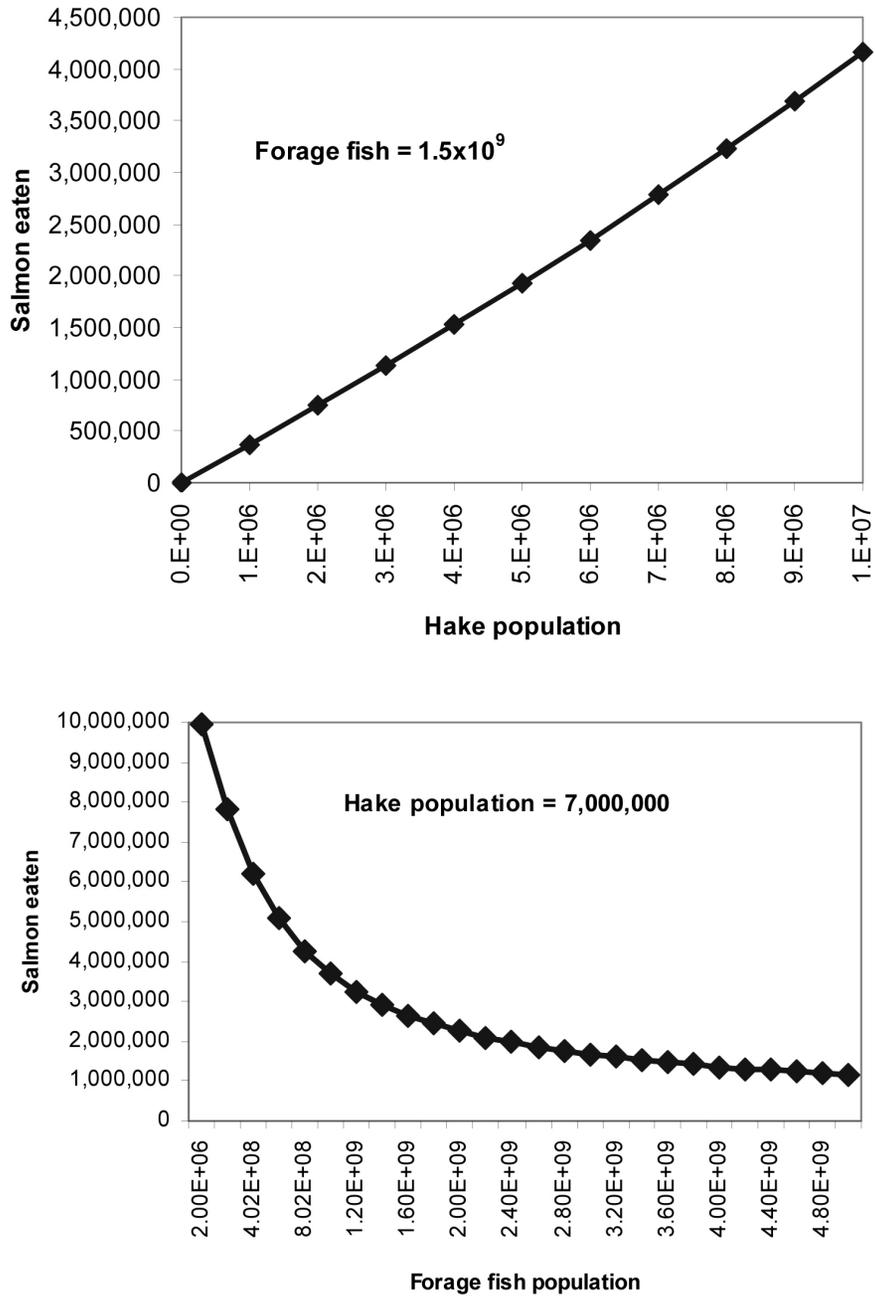


Figure 6. Model output showing the estimated number of salmon eaten at various Pacific hake (*Merluccius productus*) population sizes (top) and when the forage fish population is 1.5×10^9 , and at various forage fish population sizes (bottom) when Pacific hake are constant.

are the number of precocious males that have spent one summer at sea, are generally a good predictor of annual salmon marine survival for Chinook salmon. Annual Chinook salmon jack counts at Bonneville Dam were obtained from the Columbia River Data Access in Real Time (DART) homepage (<http://www.cbr.washington.edu/dart/dart.html>), maintained by the University of Washington. Before conducting the statistical analysis, the model-predicted number of salmon

eaten by hake was log-transformed to normalize the data.

Using multiple regression models with Columbia River Chinook salmon jack returns or coho salmon marine survival as dependent variables, we also investigated if the annual numbers of salmon eaten, as predicted by the trophic model, with Columbia River flow (average May/June flows) or average May/June sea surface temperature (SST), could account for much of the observed variation in salmon marine survival

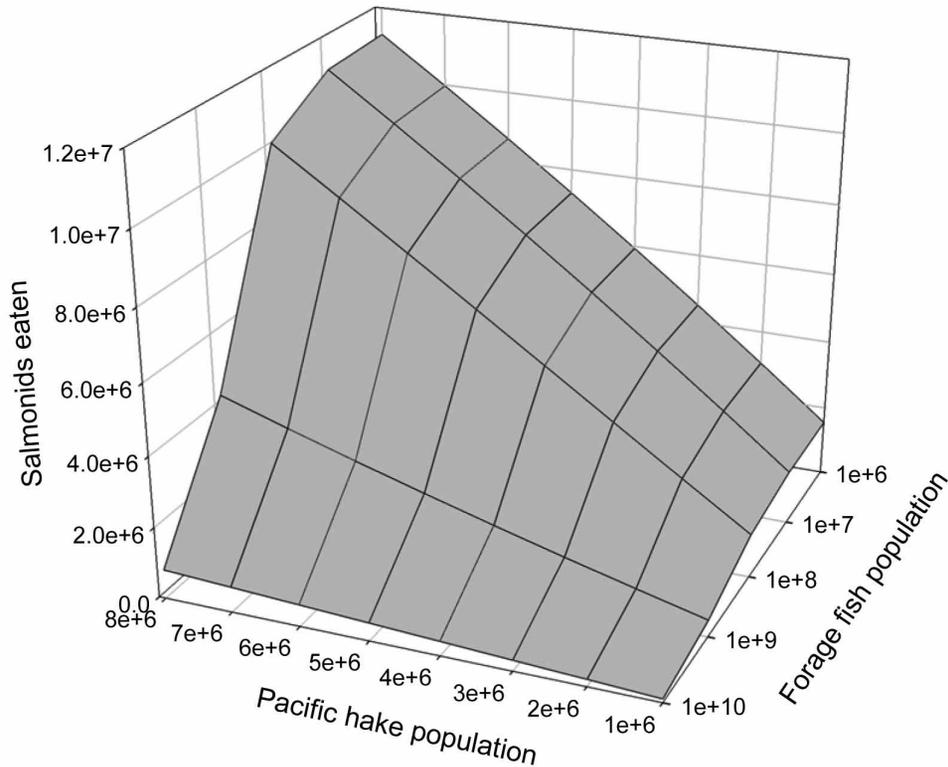


Figure 7. Output from the trophic model of Pacific hake, forage fish, and juvenile salmon interactions. Shown is the estimated number of salmon eaten under various population sizes of Pacific hake (*Merluccius productus*) and forage fishes.

RESULTS

Model simulations

We ran a variety of model scenarios to simulate how varying hake and forage fish abundances influence the number of juvenile salmon eaten. At a given level of forage fish abundance, the model predicts that the number of juvenile salmon eaten is directly related to hake population abundance (fig. 6, top panel). The model also predicts that juvenile salmon mortality is inversely related to forage fish abundance in a curvilinear fashion (fig. 6).

Under “good” ocean conditions—when hake numbers are less than 1.0×10^6 and forage fish are abundant—hake eat relatively few salmonids (fig. 7). However, when hake are abundant and forage fish are not, the number of salmon eaten by hake rises sharply (fig. 7). When forage fish are very abundant (greater than 1.0×10^9), they serve as strong alternative prey and, for a wide range of values for hake abundance, few salmonids are eaten (fig. 7).

Model estimates of salmon mortality versus salmon marine survival indexes

Seven years of average annual May/June abundance estimates for hake and forage fish in the study area were used in the model to generate model predictions of the numbers of salmon eaten. These resulting model

estimates of salmon mortality were then compared with four annual measures of salmon survival (tab. 2). The regression analysis found that Oregon OPI hatchery coho salmon marine survival was negatively correlated with the predicted number of salmon eaten (regression, $p = 0.05$, $R^2 = 0.42$). However, fall Chinook salmon jack counts at Bonneville Dam were only weakly related to the predicted numbers of salmon eaten ($p = 0.18$, $R^2 = 0.16$), and spring and summer Chinook salmon jack counts at Bonneville Dam were poorly related to the model predictions; $p = 0.91$, $R^2 = 0.0$ and $p = 0.28$, $R^2 = 0.05$, respectively.

The results of these simple regressions indicate that the simulation trophic model did not accurately mimic the observed variability in salmon marine survival. However, if average spring (May/June) Columbia River flows were included with the model-predicted numbers of salmon eaten in a multiple regression model, significant predictive relationships were obtained for OPI hatchery coho salmon smolt to adult returns ($p = 0.01$, $R^2 = 0.75$), and fall Chinook salmon jack counts ($p = 0.04$, $R^2 = 0.61$), but not spring and summer Chinook salmon jacks (fig. 8). In contrast, jack counts of Columbia River spring and summer Chinook salmon were strongly related only to May/June SST; $p = 0.002$, $R^2 = 0.79$ and $p = 0.01$, $R^2 = 0.61$, respectively (fig. 9).

TABLE 2

Average spring (May/June) abundance estimates of Pacific hake (*Merluccius productus*) and forage fishes off the mouth of the Columbia River from surface trawls 1998–2005. Trophic model predictions are the annual number of salmon eaten from 1 April through 1 August, along with observed coho salmon (*Oncorhynchus kisutch*) hatchery Oregon Production Index (OPI) area percent smolt to adult returns (SAR), and Bonneville Dam spring, summer, and fall Chinook salmon (*O. tshawytscha*) jack counts (corrected for year of ocean entry).

Year	Model prediction			Observed					
	Pacific hake	Forage fish	Salmon eaten	Coho salmon OPI % SAR	Spring Chinook salmon	Summer Chinook salmon	Fall Chinook salmon	Average Columbia River May/June flows (m ³ /sec)	Average May/June SST anomaly
1998	47,655,442	8,867,411	43,572,056	1.09	11,081	2905	23,582	10,082	0.28
1999	3,266,796	7,508,749	4,841,367	2.29	28,472	10450	55,538	10,497	-0.94
2000	81,414	1,378,052,066	31,283	4.33	22,000	11840	74,496	7,695	-0.26
2001	144,068	4,280,770,092	26,110	2.47	11,308	6141	40,215	4,621	-0.49
2002	505,760	1,202,111,144	212,987	3.76	22,245	10058	47,722	8,913	-0.42
2003	7,882,295	2,984,177,499	1,909,801	2.58	16,928	9501	38,557	7,991	-0.26
2004	3,065,483	513,088,377	2,223,774	1.89	7,016	3439	21,214	7,293	1.00
2005	544,005	598,909,525	345,270	2.01	3,856	3,407	25,549	7,461	1.10

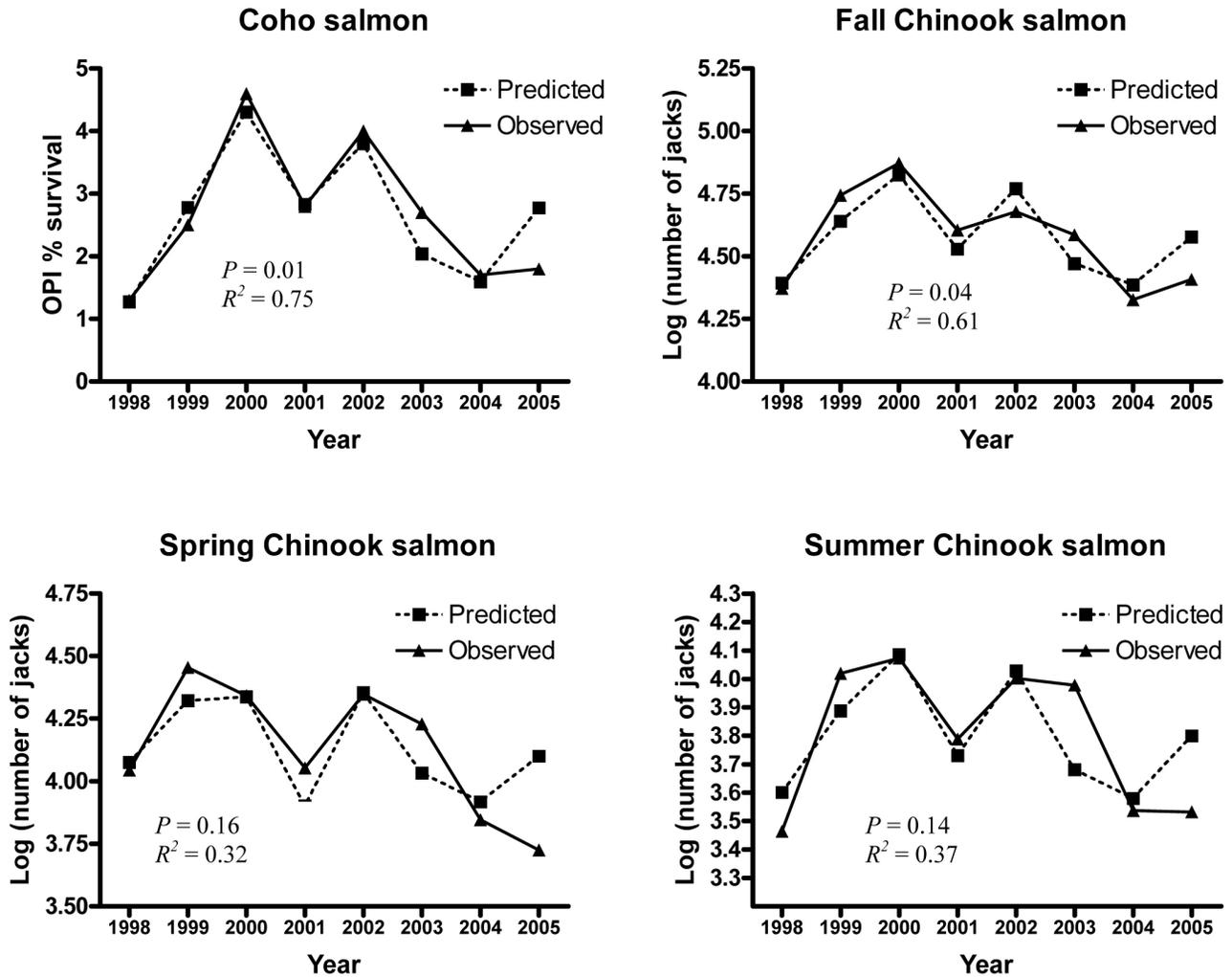


Figure 8. The relationship between observed marine survival of Oregon Production Index hatchery coho salmon (*Oncorhynchus kisutch*), and Columbia River fall, spring, and summer Chinook salmon (*O. tshawytscha*) jack counts versus values predicted from multiple regression using trophic model output and Columbia River flows.

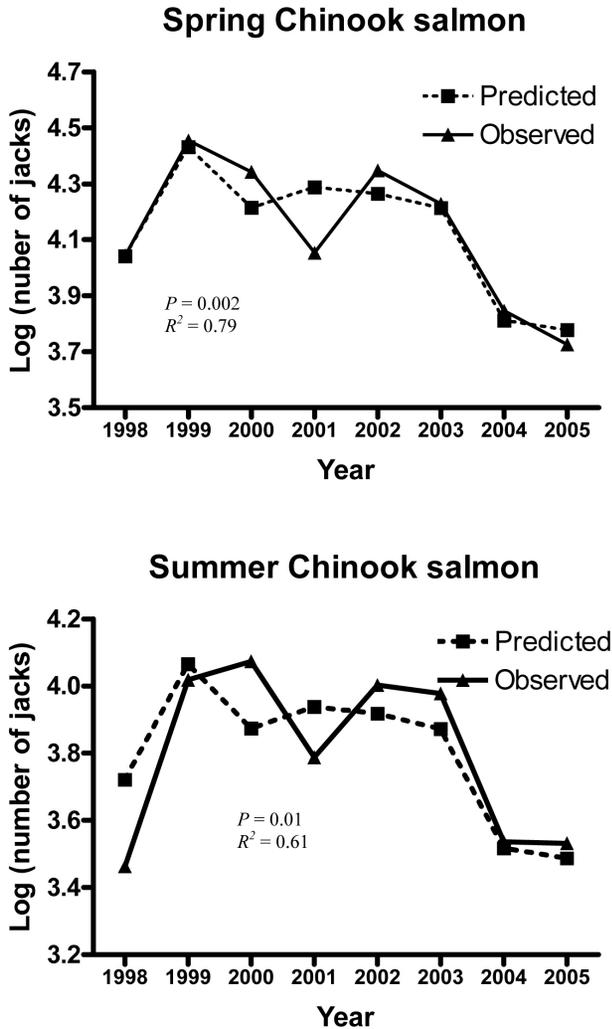


Figure 9. The relationship between observed jack counts of Columbia River spring and summer Chinook salmon (*Oncorhynchus tshawytscha*), and that predicted using average annual May/June sea surface temperatures collected off the Columbia River 1998–2005.

DISCUSSION

The goal of this study was to evaluate if predation by Pacific hake could be responsible for a large portion of the marine mortality of Columbia River salmon smolts, and if forage fish populations play a role in this mortality. We also wanted to investigate if a simple trophic predation model could replicate observed annual salmon marine survival using the hake and forage fish population data collected off the Columbia River (Emmett et al. 2006).

The model predicted relatively poor salmon survival when hake populations were abundant and forage fish populations were low in the study area. The model also predicted relatively low salmon mortality when hake were abundant, provided that forage fish were very abundant (~100 times more abundant than hake). Overall,

the model indicated that hake ate relatively few salmon smolts relative to the number migrating out of the Columbia River. However, our study area was relatively small compared to the coastal area that salmon smolts migrate through on their way north (Washington and British Columbia, Canada). If hake and forage fish densities in the coastal area are similar to those off the Columbia River, then total salmon mortalities directly related to hake predation would be proportionally higher than our estimates. Similar studies on the abundance of hake and forage fish in other locations would be of value.

A factor that strongly influences model results is the variable *Feeding Rate*, which alters the percentage of forage fish consumed by each hake as forage fish populations fluctuate. For example, when forage fish and salmon become less abundant, *Feeding Rate* declines and predators consume fewer forage fish and salmon. While stomach data indicate that the rate at which hake consume forage fish declines as forage fish become less abundant, we presently have only seven annual observations on how predator *Feeding Rate* actually changes with fluctuating predator/forage fish numbers. Laboratory studies of hake feeding at different prey concentrations would be helpful. Other estimated constants, such as residence time and number of smolts, when changed, produced smaller model responses. For example, a doubling of residence time doubled the number of salmon smolts eaten. However, holding forage fish densities constant but doubling the number of smolts did not double the number of smolts eaten, indicating that a possible “swamping” of predators can occur.

Feeding rates of large piscivorous predatory fishes are strongly affected by turbidity, while feeding rates of small fishes (juvenile salmon and forage fish) are not (De Robertis et al. 2003). In freshwater and estuarine habitats, juvenile salmon have been shown to be less vulnerable to predation at high turbidity levels (Gregory and Levings 1998). Coastal survey data indicate that juvenile salmon and forage fish are generally most abundant in nearshore turbid environments (Brodeur et al. 2004; Emmett et al. 2006), suggesting these fishes may use turbid marine waters to evade predators and for feeding. These nearshore areas also have higher zooplankton densities than offshore habitats (Lamb and Peterson 2005). We did not include turbidity in the simulation model, but doing so seems a sensible extension and it would be useful for future oceanographic surveys to measure turbidity. Laboratory experiments of predator/forage fish/juvenile salmon feeding interactions under various turbidity conditions in the Columbia River plume would also be valuable. We suspect that coastal turbidity levels are directly related to average May/June SSTs and upwelling, and to the high correlation between SSTs and spring and summer Chinook salmon jack counts.

The predictions from the simulation model correlated well with the marine survival of coho and fall Chinook salmon, but only after Columbia River flows were included in a multiple regression model. This suggests that Columbia River flows strongly influence predator/prey interactions in the Columbia River plume. Several mechanisms could be at work. Under high flow conditions juvenile salmonids would be carried quickly out of the study area and away from predators (see Pearcy 1992). Furthermore, the plume water is generally more turbid when flows are high, thus limiting Pacific hake and other predators' ability to see and capture near-surface prey (salmonids) (Gregory 1993; Gregory and Levings 1998; De Robertis et al. 2003).

In our model, we estimated that the total number of juvenile salmonids leaving the Columbia River was 100 million/year, with daily migration reflecting the numbers passing Bonneville Dam. While sufficient for this simple modeling effort, accurate estimates of the number of juvenile salmon migrating out of the Columbia River on a daily and annual basis would be extremely valuable for this model and Columbia River salmon management. Salmon runs in the Columbia River are dominated by hatchery production, so while adult salmon run sizes fluctuated widely during our study period, the actual number of juvenile salmonids migrating to sea probably did not fluctuate much. However, having the actual number of salmon smolts migrating to sea that were produced from large adult salmon returns would help parameterize our model.

The model was particularly poor at predicting salmon marine survival in 2005 (fig. 8). During that year, anomalous ocean conditions existed off the Pacific Northwest (Geophysical Research Letters special publication: <http://www.agu.org/contents/sc/ViewCollection.do?collectionCode=CALIFCUR1&journalCode=GL>). In particular, upwelling was delayed (Kosro et al. 2006; Schwing et al. 2006), zooplankton populations were low and contained few northern taxa (Mackas et al. 2006), and fish (Brodeur et al. 2006), marine birds (Sydeman et al. 2006), and marine mammals (Newell and Cowles 2006; Weise et al. 2006) were negatively affected. From these 2005 reports it was clear that the ecosystem off the Northwest was not operating "normally" but with conditions similar to an El Niño period, suggesting that during 2005 another biological mechanism, perhaps predation by Humboldt squid (*Dosidicus gigas*) or sharks (Brodeur et al. 2006), may have provided additional sources of salmon mortality.

The general trophic model we developed provides a good beginning framework to understand interactions between forage fish, predators, environmental conditions, and juvenile salmon off the Columbia River and the Pacific Northwest. As discussed above, many refinements

need to be made to create a more "realistic" model. This includes additional information on fish encounter rates and feeding efficiencies, turbidity effects, Columbia River plume size and structure, large predator/prey patches, predator and forage fish population abundances, the actual number of juvenile salmon migrating to the ocean, and their migration rates. To make the model representative of the entire Pacific Northwest, we need additional information on Pacific hake, such as better information on feeding rate, population estimates on the shelf during spring and summer, feeding behavior, and forage fish abundance. We also need information on other large fish predators, predatory birds and mammals, and forage fishes for the entire Pacific Northwest, including British Columbia. Many predators, including hake and mackerel, also eat large numbers of euphausiids. Unfortunately, estimates of Northwest euphausiid populations are presently not available, but euphausiids are important in this ecosystem because they are a primary prey for hake (Tanasichuk 2002) and many other species, and may determine the spatial distribution and movements of hake (Benson et al. 2002; Swartzman and Hickey 2003) and other predators.

This simple ecosystem trophic model is a preliminary investigation into how the Pacific Northwest pelagic fish ecosystem functions. While the trophic model appears to successfully predict marine survival of two Columbia River species/stocks of salmon, it was not successful for two other stocks. This indicates that Columbia River salmon species/stocks probably do not behave similarly nor inhabit identical coastal marine habitats. Other ecosystem processes (e.g., feeding and growth) or other piscivorous predators (e.g., marine mammals or birds) are probably acting to limit marine survival for these salmon stocks. As fishery managers move to ecosystem-based fishery management, it will be essential to identify and quantify these processes. Relatively simple trophic models, similar to the one presented here, will be useful tools to clarify which ecosystem processes are important.

CONCLUSIONS

Our trophic model indicates that predation by Pacific hake, interacting with forage fish and juvenile salmonids, and influenced by Columbia River May/June flows may help determine OPI coho salmon and Columbia River fall Chinook salmon marine survival. River flows and associated turbidity and other physical factors probably play an important role in these predator/prey interactions, and are influenced by Columbia River hydropower operations. Future ecosystem research should further quantify existing variables and explore whether adding other variables to this or other ecosystem models can produce more accurate predictions of salmon marine survival. Furthermore, this type of model would be a

useful tool to evaluate how alternative Columbia River hydropower operations could affect predator/prey interactions in the estuary and plume, and thus, salmon marine survival.

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