AN ABSTRACT OF THE DISSERTATION OF

Robert L. Emmett for the degree of Doctor of Philosophy in Fisheries Science presented on March 21, 2006.
Title: The Relationships Between Fluctuations in Oceanographic Conditions, Forage Fishes, Predatory Fishes, Predator Food Habits, and Juvenile Salmonid Marine Survival off the Columbia River.

Abstract approved:

David B. Sampson

Salmonid run sizes are strongly affected by their early marine stage. Fully understanding the life history of salmonids means understanding how they interact with their marine environment and with other fishes. Changes in the biological and physical environment off the Columbia River region affects the distribution and abundance of predatory fishes and their feeding, forage fishes, and juvenile salmonid marine survival. From 1998-2004, forage fish and predatory fish distribution and abundance off the Columbia River was quantified by surface trawling at night during spring/summer. The effect of predation on salmonids was measured by stomach analysis of predatory fishes. During the study period (1998-2004), forage fishes increased in abundance by orders of magnitude and were strongly related to the abundance of cold-water copepods the previous year. Higher forage fish populations were also linked to cooler ocean conditions and perhaps fewer predatory Pacific hake (*Merluccius productus*). Most forage fishes were distributed nearshore while predators had a more offshore distribution. Pacific hake was most abundant in 1998, 2003, and 2004; warm ocean years. Jack mackerel (*Trachurus symmetricus*) was most abundant during 1999-2002; relatively cool ocean years. Deep (50-m) ocean temperatures and the date of the spring transition, when nearshore currents switched from northward to southward, were good predictors of Pacific hake abundance in the study area. Forage fish or salmonid occurrence in a haul was negatively related to the occurrence of predators. Pacific hake and jack mackerel ate primarily euphausiids and small fishes. Salmonids were rarely eaten by either predator. However, because the Pacific hake population can be very large, hake predation can be a significant source of juvenile salmon mortality off the Columbia River during some years. A trophic model showed that marine mortality of Columbia River juvenile salmonids may be related to the abundance of Pacific hake and forage fishes. A multiple regression using the predictions from the trophic model of annual numbers of juvenile salmonids eaten by hake and Columbia River spring flows as independent variables, accounted for much of the variation observed in the annual marine survival of Columbia River coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*), the dependent variable. Future research should identify the physical and biological forces that alter the feeding habits, migration and movements of Pacific hake and jack mackerel off the Northwest, and how Columbia River flows affect trophic interactions.

The Relationships Between Fluctuations in Oceanographic Conditions, Forage Fishes, Predatory Fishes, Predator Food Habits, and Juvenile Salmonid Marine Survival off the Columbia River

by
Robert L. Emmett

A DISSERTATION

submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March 21, 2006

Commencement June 2006

Doctor of Philosophy dissertation of Robert L. Emmett presented on March 21, 2006

APPROVED:

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Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Robert L Emmett, Author

ACKNOWLEDGEMENTS

First, I wish to thank David Sampson, my major advisor, and my graduate committee, William Pearcy, William Peterson, Douglas Markle, and John Bolte, for their excellent advice and their extensive patience. This dissertation has been a long time coming. My supervisors at National Marine Fisheries Service, Northwest Fisheries Science Center, Mike Schiewe, and Edmundo Casillas and the Center Director, Usha Varanasi, provided encouragement, financial support, and time to pursue this Ph.D. Conversations with William Peterson on a variety of topics were always fruitful, motivating, and fun.

Many people willingly assisted with this project, they include Joe Fisher, Todd Miller, Cheryl Morgan, Leah Feinberg, Jesse Lamb, Toby Auth, Leah Stamatiou, Jason Phillips, Ben Sandford, William Muir, Jeff Muir, and Laurie Weitkamp. Discussions and encouragement from Rick Brodeur were always helpful. Very large thanks to Susan Hinton for always being ready and able to help with, and accomplish, the impossible.

This work would have not been possible with the able assistance of Captains D. Parker and R. Williams and the crews of the F/V Sea Eagle and F/V Piky, respectively.

I can not thank Paul Bentley and Greg Krutzikowsky enough for everything they did. They put in many days at sea in good and bad weather, and helped to collect these data. They provide assistance with all aspects of the research, and always made it fun even under harsh conditions.

Finally I would like to thank my family for their support through this long process, particularly my days at sea, in the library, or in thought. To my wife, Amy, I am most grateful. Through all of this lengthy process she was unwaveringly considerate, supportive, and understanding. Without her assistance this Ph.D. dissertation would not have been completed.

DEDICATION

This dissertation is dedicated to my mother and father. The 12 foot aluminum boat they bought began a ride I am still on.

The ocean is the big chomp. Annie Dillard, Pilgrim at Tinker Creek

CONTRIBUTION OF AUTHORS

Richard Brodeur (NOAA Fisheries, Newport, OR) provided historical information on pelagic fish abundances in the 1980s used in Chapter 1. Paul Bentley (NOAA Fisheries, Hammond, OR) and Greg Kurtzikowsky (Cooperative Institute for Marine Resource Studies, Newport, OR) assisted in all aspects of sample collections taken during 1998-2003 and used in Chapters 2 and 3. Greg Kurtzikowsky helped with database creation and management, and fish stomach analysis in Chapters 4. Dr. David Sampson was instrumental in the development of the trophic model in Chapter 5.

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The Relationships Between Fluctuations in Oceanographic Conditions, Forage Fishes, Predatory Fishes, Predator Food Habits, and Juvenile Salmonid Marine Survival off the Columbia River

INTRODUCTION

To some degree, this dissertation actually began in 1977. This was when I started working for the National Marine Fisheries Service (NMFS) at Hammond, Oregon, a very small town located at the mouth of the Columbia River. The Columbia River once had the largest salmon run in the continental U.S. In 1977, Northwest salmon runs were still relatively large and supported healthy commercial and sport fisheries. Little did I know at the time, but the oceanic regime was shifting (Mantua et al. 1997), and much lower salmon runs and Endangered Species Act listings were the future.

After staring my NMFS job, I often went salmon fishing in the adjacent ocean. From 1977 through 1982, large numbers of forage fishes, particular northern anchovy (*Engraulis mordax*) were apparent in the ocean and estuary. Bait-balls were common and easy to spot, by watching for foraging birds. Most importantly, the salmon fishing was great. However, the effect of poor ocean conditions soon became very evident during the strong 1983 El Niño. During that year, it was obvious that the ocean was not the same as the one I had observed in previous years. In 1983, forage fishes were clearly not abundant and all the large fauna that depended on this resource suffered. Not only were the adult salmon skinny and in poor condition (Pearcy 1992), but seabird reproduction was much reduced and deaths of common murre (*Uria aalge*) increased (Graybill and Hodder 1985). I hooked numerous gulls and common murres while fishing for salmon in 1983, something that rarely occurred during previous years. By late summer it was difficult to get any bait [northern anchovy or Pacific herring, (*Clupea pallasii*)] below the surface quick enough before it was preyed upon by a diving seabird. I was not surprised when salmon returns resulting from the 1983 outmigrants were extremely low. From these ocean observations, and the many since, I have been interested in predator/prey interactions in the nearshore ocean and the role these intereactions play in the marine survival of salmonids.

Federal and State natural resource agencies have spent lots of money addressing habitat issues related to reduced freshwater salmonid production and mortality, but relatively little on salmon marine habitat issues. Nonetheless, salmon marine survival reportedly equals freshwater survival (Bradford 1997). As such, small increases in marine survival can produce large increases in adult run size. As noted by Ryding and Skalski (1999), small increases in freshwater survival of smolts, from 50 to 51%, would increase overall adult run sizes by 2%, (given the same marine survival rate), but small increases in smolt marine survival rate, from 1 to 2%, would double adult returns. If we knew what controls salmon marine survival, and could influence it even a small amount, the results could significantly help depressed salmon runs.

While there is some evidence that over-winter mortality may play a role in salmon marine survival (Beamish and Mahnken 2001), there is also evidence that indicates salmonid marine survival is determined early in the migrational period – probably the first couple of months at sea (Pearcy 1992; Logerwell 2003). The strongest evidence for this early marine “critical period” is that return of precocious “jacks”, which only spend one summer [e.g., coho salmon (*Oncorhynchus kisutch*)] or one summer and one winter in the ocean [e.g., Chinook salmon (*O. tshawytscha*)], are highly correlated with adult salmon returns, indicating that most juvenile salmon mortality must be occurring early in the marine environment (Pearcy 1992; Weitkamp 2004).

Salmon marine survival has been linked to physical oceanographic conditions (Ryding and Skalski 1999; Cole 2000; Logerwell 2003), but the biological/physical mechanisms driving salmon marine survival and large fluctuations in marine fish recruitment have not been identified (Baumann 1998). For example, cold ocean sea surface temperatures are correlated with good salmon marine survival (Cole 2000; Logerwell et al. 2003), but the mechanisms by which these cooler ocean temperatures actually affect survival is uncertain. It is assumed to be linked to increased coastal ocean productivity, which in turn increases juvenile salmon forage and salmon growth rates and thus survival. However, growth information from various years (warm and cold), indicate that juvenile salmonids are growing at near peak rates, independent of year (approximately 2%/day) (Fisher and Pearcy 1988, 1995, 2005; J. Fisher, Oregon State Univ., pers comm.).

Marine predation is thought to have a major influence on salmon marine survival and eventual adult returns (Parker 1971; Fisher and Pearcy 1988; Pearcy 1992; Beamish and Neville 2001; Willette et al. 2001; Weitkamp 2004). However, while seabirds and marine mammals are known to feed on juvenile salmonids (Matthews 1983; Emmett 1997; Riemer and Brown 1997; Roby et al. 2003), their feeding alone does not appear to account for all the juvenile salmon marine mortality that occurs. While predation by fishes on juvenile salmonids has been found to be a significant source of mortality in some areas (Beacham 1990; Beamish et al. 1992; Beamish and Neville 1995, 2001;

Willette et al. 2001) it is not well documented off the Oregon/Washington coast (Brodeur et al. 1987; Pearcy 1992).

This research investigates the proposition that predation from marine fishes has a large impact on marine survival of Columbia River salmon. It also investigates how forage fishes and oceanographic conditions may affect predator fish distributions, their abundances and food habits, and thus juvenile salmon marine survival.

DOCTORAL RESEARCH

The primary objective of this dissertation research was to test the working hypothesis that predatory and forage fishes affect marine survival of Columbia River salmon. To accomplish this I measured the abundance and distribution of predatory fishes and forage fishes off the Columbia River, the oceanographic conditions that affect forage fish and predatory fish abundance, and the food habits of predatory fishes. These factors were then integrated using a trophic model to explore whether fish trophic interactions were related to marine survival of Columbia River juvenile salmon.

DISSERTATION ORGANIZATION

The research was broken into five separate work elements and written in separate, publishable chapters.

Chapter One: “Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions”, has been published (Emmett and Brodeur 2000). Using historical and some recent pelagic fish catch and population information, this paper analyzes the relationship between predatory fish and forage fish abundance and ocean conditions.

Chapter Two: “The relationship between fluctuations in the abundance of forage fishes and juvenile salmonids off the Columbia River, changing oceanographic conditions, and salmon marine survival, 1998-2004”, identifies the relationship between fluctuations in forage fish abundance and oceanographic conditions. It also discusses the “alternative prey” hypothesis and presents information on the relationship between oceanographic conditions, forage fish abundance and salmon marine survival.

Chapter Three; “Abundance and distribution of pelagic piscivorous fishes in the Columbia River Plume during spring/early summer 1998-2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids”, focuses on the temporal and spatial distributions of predator, forage fishes, and juvenile salmonids. This chapter also presents information on fish distributions relative to oceanographic conditions. This paper has been published in Progress in Oceanography (Emmett et al. 2006).

Chapter Four: “Nocturnal feeding of migratory Pacific hake (*Merluccius productus*) and jack mackerel (*Trachurus symmetricus*) off the mouth of the Columbia River, 1998-2004”, focuses on the feeding habits of the most common large fish predators off Oregon during the study period. It presents information on the direct feeding of Pacific hake and jack mackerel on juvenile salmonids and forage fishes.

Chapter Five: "The relationship between predatory fishes, forage fishes, and juvenile salmonid marine survival off the Columbia River: a trophic model analysis", presents a trophic model of the species interactions identified from field and laboratory data.

Chapter Six: "General discussion", is a short discussion of the key finding from this research, and recommendations for future research.

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Chapter 1. Recent Changes in the Pelagic Nekton Community off Oregon and Washington in Relation to Some Physical Oceanographic Conditions

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Bulletin of the North Pacific Anadromous Fish Commission
Suite 502, 889 West Pender Street
Vancouver, British Columbia
Canada, V6C 3B2
Volume 2: 11-20

ABSTRACT

Since approximately 1977, there have been dramatic declines in West Coast salmonid (*Oncorhynchus* spp.) resources and salmonid marine survival. At the same time, there are indications that the pelagic nekton fauna off Oregon and Washington has shifted in species composition and abundance since the late 1970s. While Pacific hake (*Merluccius productus)*, Pacific herring (*Clupea pallasii*), American shad (*Alosa sapidissima*), chub (*Scomber japonicus*), and jack mackerel *(Trachurus symmetricus*), and Pacific sardine (*Sardinops sagax*) populations off the Northwest coast have increased in abundance since 1977, ocean survival of salmonids, and populations of northern anchovy (*Engraulis mordax*), eulachon (*Thaleichthys pacificus*), and market squid (*Loligo opalescens*) declined. Northwest sea surface temperatures have shown a strong warming trend since 1977. Our results suggest that salmon marine survival is affected by the interplay between biological and physical factors in the northern California Current.

INTRODUCTION

Recent studies indicate that the biological community structure and dynamics of the California Current ecosystem are affected by a complex series of atmospheric/ocean interactions occurring remotely and locally at varying time scales (Francis and Hare 1994; Brodeur et al. 1996). There is also evidence that both lower and higher trophic levels undergo substantial shifts in abundance and species composition, and that these changes are usually out of phase with those occurring in the Gulf of Alaska (Hollowed and Wooster 1992, 1995; Brodeur et al. 1996; Hare et al. 1999). Examples of large fluctuations in pelagic fish composition include long-term changes in the abundance of northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) populations in the California Current system (Baumgartner et al. 1992) and the synchronous rise and fall of anchovy and sardine populations off Peru and other regions (Lluch-Belda et al. 1992). Furthermore, large annual fluctuations in pelagic and demersal fish recruitment have been documented for the Northeast Pacific Ocean (Hollowed et al. 1987; McFarlane and Beamish 1992; Beamish 1993).

Since approximately 1977, there have been dramatic declines in West Coast salmonid (*Oncorhynchus* spp.) populations. While much of this decline undoubtedly relates to loss and impairment of freshwater habitat (Gregory and Bisson 1997), ocean conditions have changed markedly since the 1970s, coinciding with the declines in salmonid marine survival (Pearcy 1992, 1997; Francis and Hare 1994; Beamish et al. 1995; Hare et al. 1999). At the same time, there are indications that the pelagic nekton off Oregon and Washington has shifted in both species composition and abundance since the late 1970s. Evidence includes reduced abundance of northern anchovy and market squid (*Loligo opalescens*), and the increased abundance of Pacific sardine, chub mackerel (*Scomber japonicus*), jack mackerel *(Trachurus symmetricus*), and Pacific hake (*Merluccius productus)* (NMFS unpublished data, and personal observations).

The purpose of this paper is to summarize pelagic nekton collections off Oregon and Washington since 1977, and relate these data to ocean environmental conditions. We also relate changes in a Northwest salmon population [i.e., ocean survival for Oregon

Production Index Area coho salmon (*Oncorhynchus kisutch*)] to changes in the abundance and species composition of the pelagic nekton.

METHODS AND MATERIALS

Nekton data

Pelagic nekton abundances and species compositions came from four different sources. The first was the direct measurement of Pacific hake and incidental catches of pelagic fishes captured during the National Marine Fisheries Service's (NMFS) Triennial Trawl Survey of groundfish resources on the Northwest shelf (Dark and Wilkins 1994; Wilkins 1996). Triennial survey data were available from 1977 through 1998. Although the survey was not designed to target small pelagic species, the survey consists of a randomized design with standardized effort each year, thus permitting comparisons of catches between survey periods. All trawling was done using a Nor'Eastern trawl constructed with 8.9-cm nylon mesh in the body and lined with 3.2-cm mesh to retain small fish. Surveys were conducted from July to October from northern Washington to Monterey Bay, California. Typical trawl sampling locations and the geographic range of fishery statistical regions are shown in Figure 1.1. For this study, only data from the Columbia Statistical Region, which extends from northern Washington to southern Oregon, were used. This region overlaps with the Oregon Production Index Area used to estimate coho salmon marine survival and all other pelagic nekton data sources used in this study.

The second source of data on pelagic nekton abundance off Oregon and Washington was from purse seine collections conducted from May to September of 1981 to 1985 by Oregon State University (OSU) [see Brodeur and Pearcy (1986) and Pearcy and Fisher (1990) for sampling dates and details]. Briefly, fine mesh (32-mm) herring purse seines were fished along east-west transects from Cape Flattery off Northern Washington to Cape Blanco off Oregon. The net size varied from 457 m to 495 m in length and 20 m to 60 m in depth among the 15 cruises. It is important to note that most of these collections were conducted during daylight. These data will be referred to as the OSU 1981-1985 Survey. Locations of their sampling stations are shown in Figure 1.2.

The third data set consists of the nekton captured during a NMFS pelagic trawl survey for juvenile salmonids off Washington and Oregon during June and September of 1998, and May, June, and September of 1999. This survey sampled as far north as La Push, WA and south to Cape Perpetua, OR (Fig. 1.2). Sampling consisted of one-half hour surface tows of a 264 Nordic rope trawl (built by Nor'Eastern Trawl Systems, Inc.) along transects perpendicular from shore, at a variety of locations. The Nordic rope trawl, which has variable mesh sizes (162.6 cm at mouth to 8.9 cm at cod end with a 1.5 cm cod-end liner), has a fishing mouth opening of approximately 30 m x 20 m. Initial trawls were conducted in as shallow water as was possible (30 m depth); farthest seaward sampling was conducted approximately 50 km from shore. Except for a couple of trawls, all sampling was conducted during daylight. These data will be referred to as the NMFS Salmon Survey.

The fourth data set came from the NMFS 1998 and 1999 pelagic and midwater trawling survey of juvenile salmonid fish predators off the mouth of the Columbia River (Fig. 1.2). This sampling consisted of trawling for two nights every two weeks from April to mid-August. Initial sampling gear was a standard Pacific hake net, which is a large variable-mesh rope trawl (mouth opening 60 m x 28 m) fished as close to the surface as possible. However, from mid-June on, a Nordic 264 surface rope trawl (as in the NMFS salmon survey) was used. All sampling during this study was conducted chiefly at night. Pacific hake and many other semi-demersal and pelagic species have nocturnal behavior and move near the surface, where juvenile salmonids appear to reside, during night. These data will be referred to as the NMFS 1998 Predator Survey.

To compare among the last three data sets, and to adjust for different gear (purse seine catches and trawl catches) and effort, all data were transformed to percentage of total catch for a particular year. The NMFS triennial survey data, however, are presented as estimates of species biomass by metric ton (mt) (Wilkins 1996, and personal communication, Alaska Fisheries Science Center, Seattle, WA). Finally, to examine long-term changes in small fish and squid commonly eaten by predatory fishes and birds, these species numbers were summed and represented as a forage nekton category while large pisciverous fishes were grouped as predators.

Hatchery coho salmon ocean survival data from the Oregon Production Index Area were used as a general description of annual ocean salmon survival. However, wild salmon generally survive at much higher rates (Nickelson 1986) and salmonid ocean survival can vary widely depending on species, stock, and location. Percent hatchery coho salmon marine survival was determined by dividing estimated adult hatchery returns (catch and escapement) by number of juvenile hatchery releases (see Pacific Fishery Management Council 2000 for data).

Physical data

Physical oceanographic data were obtained from a variety of sources. Of particular interest were long-term records of physical conditions relevant to the Pacific Northwest. Sea surface temperatures were obtained from the Scripps Institute of Oceanography Shore Station web site (http://www-mlrg.ucsd.edu/shoresta.html) for Charleston, OR, and Neah Bay, WA (ftp://nemo.ucsd.edu/pub/shore/monthly_means/). Upwelling data were obtained from NOAA's Pacific Fishery Environmental Laboratory, Pacific Grove, CA (Jerrold Norton, PFEL, pers. comm., and http://www.pfeg.noaa.gov/index.html).

RESULTS

NMFS Triennial Trawl Survey

The estimated abundances of the dominant pelagic fishes, separated by adult size and feeding habits into either forage fishes or predators, during the NMFS triennial trawl surveys indicate that a large change in the pelagic fish community occurred between 1977 and 1995 (Fig. 1.3). Pacific sardine, chub mackerel, jack mackerel, Pacific herring, American shad and Pacific hake increased in abundance while northern anchovy and eulachon (*Thaleichthys pacificus*) declined. The Pacific hake population showed over a five-fold increase, from less than 50,000 mt in 1977 to over 284,000 mt in 1995. Both forage nekton and predatory nekton increased substantially beginning in 1989 (Fig. 1.3).

There appears to be a relatively strong inverse relationship between jack mackerel abundance and coho salmon marine survival [linear regression of ln(jack mackerel abundance) on percent coho salmon marine survival, $P = 0.12$, $R^2 = 0.41$] given the small data set. There was an even stronger inverse relationship between Pacific hake abundance and coho salmon marine survival [linear regression of ln(Pacific hake abundance) on percent coho salmon marine survival, $P = 0.068$, $R^2 = 0.52$].

However, if we assume that hake predation on salmon is mediated by northern anchovy abundance (i.e., when anchovy is abundant, predation on salmonids is reduced), we can build a more realistic model of hake predation effects. The regression of ln(Pacific hake)-ln(northern anchovy) on percent coho salmon survival produces a $P = 0.01$ with a $R^2 = 0.62$ (Fig. 1.4).

OSU 1981-1985 Survey

The pelagic nekton species composition off Oregon and Washington also changed from 1981 to 1985. The percentage of forage nekton (Fig. 1.5), in particular, varied greatly among the five years. In 1981, forage nekton comprised over 87% of the catch, dropped to 8% in 1984, and then rebounded to 52% in 1985. Northern anchovy showed the largest drop in percent abundance from 1981 to 1985, declining from 34% to 3%, respectively. One forage species, Pacific herring, increased from 7.2% of the catches in 1981 to 19.3% in 1985. Meanwhile, the large predatory fish Pacific hake showed increases in relative abundance from 1981 to 1985 (Fig. 1.5). Chub and jack mackerel were very large percentages of the catches only in 1983 and 1984, which were warm El Niño years.

Juvenile salmonids were an important component of the pelagic nekton community during these annual surveys (Fig. 1.6). Juvenile coho salmon were the most abundant salmonid captured, and were consistently more abundant than juvenile Chinook salmon (*O. tshawytscha*). Coho salmon were particularly abundant in 1985 (19.5% of the total pelagic nekton catch). Chinook salmon were also a large percentage of the catch in 1985 (5.6%).

NMFS Salmon Survey

The composition of pelagic nekton captured during the NMFS 1998/1999 salmon survey were much different than that identified by the OSU 1981-1985 surveys. Particularly striking was the dominance of Pacific sardine in the catches, 18% and 59% in 1998 and 1999, respectively (Fig. 1.7), whereas sardines were rarely captured during the OSU 1981-1985 surveys. Other dominant forage nekton included Pacific herring, 59% of the catch in 1998 and 18% in 1999. In contrast, market squid (*Loligo opalescens*), an important component of the pelagic nekton in the early 1980s (Brodeur and Pearcy 1992), were only 2% and 7% of the NMFS catches in 1998 and 1999, respectively. Overall, forage nekton composed over 90% of the catches during 1998 and 1999. However, the forage nekton species were different than those during the OSU 1981-1985 surveys. The major predator in 1998 was Pacific hake, but it only comprised 2.3% of the total catch in 1998 and 0.3% in 1999 (Fig. 1.7).

Unlike the OSU 1981-1985 survey, few juvenile coho salmon were captured and they comprised a very small portion of the catches (0.4% in 1998, and 1.2% in 1999) (Fig. 1.6). However, the percentage of the catch made up by juvenile Chinook salmon (3.0% in 1998 and 5.0% 1999) was not much different than that observed during the OSU 1981-1985 surveys.

NMFS 1998 Predator Survey

This survey showed similar catches to the NMFS Salmon Survey, with Pacific sardine and Pacific herring being the dominant forage nekton (Fig. 1.7). However, this survey also caught large numbers of Pacific hake (33% and 8% of the catch in 1998 and 1999, respectively). This was probably related to the timing of the collections, which were conducted at night. The percentages of forage fish catches were lower than the NMFS salmon survey due to the preponderance of adult Pacific hake and jack mackerel, but both surveys were relatively similar in species composition.

Physical data

Upwelling

Seasonal upwelling has been shown to be a significant predictor of salmon ocean survival in the past (Nickelson 1986; Lawson 1997). We used cumulative sum plots of upwelling anomalies at 45°N 125°W as an indicator of upwelling intensity and trends (Fig. 1.8). From about 1982 until 1998, spring upwelling anomalies were consistently negative (less spring upwelling). Fall upwelling during the same period showed the opposite trend with relatively consistent positive anomalies (Fig. 1.8). Summer upwelling showed no consistent trends.

Sea Surface Temperatures

Lawson (1997) found that winter sea surface temperatures at Charleston, OR explained a significant amount of the variation in salmon ocean survival. While sea surface temperatures (SST) at Charleston, OR appear to be warmer since 1985, early trends in SST data are unclear because of missed data points. The more complete SST series from Neah Bay, however, showed a strong warming trend since 1977, with April-May averages rising from slightly below 10.0^{o} C in 1977 to 11.8^{o} C in 1994 (Fig. 1.9). When we plotted Neah Bay average SST and Pacific hake abundance, as measured by trawl survey in the Columbia Statistical Region (Fig. 1.9), we found that as summer SST increased, Pacific hake became more abundant.

DISCUSSION

During the past 20 years many studies have indicated that changing ocean conditions play a large role in the recent decline in abundance of many salmonid stocks (Pearcy 1992, 1997; Beamish et al. 1995; Coronado and Hilborn 1998). While physical factors and food supply are generally thought to be important mechanisms regulating salmon early ocean survival, interspecific interactions (competition and predation) with other nekton species are coming under increasing scrutiny (Pearcy 1992; Emmett 1997; Fresh 1997; Nagasawa 1998). Unfortunately, no regular systematic surveys of the pelagic nekton and the associated oceanographic physical conditions were made off the Oregon/Washington coast from 1986 to 1997. In this paper, we have examined changes in pelagic nekton species composition and biomass trends over the last two decades off the Pacific Northwest using a variety of data sources. While the data compiled during this study were from different fishing survey designs, gear types and years, they nevertheless provide evidence that the pelagic nekton community of the northern California Current has changed dramatically since the late 1970s.

The decline in the percentage of coho salmon in the pelagic nekton community off Oregon and Washington from the early 1980s to 1998/1999 probably reflects a variety of factors. A major factor has been the reduced number of hatchery salmon being released. In the early 1980s commercial (for profit) salmon hatcheries were releasing millions of coho salmon smolts (Weitkamp et al. 1995), but now these hatcheries are shut down. Other causes of reduced ocean abundance of juvenile coho salmon include less freshwater production and decreased marine survival. The reduced percentage of chum salmon captured in 1998/1999 versus the 1980s may reflect their overall decline in abundance. However, while Columbia River and Hood Canal chum salmon stocks are presently listed as threatened, most coastal stocks do not appear to be declining in abundance (Johnson et al. 1997). The relatively stable percentages of Chinook salmon in nekton catches (between 1980s and 1998/1999) probably relates to continued large hatchery releases, adequate freshwater production, and perhaps better marine survival than coho salmon.

The NMFS triennial trawl survey results suggest that Pacific hake, Pacific herring, American shad, chub and jack mackerel, and Pacific sardine populations off the Pacific Northwest have increased, while northern anchovy and eulachon populations have decreased. These changes are concurrent with the decrease in survival of juvenile salmon. Although we do not have any direct evidence that this relationship is causal, species interactions undoubtedly occur, and probably play a role in determining pelagic nekton species composition. Off British Columbia, predation by increased numbers of Pacific hake since 1977 caused a marked decline in their primary forage fish, Pacific herring (Ware and McFarlane 1995). Furthermore, there appears to be a relationship between forage fish abundance and salmon ocean survival. Holtby (1988) showed that smolt-to-adult survival rates of Carnation Creek, B.C., coho salmon were significantly greater during years when age-1 Pacific herring were abundant in and around Barkley Sound, Canada. Our data also appear to support the Fisher and Pearcy (1988) hypothesis that increased predation, perhaps resulting from decreased alternative prey (i.e., forage fish such as anchovy), was responsible for the low coho salmon marine survival in the early 1980s.

The data presented here, unlike those for British Columbia waters, indicate that Pacific herring off Oregon and Washington have increased since the late 1980s, where northern anchovy has, until recently, been the dominant forage fish (Richardson 1981). The decline in northern anchovy may be related to a host of factors, including increased predation by Pacific hake and mackerel, competition with other similar sized species such as sardines and herring, or changes in wind stress, upwelling and other oceanographic conditions during spawning and larval development. Older and larger Pacific hake and mackerel feed on northern anchovy (Livingston and Alton 1982; MBC Applied Environmental Sciences 1987). We suggest that increased predation on northern anchovy has been a factor reducing its abundance since 1977. Furthermore, because anchovy have a smaller adult size than Pacific herring and Pacific sardines (Hart 1973), they may suffer a higher predation rate throughout their entire life history.

One of the most obvious changes that occurred in the pelagic nekton community off Oregon and Washington since 1977 is the present high abundance of Pacific sardines. Although they were reported as early as 1984 (Brodeur and Pearcy 1986), Pacific sardines apparently arrived in great numbers to waters of the Pacific Northwest sometime between 1989 and 1992 (Hargreaves et al. 1994). There is evidence that the West Coast population of Pacific sardines, which is centered in California, is rapidly increasing and has expanded its range north into British Columbia and even into Alaskan waters (Hargreaves et al. 1994; Beamish et al. 2000). Sardines are now spawning off Oregon and Washington (Bentley et al. 1996) and British Columbia (Beamish et al. 2000). At about the same time, the northern anchovy population in this region evidently declined (Emmett et al. 1997). They have declined from being one of the dominant fish caught in the early 1980s cruises to mainly an incidental species in the 1990s. Historically a relatively large population of northern anchovy used to spawn in the plume of the Columbia River (Richardson 1981), but spawning now appears to be restricted to a narrow nearshore area adjacent to Willapa Bay, WA (Emmett et al. 1997; unpublished data).

Pacific hake, one of the most abundant pelagic fish in the California Current system, also appears to be altering its range and distribution. Evidently, recent warmer ocean temperatures and slower southerly-flowing currents have prompted Pacific hake to migrate faster and earlier from their California spawning grounds (Dorn 1995; Ware and McFarlane 1995; McFarlane and Beamish 1999). There are also indications that Pacific hake may have shifted their spawning area farther north (Horne and Smith 1997; Beamish et al. 2000). Finally, Pacific hake has had several years of good recruitment since 1977, so that their overall abundance is relatively high (Dorn 1996; Wilkins 1996). The OSU purse seining survey and the NMFS salmon survey surface trawling were conducted primarily during daylight, and evidently underestimated Pacific hake abundance because of hake’s diel migrational behavior. During darkness Pacific hake migrate to the surface layer, where they are susceptible to capture by surface trawl during the NMFS predation study.

Chub and jack mackerel have also become an important component of the pelagic ecosystem off Oregon and Washington, at least during the summer months. They apparently invaded the region around the time of the 1983 El Niño and became the dominant fishes caught in the purse seine sampling during 1983 and 1984 (Brodeur and Pearcy 1986, 1992). Chub mackerel were also common in British Columbia at that time (Ashton et al. 1985) and in recent years, they have been found as far north as northern British Columbia (Beamish et al. 2000). Although a large proportion of the chub mackerel population is believed to return to Southern California in the winter to spawn, some chub mackerel eggs and larvae and have been found off Oregon (Emmett, unpublished data).

Perhaps the only study off Washington and Oregon comparable to ours in terms of spanning several decades was the analysis of Soviet bottom trawl data collected from 1965 to 1985 by Ermakov and Stepanenko (1996). They also showed dramatic fluctuations in the catch of pelagic forage species such as Pacific herring, American shad, northern anchovy and smelts, but the overall biomass was dominated by Pacific hake throughout this period. They found, as we did, that chub mackerel and sardines only began to occur in their catches from 1980 to 1985. They attributed some of the declines in fish populations to fishing, but many species that were not the direct target of fisheries also fluctuated in abundance.

The change in the pelagic nekton community off the Pacific Northwest appears to be related to changes in atmospheric and oceanic circulation since 1977 (Mantua et al. 1997). In particular, the increasing ocean temperatures and less southerly current transport may be related to an unprecedented series of El Niño events, especially in the 1990s (Trenberth and Hoar 1996). These warming events, beginning with the 1982-83 event, undoubtedly increased the geographic range species such as chub mackerel and other warm water species can occupy, from waters off California to off the Pacific Northwest (Pearcy et al. 1985; Brodeur and Pearcy 1992). There is increasing evidence for a 1989 regime shift (Beamish et al. 2000; Hare and Mantua 2000), and this is reflected in a dramatic increase in both forage and predator nekton at this time. In this example, the response is far too rapid to be related to an influx of new recruits, but is more likely a shift in distribution of these species.

This pelagic fish community change coincides with the decline in coho salmon ocean survival. We suspect that ocean-migrating juvenile coho salmon are being "squeezed" by both competitors and predators, and that smolts are finding reduced ocean habitats containing appropriate or optimum water temperatures and feeding conditions (Fisher and Pearcy 1988; Pearcy 1992). Besides having to evade numerous predators (large mackerel and Pacific hake), coho salmon may also be suffering from competition with small individuals of these and other species. Small mackerel and hake feed primarily on euphausiids, a common prey of juvenile salmonids (Peterson et al. 1982; Brodeur et al. 1987; Brodeur and Pearcy 1992). At the same time, northern anchovy, eulachon, and market squid populations appear to have declined, thus diminishing any predatory "buffer" or alternative prey to predators in place of salmonids. Sardines could also be acting as competitors with juvenile salmon for food. As a potential result of this competition, juvenile salmon ocean growth may now be reduced, thus prolonging their availability to predators. Studies are presently underway by NMFS and others to identify the growth rates and fish predators of juvenile salmonids and to quantify their predation rates in coastal waters.

CONCLUSIONS

The pelagic nekton fauna off the Oregon coast has changed markedly since 1977. In the late 1970s and early 1980s market squid, eulachon, and northern anchovy were a large proportion of the pelagic nekton fauna. Starting in the late 1980s and early 1990s, however, these species were replaced by Pacific sardine, chub mackerel, and jack mackerel. Pacific hake also became more abundant beginning in the late 1980s. The cause of this species change is uncertain; however, it correlates well with increasing sea surface temperatures and other oceanographic conditions. The shift in the pelagic nekton fauna (particularly the increase in Pacific hake and the decrease in northern anchovy) appears to be strongly associated with the decline in coho salmon ocean survival. The actual mechanisms whereby Pacific hake, northern anchovy, or possibly mackerel affect ocean survival of salmonids are uncertain but predation and competition could both be playing a role.

ACKNOWLEDGMENTS

We thank Mark Wilkins of the NMFS Alaska Fisheries Science Center, Seattle, for generously providing catch data from the West Coast surveys, and Dr. William Pearcy for critically reviewing the manuscript. We also thank Joe Fisher, Paul Bentley and Dr. Edmundo Casillas for assisting with field work and logistics. Funding for this study was provided by Bonneville Power Administration and by the NMFS Northwest Fisheries Science Center.

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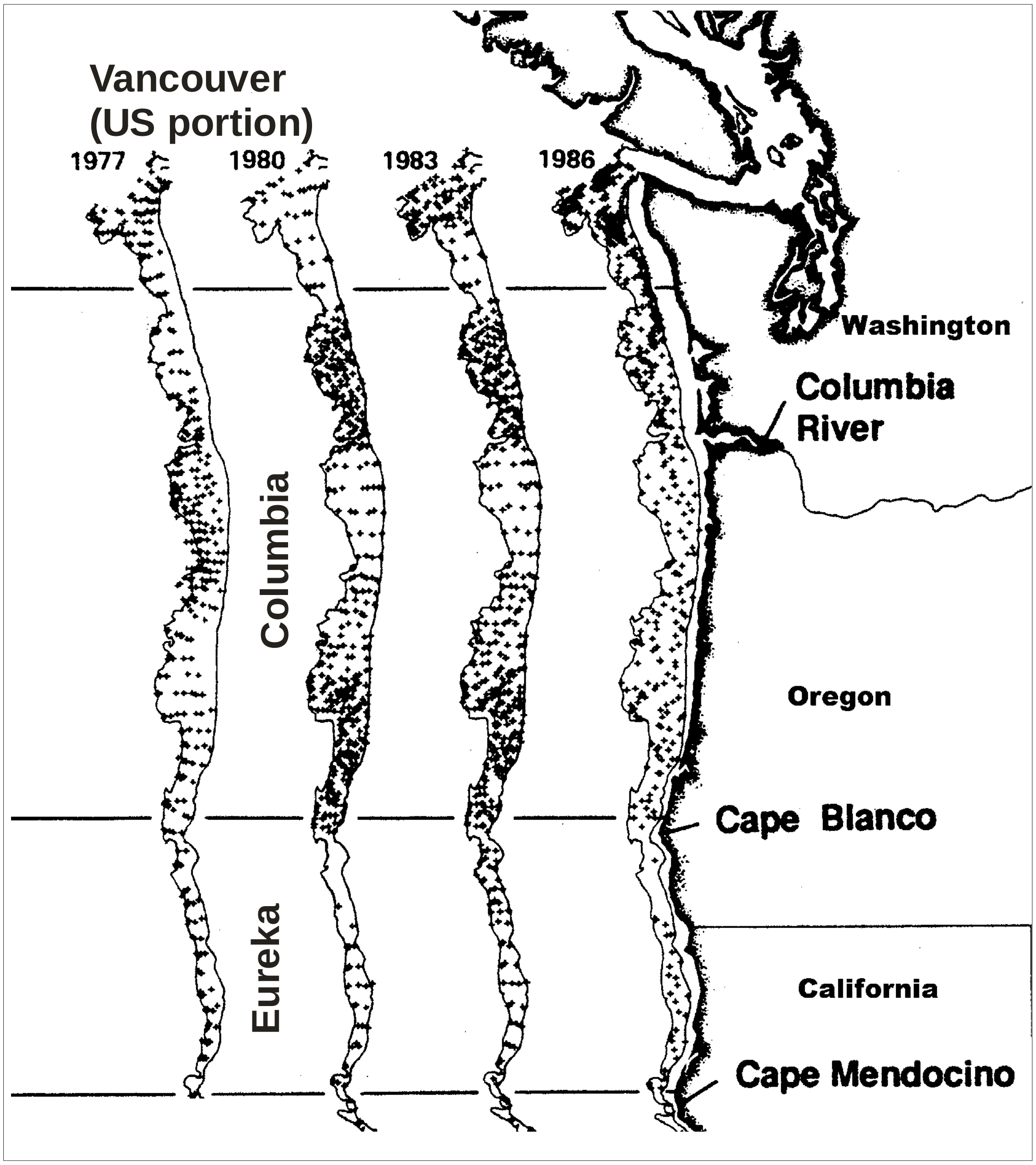

Figure 1.1. Examples of geographic distribution and sampling effort of the NMFS Triennial Trawl Survey on the US continental shelf from 1977 to 1986. Also shown are three fishery statistical regions, Vancouver (U.S. portion), Columbia, and Eureka (modified from Dark and Wilkins 1994).

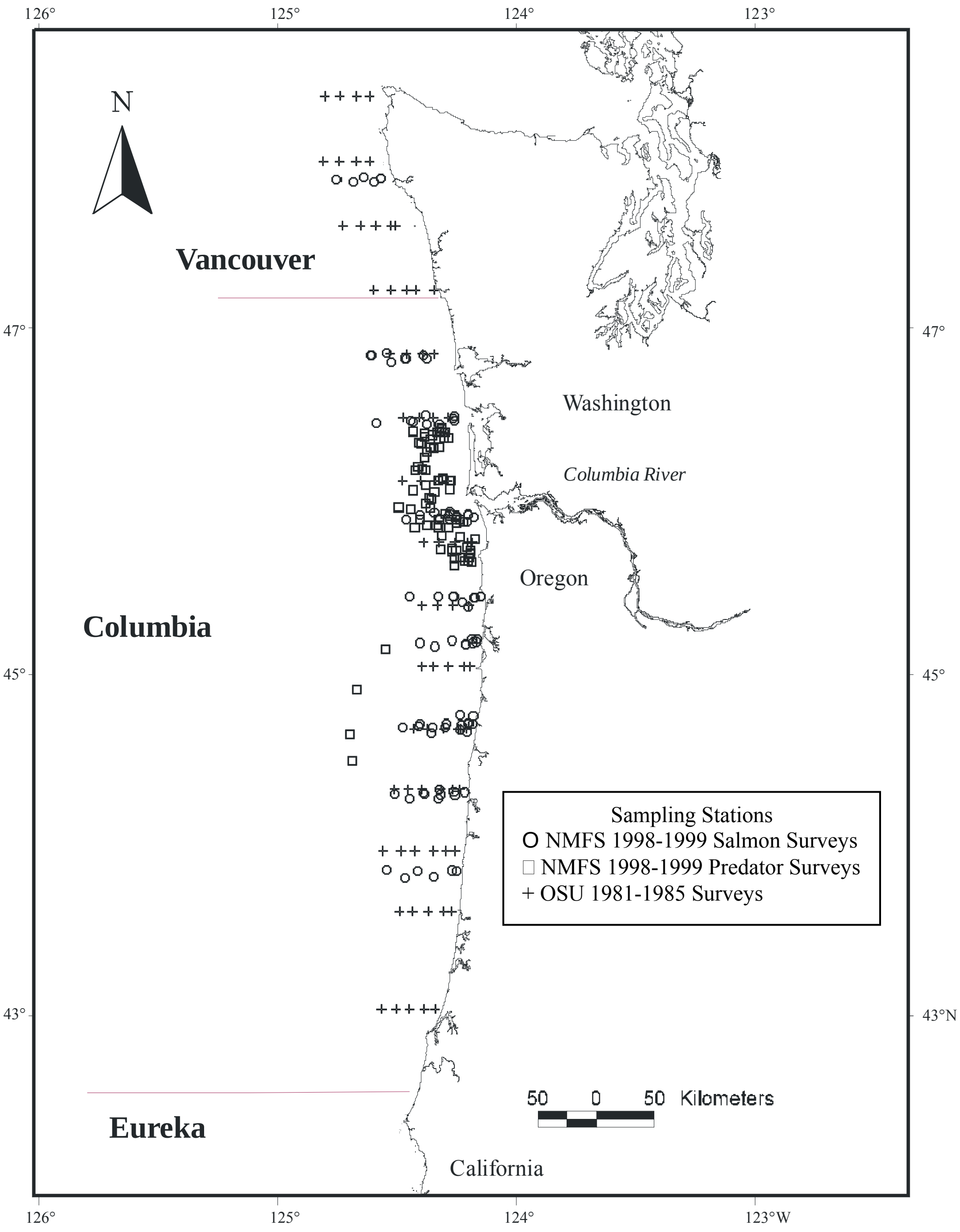

Figure 1.2. Location of stations sampled by surface trawl during the NMFS Salmon Survey, Predator Survey and OSU purse seine survey. Also shown are three fishery statistical regions, Vancouver (U.S. portion), Columbia, and Eureka.

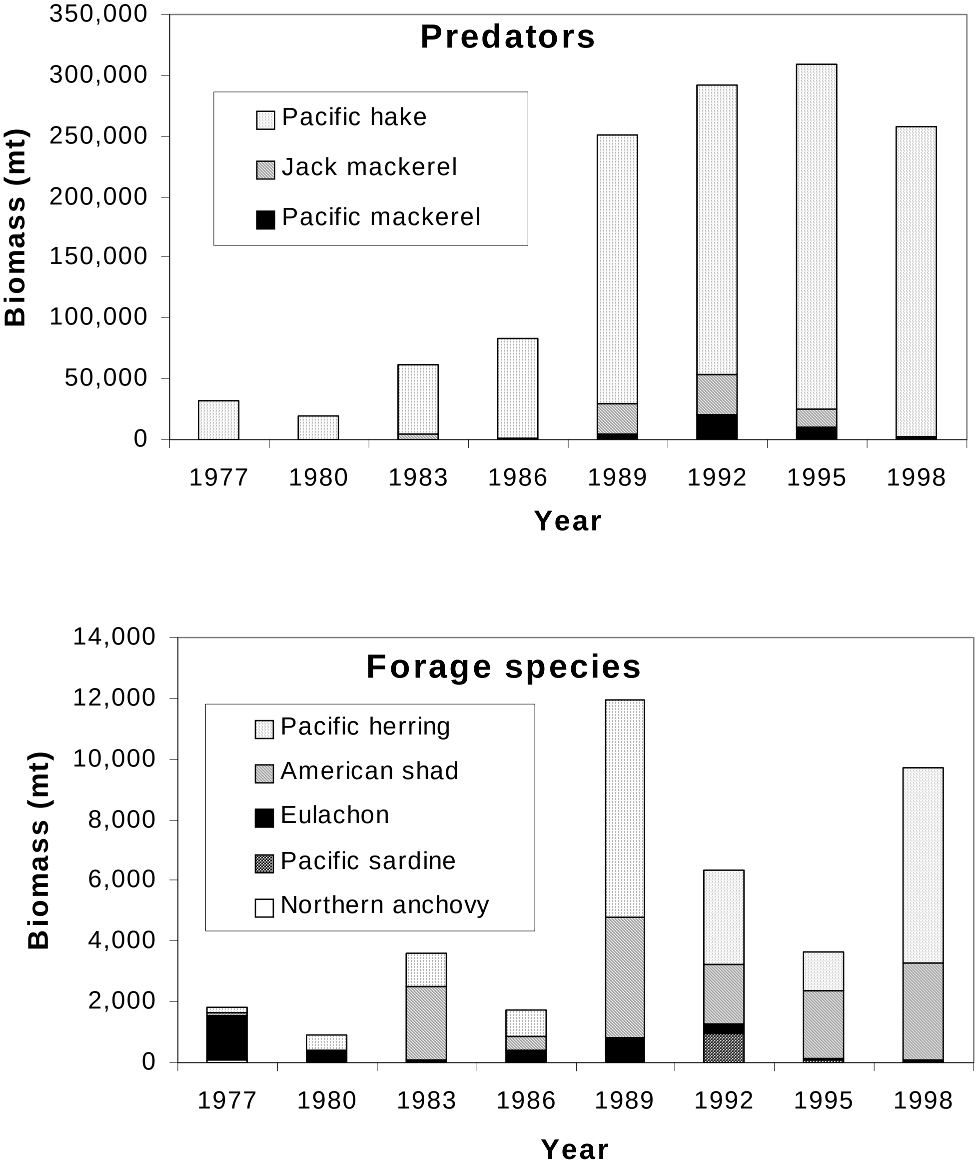

Figure 1.3 Estimated biomass of three fish predators (A) and five forage fish (B) species caught during National Marine Fisheries Service (NMFS) triennial trawl survey of fish abundance on the continental shelf in the Columbia Region (data provided by Mark Wilkins, NMFS, 7600 Sandpoint Way NE, Seattle, WA).

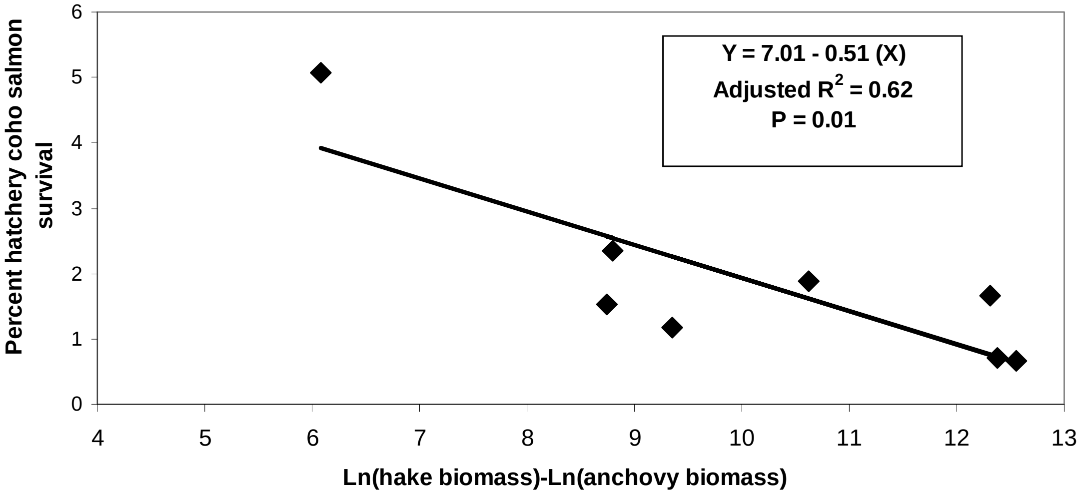

Figure 1.4. Relationship between Oregon Production Index hatchery coho salmon percent marine survival and predation pressure of Pacific hake [defined by ln(hake biomass)-ln(anchovy biomass)].

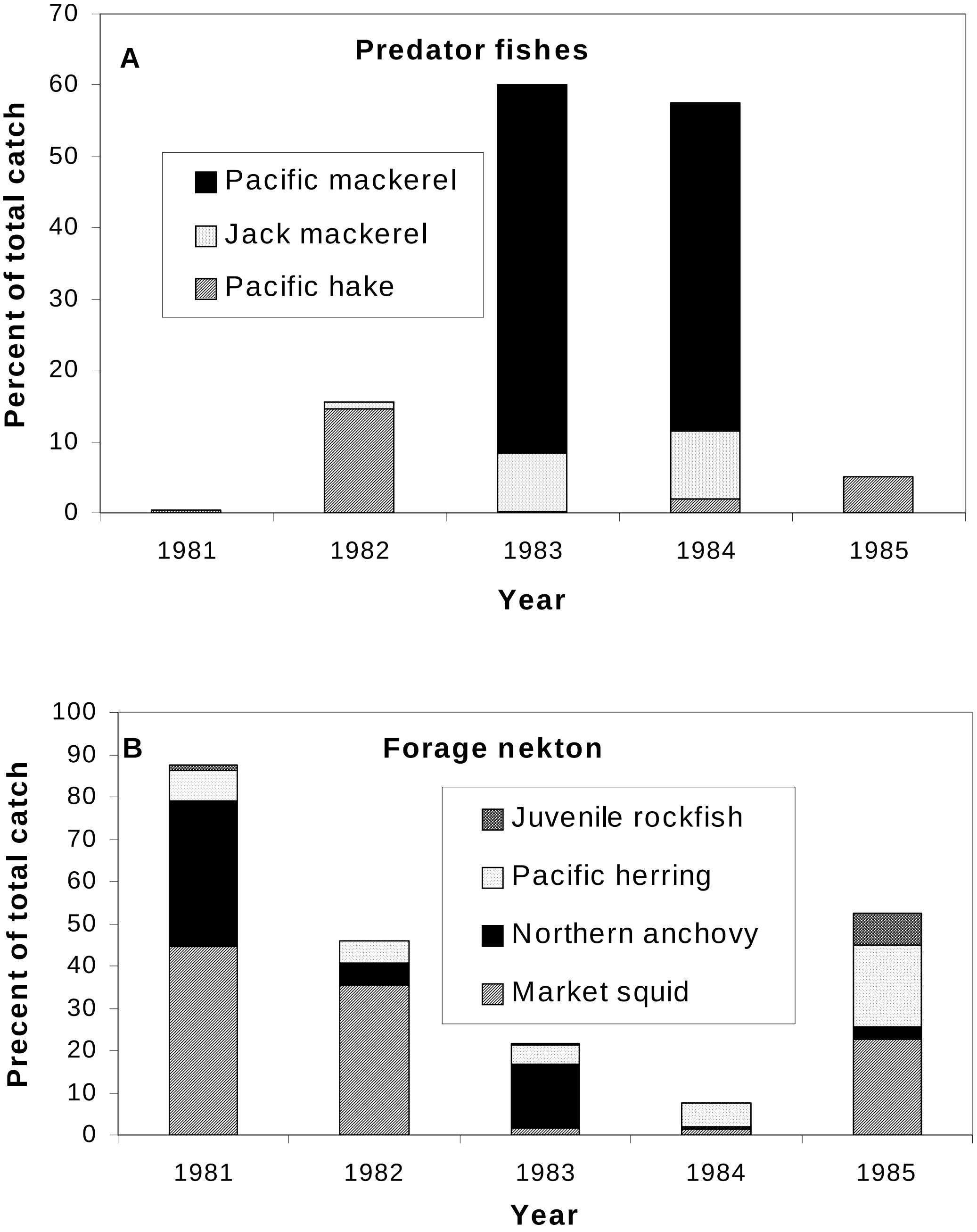

Figure 1.5. Percent of total purse seine catches of major species of predator fishes (A) and forage nekton (B) off Oregon/southwest Washington from 1981 to 1985 by Oregon State University.

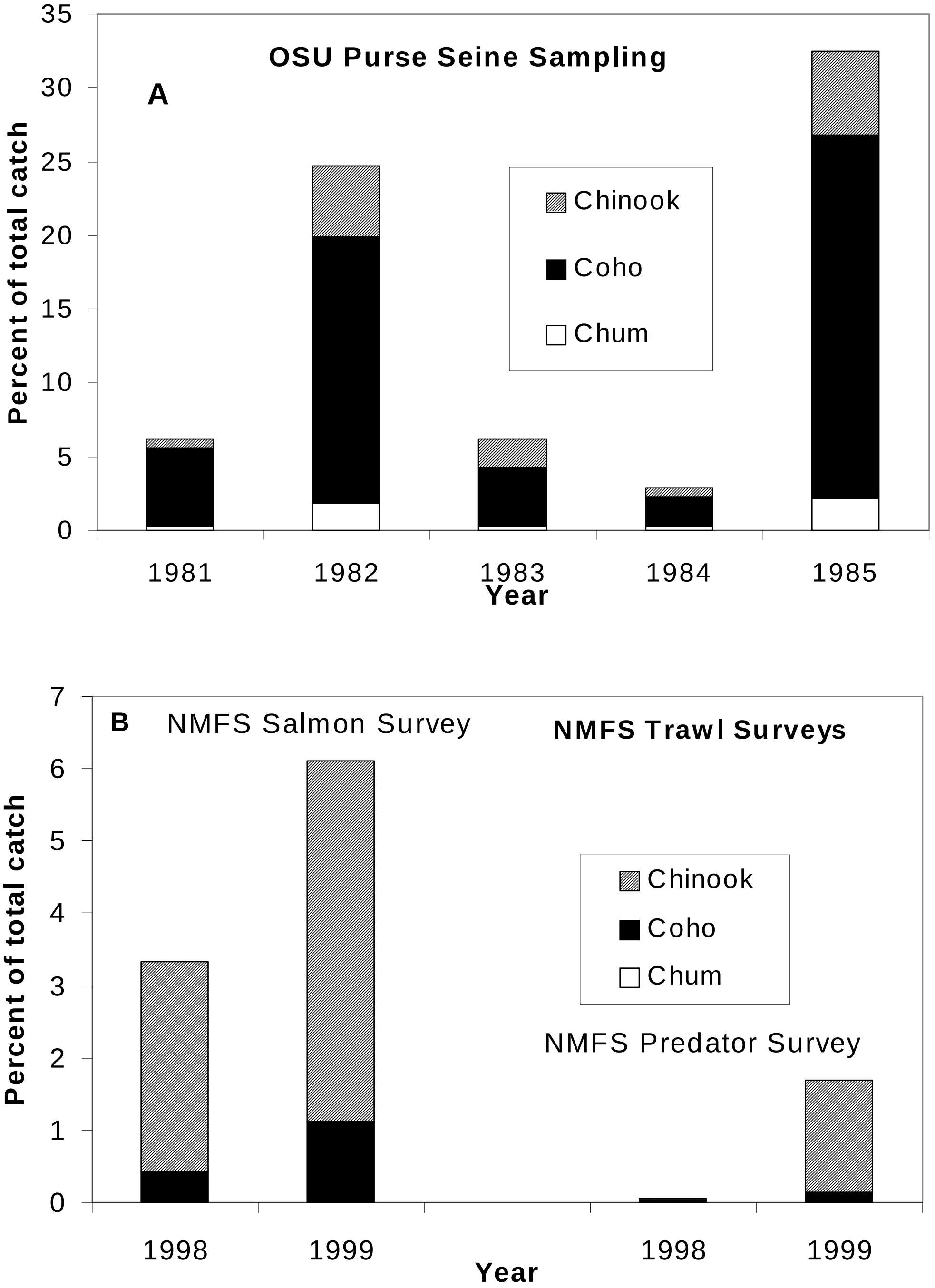

Figure 1.6. Percent of total catch comprised of salmonids during the OSU purse seine survey (A) and the NMFS trawl surveys (B).

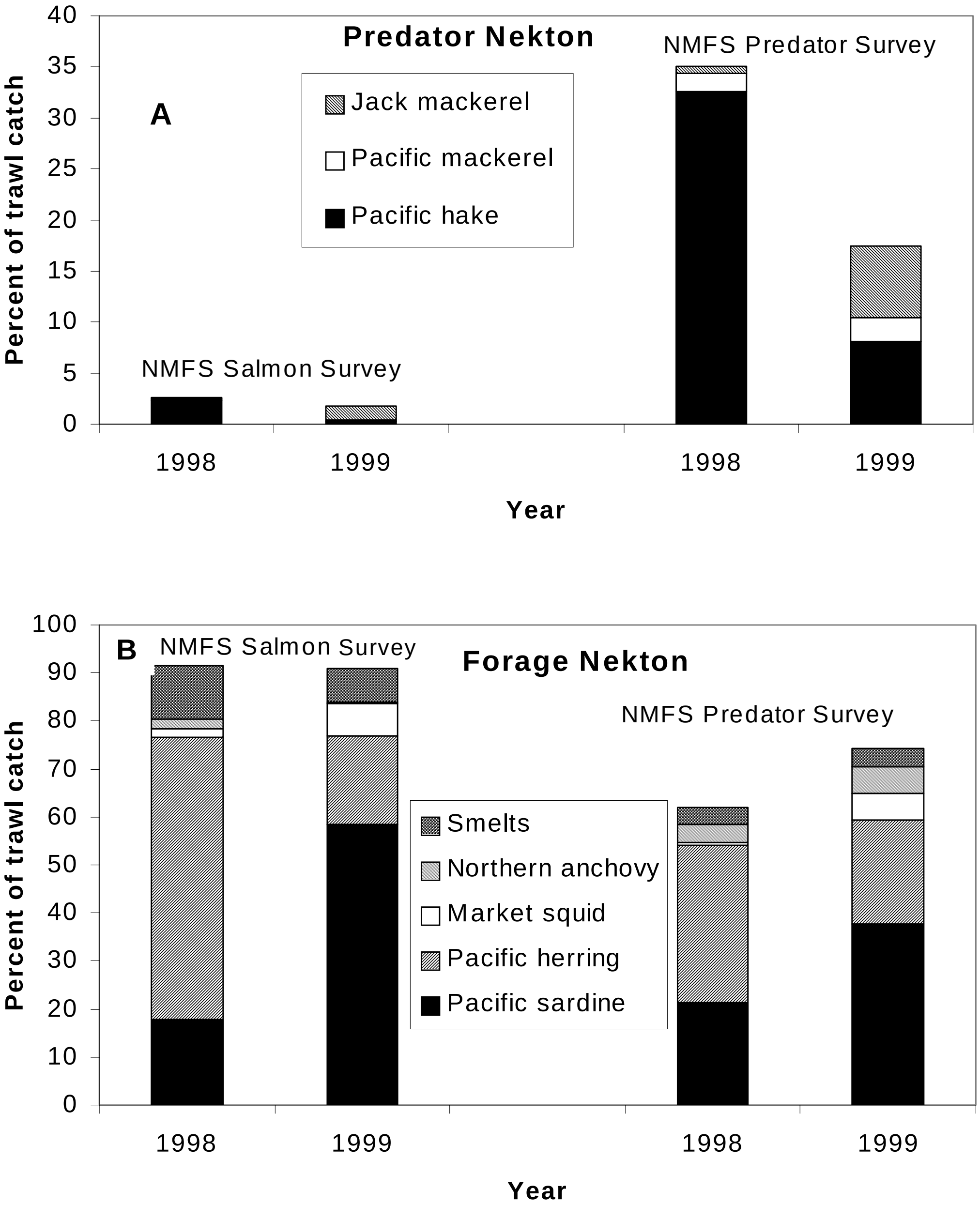

Figure 1.7. Percent of total surface and near-surface trawl catches off Oregon/southwest Washington composed of predator fishes (A) and forage fishes (B).

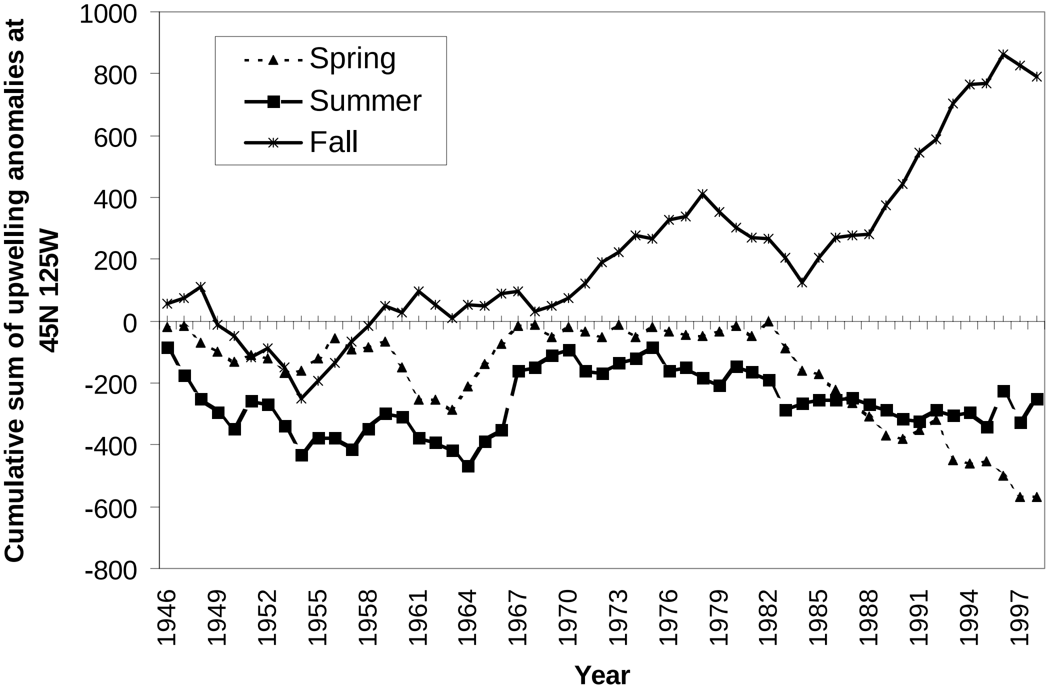

Figure 1.8. Cumulative sum of spring, summer, and fall upwelling anomalies at 45°N 125°W.

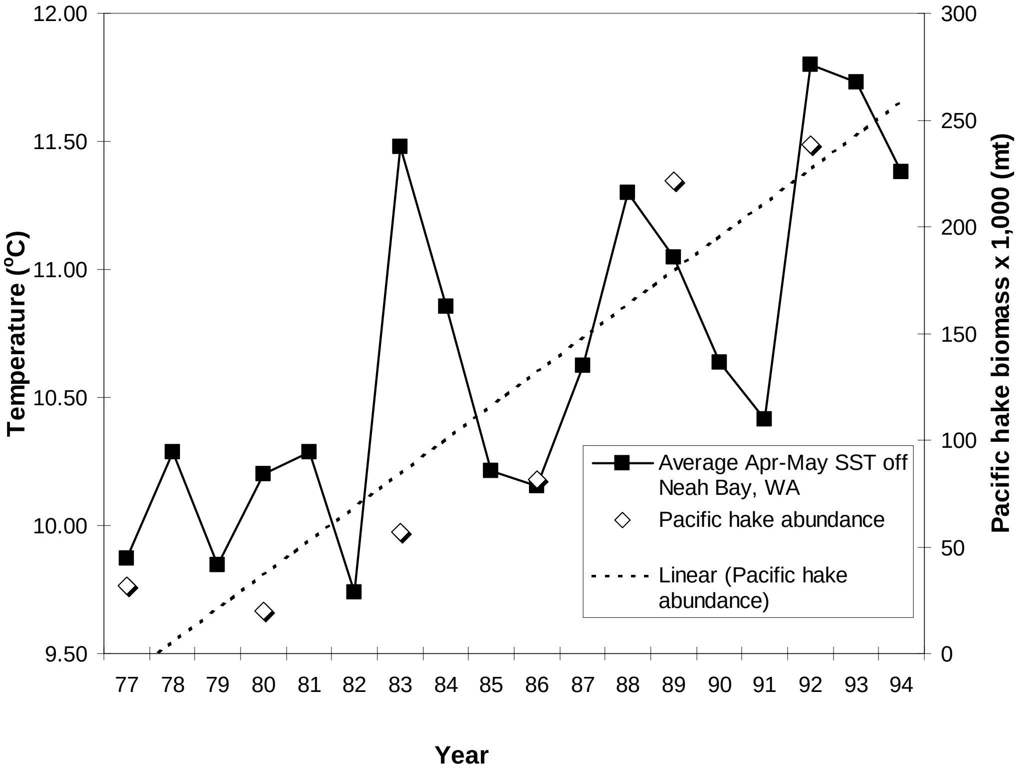

Figure 1.9. The relationship between Pacific hake abundance in the Columbia Statistical Region and sea surface temperatures off Neah Bay, Washington.

Chapter 2. The Relationship Between Fluctuations in the Abundance of Forage Fish and Juvenile Salmonids off the Columbia River, Changing Oceanographic Conditions, and Salmon Marine Survival, 1998-2004

ABSTRACT

From 1998-2004 the abundance of forage fishes and juvenile salmonids off the Columbia River during spring/early summer was assessed and the relationship between forage fish abundance, oceanographic conditions, and salmonid marine survival investigated. Forage fish numbers increased significantly after 1999 and appeared to be related to cooler ocean conditions, earlier spring transition, and an increase in the relative proportion of subarctic waters. These changes were reflected in the negative values of the Pacific Decadal Oscillation and Multivariate ENSO indices. Annual densities of forage fish were positively related to the abundance of the previous year's cold-water copepods. Seasonally, forage fishes generally became most abundant in spring (May/June), when many Columbia River juvenile salmonids migrate to sea. Forage fishes were of similar size and resided in similar habitats as juvenile salmonids. When abundant, forage fishes may increase salmonid marine survival by acting as "alternative" prey for piscivores that also eat juvenile salmonids. However, statistical analysis indicated no relationship between the abundance of forage fishes and Columbia River coho salmon marine survival, indicating that other environmental factors are also important.

INTRODUCTION

The term “forage fishes” refers to small pelagic fishes that occupy a critical link in marine food webs by transferring production from lower levels (primary and secondary) to upper trophic levels (Cury et al. 2000). Marine forage fishes, such as northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), smelt (Osmeriidae), and Pacific herring (*Clupea pallasii*) are particularly important forage fishes in the coastal region along the west coast of North America and the California Current (PFMC 1983; Kucas 1986; Lassuy 1989; Emmett et al. 1991; Emmett and Brodeur 2000). They are also prey for many species of seabirds (Wiens and Scott 1975; Matthews 1983; Emmett et al. 1991), marine mammals (Beach et al. 1985; NMFS 1997; Reimer and Brown 1997), and large fishes (Livingston and Alton 1982; Ashton et al. 1985; Livingston and Bailey 1985; Brodeur et al. 1987; Tanasichuk et al. 1991; Brodeur and Pearcy 1992), including adult salmonids (Fresh et al. 1981).

While Pacific herring and smelt feed at the secondary production level (euphausiids and copepods), anchovy and sardines feed upon both phytoplankton and zooplankton (King and Macleod 1976; Emmett et al. 1991; McFarlane and Beamish 2001; Emmett et al. 2005). Anchovy and sardine populations are particularly abundant in productive upwelling regions around the world, such as off the west coast of North and South America, and in the Bengeula Current off the southwest coast of Africa (Bakun 1996). Worldwide anchovy and sardine populations appear to cycle in concert, indicating global or basin-wide forcing mechanisms affect recruitment processes (Lluch-Belda et al. 1992; Chavez et al. 2003).

Populations of small pelagic forage species often become very large and support intense fisheries (FAO 2002). However, the productive upwelling areas that support these populations undergo regular disruptions by El Niño events (Bakun and Broad 2003) and decadal regime shifts (Mantua et al.1979; Hare and Mantua 2000), altering primary and secondary production levels and causing pelagic fisheries to decline (Cushing 1982; Bakun 1996; McGowan et al. 1998; Alheit and Bernal 1999). Pacific Northwest salmonids are also negatively affected during El Niño events, which cause low juvenile salmonid marine survival and reduced adult salmon body size (Pearcy 1992).

Upwelling ecosystems appear to have a low diversity of forage fish species that may act as “alternate” prey species to piscivores when productivity shifts occur. Rice (1995), Bakun (1996) and others have called upwelling systems, “wasp-waist” systems, because only a few forage fish species are responsible for transferring lower trophic production (primary and secondary) to a wide range of upper-level species. As a consequence, when these forage fish populations’ decline, upper-level piscivore populations also are affected (Arntz and Tarazona 1990; Cury et al. 2000). This is particularly obvious in piscivorous bird populations (Graybill and Hodder 1985; Tovar et al. 1987; Crawford and Jahncke 1999).

Besides showing wide fluctuations in overall forage-fish abundance, upwelling ecosystems also show large shifts in species structure in relation to fluctuating oceanic regimes (i.e., switching from an ecosystem dominated by sardines to one dominated by anchovy; Chavez et al. 2003). Varved scales deposited in the Santa Barbara Basin, California, show that sardine and anchovy have had a long history of fluctuations in abundance and species dominance (Baumgartner et al. 1992). During the 1990s the California Current (which included the Pacific Northwest) appeared to be in a "sardine regime" whereby the Pacific sardine population rapidly increased and northern anchovy decreased (Chavez et al. 2003).

Is there a relationship between forage fishes and Pacific Northwest salmon marine survival? There have been many studies attempting to identify the biological/physical oceanographic conditions that affect salmonid marine survival (Pearcy 1992; Beamish and Bouillon 1993; Beamish et al. 1999; Cole 2000; Hobday and Boehlert 2001, Logerwell et al. 2003). However, few studies have attempted to identify the biological mechanisms that actually cause salmonid marine mortality and how these mechanisms are correlated with physical oceanographic factors. It has been hypothesized that predation, occurring primarily when salmonids first enter the ocean, is a prime factor determining marine survival for salmonids off the Pacific Northwest (Parker 1971; Hargreaves and LeBrasseur 1985; Pearcy 1992). Forage fishes, by acting as alternative prey for piscivores, are thought to influence this predation (Pearcy and Fisher 1988; Pearcy 1992) and thus play an important role in juvenile salmonid marine survival. The basic premise of Pearcy and Fisher's hypothesis is that when alternative prey (northern anchovy, Pacific herring, smelt, etc.) are abundant, piscivorous predators will eat fewer salmon, consuming forage fishes instead, thus permitting a higher marine survival of juvenile salmonids.

There are studies that indicate a relationship between forage fish abundance and salmonid marine survival. During the 1970s and 1980s in Barkley Sound, British Columbia, Canada, coho salmon (*Oncorhynchus kisutch*) marine survival appeared to be directly related to the abundance of age-1 and -2 Pacific herring (Holtby et al. 1990; Pearcy 1992). During the 1983/84 El Niño, forage nekton, especially northern anchovy and market squid (*Loligo opalescens*) populations declined considerably, and predatory fishes increased markedly, particularly jack (*Trachurus symetricus*) and chub mackerel (*Scomber japonicus*) (Brodeur and Pearcy 1992; Emmett and Brodeur 2000). Probably not coincidentally, the marine survival of 1983 juvenile coho salmon migrants was very low, and adult coho salmon returning in 1984 were very small in size (Johnson 1988, Pearcy 1992). However, by 1985, market squid (*Loligo opalescens*), northern anchovy and Pacific herring populations rebounded (Emmett and Brodeur 2000) as did coho salmon ocean survival (Logerwell et al. 2003).

Nickelson (1986) showed that Oregon coho salmon marine survival and the abundance of northern anchovy off California both declined in the 1980s. Unfortunately, I have only limited data showing that the northern anchovy subpopulation, which spawns off Oregon (Richardson 1981), also declined. However, purse-seine data off Oregon/Washington revealed large fluctuations in northern anchovy and other forage fishes during the mid-1980s (Emmett and Brodeur 2000). Ichthyoplankton surveys off Oregon/southern Washington also indicated low northern anchovy spawning biomass in the 1990s (Emmett et al. 1997; Emmett unpublished data). These were years with poor salmon marine survival as well.

Forage fish abundance is probably strongly linked to ocean productivity and trophic interactions. For example, there is evidence that from 1977-1998 the entire California Current ecosystem was relatively warm and non-productive (Roemmich and McGowan 1995; McGowan et al. 1998), and the North Pacific Ocean entered a warm oceanic regime (Mantua et al. 1997; Hare and Mantua 2000). As a result of this warm regime, northern anchovy became less abundant off California, but Pacific sardine increased markedly (McFarlane et al. 2000, 2002; McFarlane and Beamish 2001; Chavez et al. 2003).

With this background, I initiated a study in 1998 to identify the abundance of forage fishes off the Columbia River. The goals of this study were to measure a) the abundance of forage fishes and juvenile salmonids off the Columbia River, b) the relationship between forage fish abundance and ocean conditions, and c) the relationship between the abundance of forage fish off the Columbia River and salmonid marine survival.

METHODS

Field sampling

I began to examine the abundance and distribution of forage and predatory fish off the Columbia River during the annual salmonid smolt migration period (April through July) in 1998. The first year (1998) was used principally as a pilot study to identify the appropriate gear type and sampling scheme to collect pelagic fishes near the surface. As a result, many different stations were sampled in 1998 (Fig. 2.1). In 1998 the fishing gear was deployed one or two times each night when the depth sounder indicated fish (undetermined species) were around the vessel and near the surface, as one of the initial study objectives was to identify whether the surface trawl gear fished effectively. Blind tows (no prior information about fishing conditions) were also conducted. I report 1998 data only from collections when a rope trawl was used (1 June 1998-on), as this was the fishing gear finally identified as most effective. Because the 1998 sampling scheme differed from that in 1999-2004 (different stations) and number of surveys, fish densities calculated for 1998 may not be completely comparable to later years. However, fish catches and oceanographic conditions differed widely between 1998 and 1999-2004, thus the 1998 data provided valuable contrasting information on fish/oceanographic relationships that I believe are important to include in this analysis.

From 1999-2004, all samplings were conducted at specific locations off the mouth of the Columbia River (Fig. 2.1). Large piscivores, primarily Pacific hake (*Merluccius productus*), chub mackerel, and jack mackerel; forage fishes (Pacific herring, northern anchovy, Pacific sardine, etc.); and market squid were collected by surface trawling. Sampling was conducted at night (dusk to dawn) using a chartered commercial trawler. I sampled at night to take advantage of the diel migratory behavior of many fishes and because surface trawls are usually more effective at night due to visual avoidance during daylight (Dotson and Griffith 1996). Moreover, fishes such as Pacific hake (Bailey et al.

1982) and clupeids (Blaxter and Holiday 1963) migrate from depth to the surface at night (diel vertical migration), and thus are more easily sampled.

All surface trawling was conducted with a 264-rope trawl with 3-m foam-filled Lite doors, designed and built by NET Systems, Bainbridge, WA. The trawl is 100-m long with a fishing mouth area approximately 28-m wide and 12-m deep. Time depth sensors placed on the head ropes indicate the net fished near the surface, from 1.0-13.0 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 effectively capture small fishes and invertebrates. The 264-rope trawl was towed 137 m (75 fathoms) behind a chartered commercial fishing trawler, traveling approximately 2.9 knots (1.5 m/sec) for 30 minutes. Starting in 2001, trawl time was often shortened to 15 minutes to reduce the catches because very large catches of forage fish were difficult to process effectively. Forage fish abundance was standardized by calculating densities (number/$10^6 m^3$) by multiplying distance towed (geographic distance between begin and end of trawl tow) by the effective mouth area of the net (336 m^2). The effective mouth area was identified using a backward looking net sounder (Emmett et al. 2004).

From 1999-2004 I sampled at pre-determined stations along two transect lines north and south of the entrance to the Columbia River (Fig. 2.1). Six stations were sampled along each transect, with the first station being as close to shore as possible (30-m deep), and the farthest station approximately 30 km from shore. Sampling was conducted approximately every 10 days from mid-April through July or early August from 1998 to 2004, for a total of 20 sampling days (10 sampling cruises per year). From each trawl, all forage fish species and potential salmonid predators were identified, enumerated, and measured, except when large catches occurred. For large catches, a random sample of 30 individual fish from each species was measured, subsamples of each species were counted and weighed, and the remaining catch mass weighed by species. Total number of each species actually captured for that haul was determined by adding the number counted to the number calculated by dividing the mass weight by the average weight/individual.

Chinook salmon were separated into yearling (1.0-age, where the first number represents years in fresh water and the number to the right of the decimal, years in the ocean) and subyearling (0.0-age) by size. Size of each age group varied by month and was identified by length frequency analysis and historical salmon size information (J. Fisher, Oregon State University, Corvallis, OR. pers. comm.).

Annual trawl surveys were conducted on similar days each year, but not exactly the same days, due to weather and other factors. To allow annual comparisons, 1999 sampling dates were identified as the "base" sampling dates and those of other years samplings were shown relative to those dates. For example, figures showing 22 April annual data include trawl information collected during 21 April 1999, 20 April 2000, and 22 April 2001, etc.

Temperature and salinity profiles were collected at all trawl stations by lowering a SeaBird SB-19 conductivity, temperature, and depth (CTD) probe to 100 m depth (or just off the bottom in shallower water). Chlorophyll *a* values were determined from two stations located just south of the Columbia River mouth. Water samples were collected at 3 m depth, filtered on glass fiber filters at sea, and frozen. At the laboratory chlorophyll samples were treated with acetone and chlorophyll measured with a Turner Designs 10-AU fluorometer. Additional sea-surface temperature data were obtained from the NOAA buoy 46029 located off the Columbia River (National Data Buoy Center, http://www.ndbc.noaa.gov/). Other physical data gathered to evaluate changes in the nearshore ocean environment were Columbia River flows at Beaver, OR (US Geological Survey, http://waterdata.usgs.gov/nwis/nwisman/), sea-surface height at South Beach, Oregon (NOAA's Center for Operational Oceanographic Products and Services, http://www.co-ops.nos.noaa.gov/), upwelling anomalies at 45°N (NOAA/NMFS Pacific Fisheries Environmental Laboratory, http://www.pfeg.noaa.gov/) and the date of the spring transition. The spring transition, defined by when upwelling, northwest winds, and equator-ward currents consistently begin, was identified by changes in upwelling anomalies and sea level along the Oregon/Washington coast (Loggerwell et al. 2003; E. Loggerwell, NOAA Fisheries, Seattle, WA, pers. comm.). Other information of interest included the Multivariate El Niño/Southern Oscillation (ENSO) Index (NOAA-CIRES Climate Diagnostics Center, http://www.cdc.noaa.gov/ENSO/), Pacific Decadal Oscillation (PDO) index (Joint Institute for the Study of the Atmosphere and the Oceans, http://jisao.washington.edu/pdo) and Northern Oscillation Index (NOI) (NOAA/NMFS Pacific Fisheries Environmental Laboratory, http://www.pfeg.noaa.gov) (Schwing et al. 2002). Since there appeared to be a “shift” in ocean conditions in 1999 (Peterson and Schwing 2003) and perhaps again in 2003, I compared the average oceanographic data from 1991-1998 to that of 1999-2002 and 2003-2004 to identify any statistical differences in Columbia River buoy sea surface temperatures and sea surface heights between periods.

Data analysis

A Kruskal-Wallis Test was used to test for statistical differences in forage fish densities (by species and combined) between years because densities were not normally distributed. Dunn's Multiple Comparisons Test was used to identify which years differed. Statistical differences in physical oceanographic conditions between the three time periods (1991-1998, 1999-2002 and 2003-2004) were also identified using a Kruskall-Wallis Test. An analysis of variance (ANOVA) was used to test for statistical differences between 3-m temperatures, salinities, and chlorophyll, with Tukey's Multiple Comparisons Test used to identify different periods/years.

Regression analysis (single independent variable and a multiple linear model) was used to identify the physical factors that were related to the annual variation in average forage fish densities (all species combined). Average annual forage fish densities per year were log transformed before analysis. Physical factors included in the analysis were date of the spring transition, average April-June Columbia River flows, maximum April-June flows, and northern (i.e., cold-water) copepod anomaly (Peterson and Schwing 2003). Spring transition was identified in Julian days. Since many of the forage fishes, especially whitebait smelt (*Allosmerus elongatus*), Pacific herring, and northern anchovy were composed primarily of yearling fish (i.e., were spawned during the previous year), physical/biological variables used in statistical analysis were lagged one year (*t*-1). I hypothesized that physical conditions during spawning, larval development, and early juvenile stage, largely determined the abundance of forage fish species the following year. Age determination of forage fishes were determined by looking at otoliths and length frequency distributions (unpublished data).

To identify if there was a relationship between forage fish abundance and salmon marine survival, I compared (regression analysis) data on the marine survival of coho salmon from the Oregon Production Index (OPI) area with average annual forage fish densities. Coho salmon OPI represents the marine survival of hatchery coho salmon in the OPI area (PFMC 2002). Percent marine survival was calculated by dividing the sum of coho salmon adult and jack returns by the number released from hatcheries.

RESULTS

Annual densities of forage fishes off the Columbia River changed significantly from 1998 to 2004 (Kruskal-Wallis test statistic = 82.636; $P < 0.0001$; Fig. 2.2A). Forage fish densities were significantly lower in 1998 than 2001 and 2003, and in 1999 compared to all other years (Dunn's Multiple Comparison Test, $P < 0.0001$). Forage fish densities were not statistically different (Dunn's Multiple Comparison Test, $P > 0.05$) for all other years. In 1999 mean forage fish densities were less than $170/10^6m^3$, whereas by 2000, densities were twenty times greater ($3,317/10^6m^3$). Densities doubled in 2001, but in 2002, forage fish densities declined to values close to the 2000 levels, with declines observed in whitebait smelt, Pacific herring, and Pacific sardine densities (Fig. 2B). In 2003, forage fish densities again increased, coming close to matching the 2001 densities ($7{,}434/10^6 m^3$), with northern anchovy the most abundant species. However, in 2004 forage fish densities declined below 2000 densities (Fig. 2A).

Statistical analyses of density by species revealed that densities of all forage fishes were significantly different during 1998-2004 (Kruskal-Wallis test, $P < 0.05$). Densities of northern anchovy in 1998 were significantly less than those of 2002-2004, and 1999 densities lower than those in 20000-2004 (Dunn's Multiple Comparison test, $P < 0.05$). Whitebait smelt densities in 1998 were significantly less than those of 2000 and 2001, and 1999 densities were lower than those in 2000-2004 (Dunn's Multiple Comparison test, $P < 0.05$). Pacific herring densities in 1998 were significantly lower than those in 2003, and densities in 1999 and 2000 were significantly lower than densities in 2001 and 2003 ((Dunn's Multiple Comparison test, $P < 0.05$). Pacific sardine densities showed only one annual significant difference; with 1999 densities lower than those in 2004 ((Dunn's Multiple Comparison test, $P < 0.05$).

Not only did forage fish densities change from 1998 to 2004, but the species composition of the catch also changed considerably. In 1999, Pacific sardine made up more than half the forage fish catch; by 2002 they composed less than 6% (Fig. 2.2C). Northern anchovy was 6% of the forage fish catch in 1998 but 48% by 2004. Whitebait smelt abundance showed the largest fluctuations, ranging from a low of 4% of the catch in 1998 to over 56% just one year later, and remaining a large percent of the forage fish catch through 2004 (Fig. 2.2C). Pacific herring composed a high percentage of the forage fish catch in 1999 (31%); but only 9% in 2002 and 12% in 2003. Sardines were the most abundant forage fish in 1999, comprising 56% of the catch, but by 2003 comprised only 10% of the forage fishes.

Juvenile salmonids (all species combined) composed only a very small percentage of the forage fish catch (Fig. 2.3). The largest percentage of juvenile salmonids in the forage fish catch was in 1999 when they represented slightly over 2.2% of the catch (Fig. 2.3). During that year subyearling Chinook salmon comprised most of the salmonids captured, followed by yearling Chinook and coho salmon. In subsequent years, juvenile salmonids comprised little of the forage fish catch, <0.5% from 2000-2004 (Fig. 2.3). This declining percentage of salmonids over the five years reflects the large increases in forage fish species abundance, as there were slight increases in juvenile salmonid abundance. For example, average densities of coho (1.0-age), yearling Chinook (1.0-age), and subyearling Chinook salmon (0.0-age) increased in 1999 and 2000 (Fig. 2.4).

Both salmon species and age groups showed significant changes in densities between the seven study years (Kruskal-Wallis test, $P < 0.05$). Densities of yearling Chinook salmon in 1999 were significantly lower than 2000, 2001, and 2003, but not in 2002 and 2004 (Dunn’s Multiple Comparison Test, $P < 0.05$) (Fig. 2.4A). Coho salmon densities in 2000 were significantly higher than in 2002 and 2003 (Dunn’s Multiple Comparison Test, $P < 0.05$) (Fig. 2.4B), and subyearling Chinook salmon densities were significantly lower in 1999 than 2000 (Dunn's Multiple Comparison Test, $P < 0.01$) (Fig. 2.4C), but no differences were identified from other years.

Juvenile salmonids and forage fishes were captured at similar times of the year (Fig. 2.5). However, while yearling Chinook and coho salmon were generally in highest abundance from mid-May to early June, forage fish species had more constant densities through the spring, but with peak abundances differing between years (Fig. 2.5D). For example, in 2000 forage fish densities peaked near the end of June, whereas in 2001, they peaked in early May. Juvenile coho salmon catches were very low until mid-May, when they increased abruptly during three of the study years (Fig. 2.5A). Yearling Chinook salmon catches did not show a similar pattern, but generally increased, peaked in mid-May and then declined to low levels by the end of July (Fig. 4B). Subyearling Chinook salmon were most abundant in July of all years (Fig. 2.5C). This follows the known migrational timing behavior of these species from the Columbia River (Dawley et al. 1986).

Besides showing large annual differences in abundance, forage fishes and juvenile salmonids showed annual temporal abundance patterns that differed depending on species and year (Fig. 2.5). While yearling (1.0-age) Chinook and coho salmon catches showed similar migrational timing each year, their densities changed considerably during the study period, with densities for both species highest in 2001. Juvenile yearling Chinook salmon had their highest densities in late April and May during all years (Fig. 2.5B), with the highest overall density ($19.8/10^6 m^3$) occurring 13 May 2001. Peak juvenile coho salmon (1.0-age) catches occurred slightly later than peak yearling Chinook salmon catches and were about half the densities of yearling Chinook salmon (Fig. 2.5A). Highest overall juvenile coho salmon catches ($5.9/10^6m^3$) occurred in mid-May 2001. Juvenile subyearling Chinook (0.0-age) salmon showed temporal abundance similar to Pacific sardine (Fig. 2.6), becoming most abundant during late June and July (Fig. 2.5C). Highest overall juvenile subyearling Chinook salmon density ($23/10^6m^3$) was on 6 July 1999.

Forage fish species showed very high variability in temporal densities by year. For example, in 1999 a total of 1,557 total northern anchovy were captured (average density of $13/10^6m^3$), but by 2000, northern anchovy were relatively abundant (average density of $541/10^6m^3$), primarily in late April and May (Fig. 2.6A). Northern anchovy density peaked early each spring during 2001 and 2003, but relatively high densities also occurred in late July 2002 (Fig. 2.6A). Pacific herring also showed varied densities through the sampling season. This species was particularly abundant in late July in 2000, but its peak abundance shifted to earlier in the season during each following year (Fig. 2.6B). Whitebait smelt temporal densities showed a pattern of highest densities occurring in spring and then declining during summer. Peak densities also appeared to occur earlier in each year following 2000 (Fig. 2.6C). Pacific sardine densities were generally very low until late June/early July every year. In 1999 they did not appear in significant densities until late July. In other years (2000-2003) they started to appear in the catches in late June (Fig. 2.6D). Pacific sardine differed from other forage fishes by becoming more abundant later in the spring, primarily from late-June on, with highest densities in late June 2001 (Fig. 2.6D).

Lengths of salmonids and forage fishes in May/June showed a large amount of overlap when summarized annually. This length overlap is important because it allows predators to prey on forage fishes of similar size to juvenile salmonids. As shown earlier, May/June is the peak time period when yearling smolts migrate to sea (Fig. 2.5). The overall forage fish length-frequency distribution fully encompasses all juvenile salmonid lengths (Fig. 2.7). Most yearling Chinook and coho salmon captured ranged from 130 to 200 mm FL, whereas the largest portion of forage fish ranged from 135-165 mm FL, with relatively few in the 170-180 mm FL size class. In 1999 there were very few forage fishes with lengths within the 135-180 mm FL size mode. Subyearling Chinook salmon were much smaller than either yearling Chinook or coho salmon, ranging from 75-140 mm FL (averaging 112 mm FL) over all years (Fig. 2.7).

There was generally a high degree of overlap between salmonid and forage-fish lengths when fish length data were analyzed by month (all years combined; Fig. 2.8). However, in April, fork lengths of both coho and yearling Chinook salmon were slightly greater than those of most forage fishes (Fig. 2.8); only a few Pacific herring and Pacific sardine were of similar size to the juvenile salmonids. In May, juvenile yearling coho and Chinook salmon were still larger than most forage fishes, but by this month there were large numbers of northern anchovy, Pacific herring, whitebait smelt, and Pacific sardine that overlapped the yearling salmon size range (Fig. 2.8). Chinook salmon of age 0.0 in May averaged 100 mm FL and were of similar length to many forage fishes, while chum salmon captured in May were slightly smaller than most forage fishes.

By June, juvenile yearling Chinook and coho salmon averaged 197 mm and 186 mm, respectively, but some were as small as 150 mm FL (Fig. 2.8). Also by June, migratory Pacific sardine began moving into the sampling area. While the median length (244 mm FL) of Pacific sardine was larger than that of the yearling salmonids, Pacific sardine had a wide size range, between 100 and 300 mm FL (Fig. 2.8). Subyearling Chinook and chum salmon had almost exactly the same size range as whitebait smelt, but their lengths also overlapped with those of northern anchovy.

During July/early August, lengths of 0.0-age Chinook and chum salmon still strongly overlapped with those of whitebait smelt, averaging around 110 mm FL, but there was also some overlap with small Pacific herring and Pacific sardine (Fig. 2.8). Yearling Chinook and coho salmon averaged near 200 mm FL and only larger Pacific herring and smaller Pacific sardine were of similar length (Fig. 2.8) during this period. However, few yearling salmonids were captured at the end of July/early August, most had evidently migrated out of the study area.

Average April-July surface water (3-m) temperatures and salinities are heavily influenced by the Columbia River. However, both surface temperatures and salinities showed significant annual differences (ANOVA, $P < 0.001$, Fig. 2.9). Surface temperatures in 1998 and 2004 were significantly warmer (Tukey Multiple Range Test, $P < 0.05$) than other years, while surface temperatures in 1999, were significantly colder than other years (Tukey Multiple Range Test, $P < 0.05$). Surface salinities in 2001 were higher than all other years (Tukey Multiple Range Test, $P < 0.05$), reflecting the very low Columbia River flow conditions that year.

Salinity/temperature conditions at 50 m (below the effect of the Columbia River plume) were analyzed to identify if the subsurface "source" water changed during the study period. During 1998, an El Niño year, ocean waters were warmer and less saline than during other years (Fig. 2.10). From 1999 through 2001, salinities/temperatures were very similar, generally starting out in the spring at higher temperatures and lower salinities (no upwelling) and then shifting toward lower temperatures and higher salinities as upwelling caused deeper water to move up on the shelf. In 2002, waters at 50-m depth were much colder and less saline than in all other years (Fig. 2.10), reflecting intrusion of waters of subarctic origins. However, in 2003, while still colder than previous years, waters at 50-m depth did not have the strong subarctic signature as in 2002. Instead during spring these waters were relatively warm with low salinity, reflecting southerly and offshore origins (W. Peterson, NOAA Fisheries, Newport, OR pers. comm.,). This relatively warm, low salinity water was also observed in 2004 (Fig. 2.10).

Phytoplankton biomass can vary widely on the Oregon/Washington coast, but was not evident from the chlorophyll data. Chlorophyll *a* levels were similar within and among years (Fig. 2.11). However there were some extremely high levels, such as single chlorophyll measurements of 30 mg/l in 2000 and 2001. The highest annual median chlorophyll level was in 2003 (5.0 ug/l) and the lowest (1.8 ug/l) in 2001. There were significant differences in chlorophyll levels among years (Kruskal-Wallis test, P = 0.0013), with the 2003 chlorophyll values significantly higher than 2001 values (Dunn's Multiple Comparison Test, P <0.01). While ocean water temperatures and other physical parameters (both at the surface and at depth) changed significantly between years, it was not strongly reflected in the chlorophyll measures taken off the Columbia River.

The timing of the spring transition, when sustained upwelling begins along the Oregon coast, nearshore surface currents shift from northerly to southerly, and sea level drops, has been found to be important to salmon marine survival (Logerwell et al. 2003). During most of the 1990s, the spring transition each year occurred after 80 Julian days (22 March) (Fig. 2.12), but from 2000-2002, it shifted to an earlier time period (Fig. 2.12). Starting in 1999, and going through 2002, the spring transition came earlier than nearly all years between 1991 and 1998 (Fig. 2.12).

A comparison of physical oceanographic conditions off Oregon/Washington between 1991-1998, 1999-2002, and 2003-2004 revealed significant changes in sea surface temperatures after 1998 (Kruskal-Wallis, $P < 0.05$). As stated earlier, these groupings were formed because ocean conditions appeared to shift abruptly in 1999 and then again in 2003. Monthly sea surface temperatures off the Columbia River during the 1991-1998 period were significantly warmer than other periods (Dunn's Multiple Comparison Test, $P < 0.01$) (Fig. 2.13A), and 1999-2002 was warmer than the 2003-2004 period (Dunn's Multiple Comparison Test, $P < 0.01$) (Fig. 2.13A). However, these data are from the Columbia River buoy and are heavily influenced by Columbia River temperatures.

Average sea surface heights, which are indicative of geostrophic forcing, showed no statistical change between the three time periods (Kuskal-Wallis, $P = 0.14$)

(Fig. 2.13B). However, average monthly sea surface heights during 1991-1998 were higher (approximately 1 cm) than during 1999-2002.

In 2001, a drought year, Columbia River flows were much lower than normal and little if any spring (April-June) freshet occurred. Ignoring 2001 values, monthly average Columbia River flows were lower during 1999-2004 than during 1991-1998, but not strongly so (signed ranked test, $P = 0.065$; Fig. 2.13C). However, there were large fluctuations in flow during the two periods, such as February 1996, when the Columbia River had one of its highest flows on recent record (15,384 m^3s^{-1}) and May 2001, when it was lowest May flow on record (4,261 m^3s^{-1}). Columbia River flows produce a large plume off the Oregon/Washington coast and these wide fluctuations probably have biological effects.

Much of the fluctuations in the localized physical conditions off the Columbia River reflect the large-scale forcing indices of the North Pacific. Coho salmon marine survival also appears to be related to these indices (Fig. 2.14A). For example, while the local upwelling anomaly at 45ºW shows no clear pattern (Fig. 2.14E), the Pacific Decadal Oscillation (PDO) index (Fig. 2.14B), Multivariate El Niño Southern Oscillation Index (MEI) (Fig. 2.14C), and Northern Oscillation Index (NOI) (Fig. 2.14D), all show large changes starting in 1999. From 1991 to 1998, the PDO index was primarily positive, but starting in late 1998, the PDO became negative, and remained so until late 2002. The MEI was also positive for most of 1991-1998, and like the PDO, became negative in late 1998, turning positive again during the middle of 2002. The NOI, which is perhaps the best indicator of North Pacific atmospheric/oceanic conditions (Schwing et al. 2002) also showed an abrupt change in 1999, with anomalies becoming positive and staying mostly positive until 2002. The NOI anomalies remained negative all through 2003, and were similar to values observed during 1991-1998 (Fig. 2.14D).

Annual average forage fish densities (all species combined) showed a significant positive relationship with the previous year's northern copepod anomaly ($P = 0.002$, $R^2 = 91.0$) (Fig. 2.15). No other environmental variables, such as river flow, sea surface height, upwelling, etc., either singularly or in combination, showed any statistical relationship with annual forage fish densities (multiple linear regression, $P > 0.05$)

Only seven years of coho salmon OPI hatchery marine survival information were available during this study period, limiting the strength of the statistical analysis. However, annual coho salmon survival, like forage fish densities, varied widely, with hatchery coho salmon OPI marine survival ranging from 1.15% to 4.41% between 1998 and 2004 (Fig. 2.14A). There was no statistical relationship between annual average forage fish densities and coho salmon marine survival (regression, $P > 0.05$) (Fig. 2.16). Nevertheless, coho salmon marine survival from 1999-2003, years with large increases in forage fishes, were much higher than the 1990s, but still much lower than that observed during the 1970s. This indicates that while the number of forage fishes is probably an important factor influencing salmon marine survival, other environmental factors (number of predators, salmon health, salmon growth, etc.) also play a role in salmon marine survival, at least during this study period.

DISCUSSION

Is there any relationship between forage fish and juvenile salmon abundance?

Pearcy and Fisher (1988) and Pearcy (1992) hypothesized that fluctuations in the forage fish prey base play a critical link in juvenile marine survival by acting as "alternative" prey for piscivores. Large marine piscivorous predators, including large fishes, birds, and marine mammals feed on forage fishes and juvenile salmonids because they are similar in size and in the same habitat. There are three biological criteria that forage fishes must meet to act as alternative prey for juvenile salmonids in the marine environment. First, they must be abundant and occur in the same habitat as juvenile salmonid. This ensures that piscivorous fishes, birds, or mammals may find forage fishes more readily than salmon smolts. Secondly, forage fishes must arrive, or be abundant, when salmon smolts are most abundant, which is during the peak period of the smolt migration. Finally, forage fishes must be similar in size to salmonids. Piscivores are generally size selective, with fishes often preferring smaller prey and some birds and mammals preferring larger prey. Populations of northern anchovy, whitebait smelt, Pacific herring, and perhaps Pacific sardine, met these three criteria, and should have acted as alternative prey during the seven study years. However, statistical analysis indicated a poor relationship between annual forage fish abundance off the Columbia River and annual coho salmon marine survival. This suggests that other environmental factors, probably in concert with forage fish abundance, ultimately determine juvenile salmon marine survival.

Nevertheless, it is clear that when forage fishes are not available, piscivorous predators will prey upon juvenile salmonids. For example, when Caspian terns (*Sterna caspia*) nested at Rice Island in the Columbia River estuary, juvenile salmonids were their primary prey. Few other forage fishes were available at this site because low salinities prohibit marine forage fishes from inhabiting this portion of the estuary (Collis et al. 2002; Roby et al. 2002). When Caspian terns were successfully encouraged to nest in the lower Columbia River estuary at East Sand Island, an area with high salinities, they switched to feeding primarily on abundant marine forage fishes (Roby et al., 2002)

It appears that during the 1990s, forage fishes were not abundant in Oregon/Washington waters, especially in spring when salmon smolts were migrating to sea. For example, in the late 1990s the bait fishery for northern anchovy in the Columbia River estuary was eliminated because northern anchovy were unavailable (E. McClure, commercial fisherman, Ilwaco, WA, pers. comm.). The low abundance of forage fishes off Oregon/Washington during the late 1990s may be partially responsible for the poor ocean salmonid marine survival during that period. The one forage fish species that did become abundant in the late 1990s, Pacific sardine, usually does not arrive in numbers off Oregon/Washington until after the peak salmonid smolt migration (late spring and summer) (Emmett et al. 2005).

The shift in North Pacific and Pacific Northwest environmental conditions observed in 1999 (this study; Peterson and Schwing 2003), was signified by the end of an

El Niño and beginning of a La Niña period. This environmental shift initiated biophysical changes in Pacific Northwest coastal waters that were accompanied by increasing marine survival of salmonids and also increased forage fish abundance. The beginning of the forage fish increase may have actually been initiated during the El Niño of 1997/1998. During a previous strong El Niño, summer 1983, northern anchovy spawned over a wide temporal and geographic range off Oregon (Brodeur et al. 1985) and dominated the diet of juvenile coho and Chinook salmon that fall (Brodeur and Pearcy 1990). Two years later (1985), when northern anchovy from the 1983 year-class became adults, there were large numbers of anchovy off the Oregon coast (Emmett and Brodeur 2000). Perhaps not coincidentally, coho salmon marine survival in 1985 was 7.6%, the highest observed since 1975.

Northern anchovy, whitebait smelt, and Pacific herring showed large population increases after 1999. These species prefer cool ocean conditions, the same conditions that Cole (2000), Hobday and Boehlert (2001) and others have found correlate well with high salmonid marine survival. Unfortunately, while we know where and when northern anchovy spawn off Oregon, we presently do not know the spawning locations of the whitebait smelt and Pacific herring populations that reside off the Oregon/Washington coast. As such, these populations may be vulnerable to changes in Columbia River flows or other anthropogenic influences. We also do not know if the Pacific herring or whitebait smelt captured during this study are a local population (i.e., spawning in or around the Columbia River estuary) or are from adults spawning elsewhere and rearing off the Columbia River. As such, the population biology of these species needs additional study.

Pearcy (2002) noted that the strong El Niño of 1997-1998 did not lower salmon marine survival (marine survival was already very low) or cause dramatic reduction in adult salmon size, as was observed during the 1983 El Niño. I speculate that because of warm El Niño conditions, some Pacific sardine may have overwintered off Oregon during 1997-1998, and served as alternative prey, thus reducing predation on salmonid smolts. Pacific sardines were abundant off Oregon in summer and fall of 1998, and provided an abundant, high-energy prey for piscivorous adult salmonids. Adult coho and Chinook salmon have been relatively large the last few years, indicating excellent adult feeding conditions (i.e., abundant forage fish). Ultimately, large adult size is reflected in large egg size, which usually enhances egg hatching and alevin survival (Fleming and Gross 1990; Einum and Fleming 1999). This suggests that a large west coast sardine population may be important to Pacific Northwest adult salmonids during El Niño or warm ocean conditions.

Beamish et al. (2001) found no relationship between coho salmon abundance and the spawning biomass of Pacific herring in the Strait of Georgia, Canada. While this coho salmon population declined in the 1990s, spawning biomass of herring in the Strait increased. I suggest another possible explanation why no relationship was found; adult Pacific herring spawning biomass may not be an appropriate measure of forage fish resources in the Strait of Georgia. Little is known about the migrational behavior of adult and juvenile Pacific herring during spring and summer, but herring often migrate far away from their spawning grounds. If Strait of Georgia/Puget Sound Pacific herring (or other forage fish) were unavailable to salmon predators during the coho salmon smolt migration period, predators could have consumed salmonids instead. Direct measurement of Pacific herring abundance in the Strait of Georgia during the juvenile coho salmon smolt migration would be very valuable. The decrease in coho salmon survival in the Strait of Georgia, Canada, (and Puget Sound, WA) during the 1990s does correlate well with large decreases in Pacific herring spawning biomass in adjacent Puget Sound, Washington, USA. Some Pacific herring stocks in Puget Sound were at such low abundance that there were petitions to list them as threatened with extinction (Stout et al. 2001). Finally, as I observed off the Columbia River, other forage fish species probably play important roles as alternative prey for juvenile salmonid predators during the early ocean entry period. Only surveys that measure the abundance of all forage fish species during the salmonid migrational period will adequately identify which forage fish species are important to salmonid marine survival within an ecosystem.

Others have reported alternative prey or prey-switching as a factor determining juvenile salmonid early marine survival. Willette (2001) and Willette et al. (2001) showed that in Prince William Sound, Alaska, two normally planktivorous fishes, Pacific herring and walleye pollock (*Theragra chalcogramma*), switched to feeding on juvenile pink salmon (*O. gorbuscha*) when the abundance of their preferred prey (large copepods), dropped below a threshold level, and that this predation determined eventual run sizes of pink salmon. I believe the same functional relationship (predators consuming more salmonids when their primary prey are reduced in abundance) could be true off the

Columbia River and the Oregon/Washington coast. However, because densities of salmonids are so low in our study area, additional salmonid predation will be difficult to observe. Studies in Prince William Sound (Cooney et al. 2001), Barents Sea (Borgstad and Mehl 1997), Bering Sea (Livingston and Jurado-Molina 2000), northeastern USA (Overholtz et al. 1991) and other regions, indicate that predation on juvenile fishes may determine recruitment levels for many species of fishes (Bax 1998).

Why the increase in forage fishes after 1999?

Forage fish densities were positively related to the abundance of northern copepod species the previous year. The change in zooplankton species composition and densities that started in 1999 (Peterson and Schwing 2003) may have increased larval forage fish survival and recruitment. Fish larvae must have appropriate food densities and perhaps species composition to survive (Lasker 1981; Davis and Olla 1992; Watanabe 1993; Masuda 2003). Abundant northern, cold-water copepod species may be necessary food for the survival of larval anchovy, herring, and whitebait smelt. Northern cool-water copepod species have high concentrations of highly unsaturated fatty acids (HUFAs) compared to southern, warm-water copepods (Davis and Olla 1992, Peterson, pers. comm.). HUFAs are critical for larval fish survival (Davis and Olla 1992) because fish can not synthesize these necessary fatty acids from other molecules (Watanabe 1993; Masuda 2003).

Columbia River flow was not statistically related to annual forage fish densities, even after accounting for northern copepod abundances. However, river plumes have been found to be important habitat for larval fishes (Castro et al. 2000; Grimes 2001). Furthermore, Richardson (1981) noted that northern anchovy spawn in the Columbia River plume, and postulated that northern anchovy larvae gain survival benefits in this low salinity/stable water mass. River plumes also create convergent frontal regions, or eddies, locations of high zooplankton densities, which can enhance larval fish survival (Okazaki et al. 2002). If fewer, and smaller, frontal convergent regions are created under low flow conditions, low Columbia River flows may result in lower forage fish recruitment. A large drop in forage fish densities (2002) was observed one year after Columbia River flows were very low (2001), but again, no statistical relationship between flow and forage fish abundance was determined. Nevertheless, I hypothesize that forage fish recruitment off Oregon/Washington depends on both cool-water zooplankton species and densities, and adequate Columbia River spring flows. However, a longer time series and larval fish data are necessary to adequately evaluate this hypothesis.

Forage fish densities off the Columbia River appear to be responding to the copepod community changes brought on by major physical and biological changes in the Northeast Pacific. Most obvious was the strong La Niña of 1999, which ended a long period of warm ocean conditions, and the strong El Niño of 1997-98 (Durazo et al. 2001), after which many ocean indices changed sign (Figs. 2.12 and 2.14). The anomalous cold ocean conditions in 2002 are well documented (Huyer 2003; Kosro 2003; Strub and James 2003; Wheeler et al. 2003), and responsible for the high primary production and low oxygen conditions observed off the Oregon coast in 2002. These cold, nutrient rich waters resulted from an increase in the transport of subarctic waters to Oregon in 2002 (Kosko 2003; Strub and James 2003). As a result, Pacific Northwest waters became cooler, both at the surface and subsurface (Figs. 2.9 and 2.10; Bond et al. 2003), sea surface height was lower (Fig. 2.13; Strub and James 2003), and southerly transport increased. These physical factors are indicators of increased subarctic waters, increased nutrients, and primary production, which evidently led to the shift in zooplankton composition and abundance, with subarctic species replacing transition species (Peterson and Mackas 2001; Peterson et al. 2002; Peterson and Schwing 2003; Schabetsburger et al. 2003). However, the copepod abundance/species change did not affect juvenile Chinook and coho salmonids directly because juvenile salmon eat few copepods (Peterson et al. 1982; Emmett et al. 1986; Brodeur and Pearcy 1990), but the increased cold-water copepods clearly enhanced forage fish populations that do feed on copepods (this study). Coastal Pacific Northwest forage fishes, especially whitebait smelt, northern anchovy, and Pacific herring populations, responded strongly to the observed changes in primary and secondary production. Hollowed et al. (2001) and McFarlane et al. (2000) noted similar fishery recruitment responses to basin-wide changes in the Pacific Ocean.

The abundance and distribution of piscivorous predators is an additional factor that can influence forage fish abundance along the Oregon/Washington coast. There is evidence that the distribution of Pacific hake (a dominant forage fish predator) along the west coast changed markedly starting in the early 1990s (McFarlane et al. 2000). In the early 1990s, a large proportion of the west coast hake population resided in Canadian waters, with many not undertaking their ‘normal’ winter migration to southern California to spawn. Instead these hake remained off coastal British Columbia, Oregon, Washington, and northern California (McFarlane et al. 2000). Off the west coast of Vancouver Island, Canada, the large number of Pacific hake ultimately led to increased predation on Pacific herring and a crash of the western Vancouver Island herring stock (Ware and McFarlane 1995). I suspect that the same phenomenon may have occurred off Oregon/Washington, and led to reduced abundance of northern anchovy, Pacific herring, and smelt during the 1990s. Starting in late 1998 (the beginning of the La Niña), cooler ocean temperatures and increased southern transport appear to have reestablished the typical fall/winter hake migration pattern, to southern California waters, reducing predation pressure on forage fishes.

CONCLUSIONS

The recent large salmonid runs in the Pacific Northwest and the Columbia River are related to increased juvenile salmonid marine survival (NPCC 2003; Williams et al. 2005). Pacific Northwest marine survival is correlated to coastal ocean conditions linked to large changes in the North Pacific Ocean pelagic ecosystem. There have been few studies of the pelagic fish ecosystem off the Pacific Northwest to identify the relationship between the abundance of pelagic fishes, ocean conditions, and improved salmonid marine survival, perhaps because there were few commercial fisheries for small pelagic fishes. As such, population abundance and fluctuations of forage fishes off Oregon/Washington were poorly known. The pelagic fish survey data indicate that small coastal forage fish populations off the Northwest coast were depressed in 1998 and 1999, and perhaps earlier, but increased significantly after 1999, with this increase directly related to increased abundance of northern copepod species the year before and reduced hake predation. Annual forage fish densities off the Columbia River were not found to be statistically related to coho salmon marine survival, indicating that additional oceanographic factors determine juvenile salmon marine survival. Only through continued studies of the pelagic ecosystem off Oregon/Washington will scientists have a time series long enough to identify the bio/physical mechanisms that influences salmonid marine survival during any particular year.

ACKNOWLEDGEMENTS

Drs. William Pearcy, Richard Brodeur, and Edmundo Casillas provided excellent reviews and comments on earlier versions of this paper. Special thanks to the captains and crews of the FV Sea Eagle and FV Piky; Dan Parker, Bob Williams, Ed Grotting, Steve McGuire, and John Owens. Special appreciation to all the summer students, Jeff Muir, Emily Locke, Cascade Sorte, Liz Davis, and James Douglas, and NMFS and CIMRS employees, Susan Hinton, Joe Fisher, Todd Miller, Cheryl Morgan, Leah Feinberg, and Laurie Weitkamp, who provided such able assistance. It was only with their hard work and dedication that this research was undertaken. NOAA Fisheries and Bonneville Power Administration supported this research.

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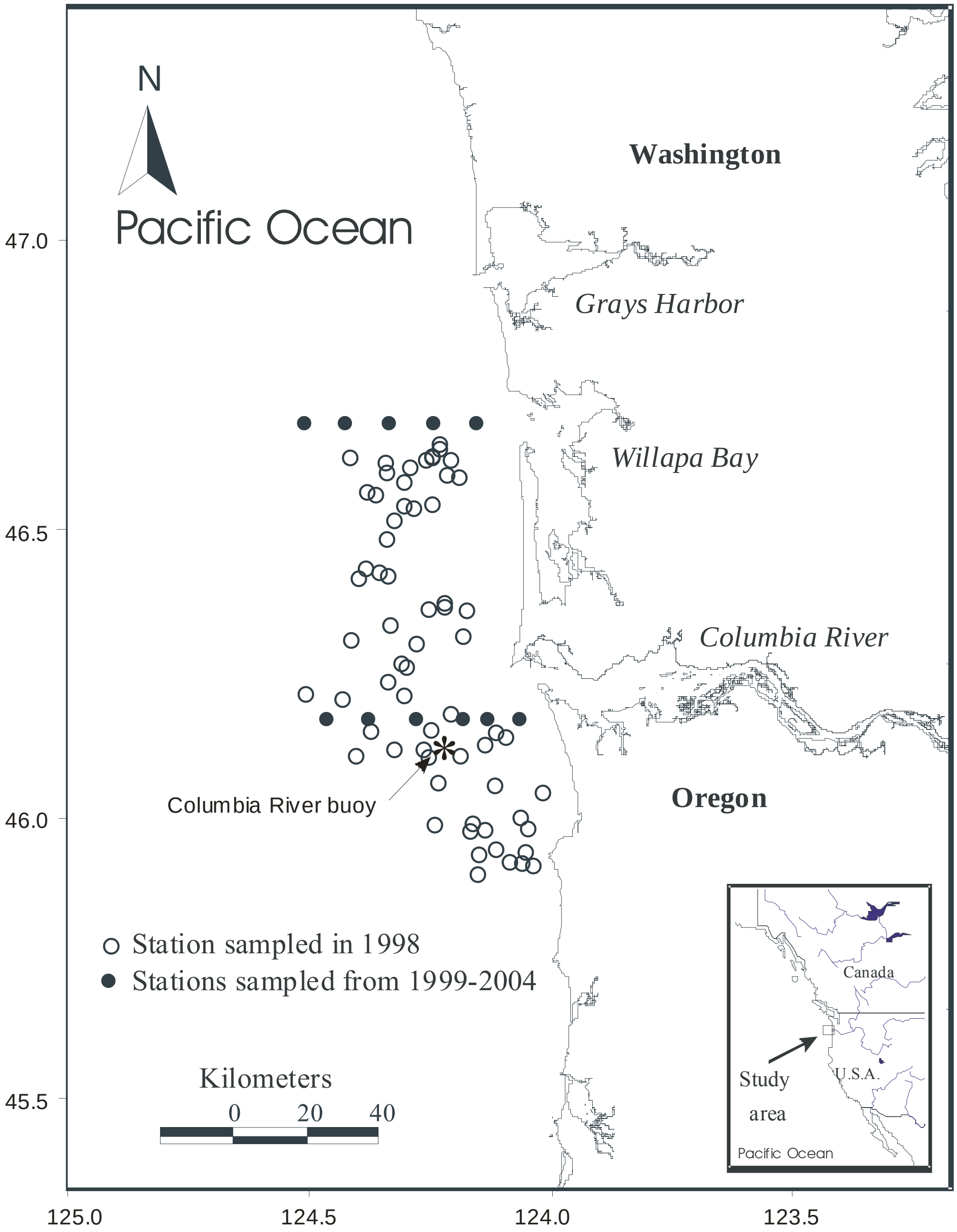


Figure 2.1. Station locations off the Columbia River sampled by surface trawl for pelagic fishes, 1998 through 2004.

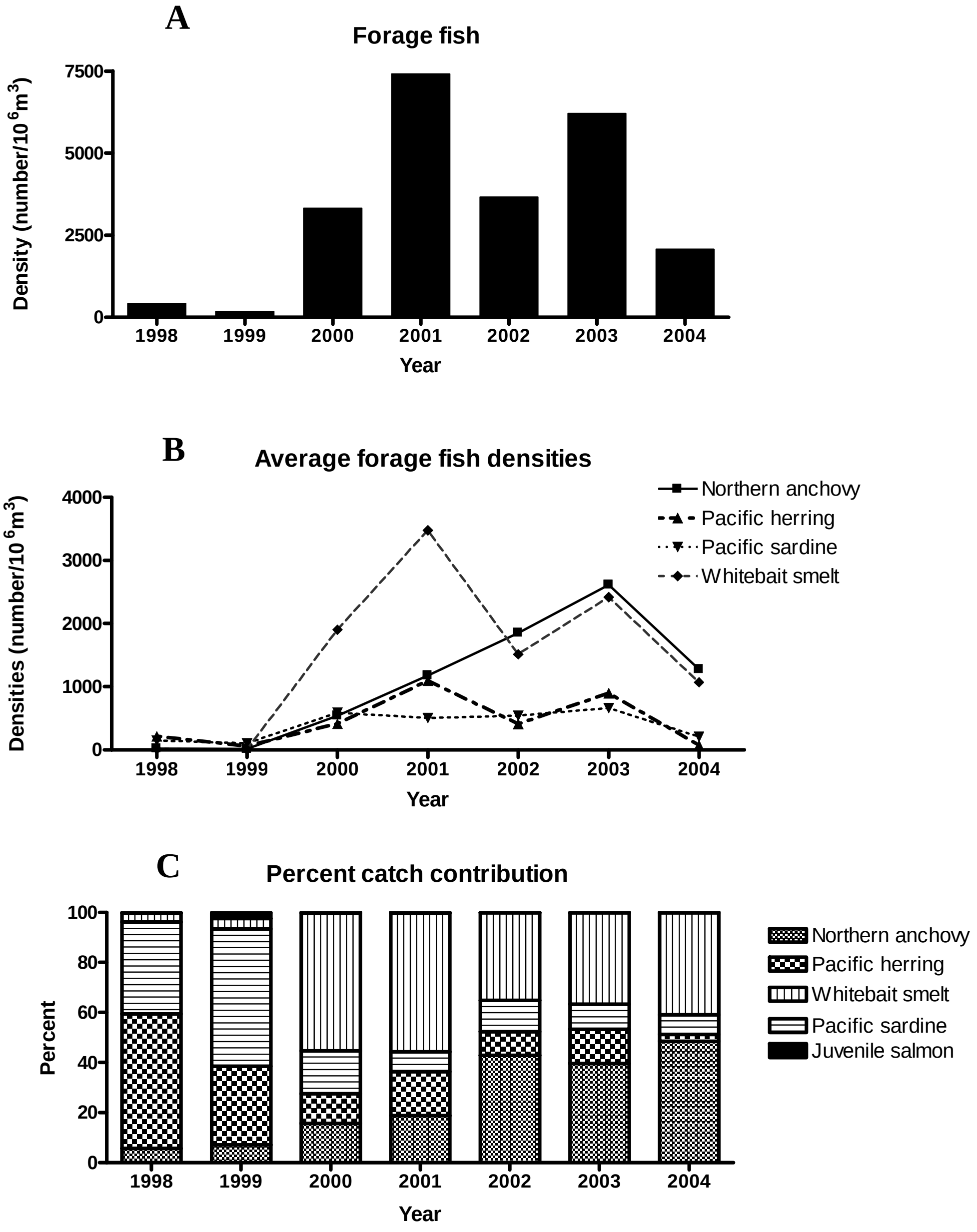


Figure 2.2. Average annual total forage fish densities (A), annual average densities by forage fish species (B), and annual percent catch contribution by species (C) off the Columbia River, 1998 through 2004. Forage fishes include whitebait smelt (*Allosmerus elongatus*), Pacific sardine (*Sardinops sagax*), Pacific herring (*Clupea pallasii*), and northern anchovy (*Engraulis mordax*). Juvenile salmon include Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*).

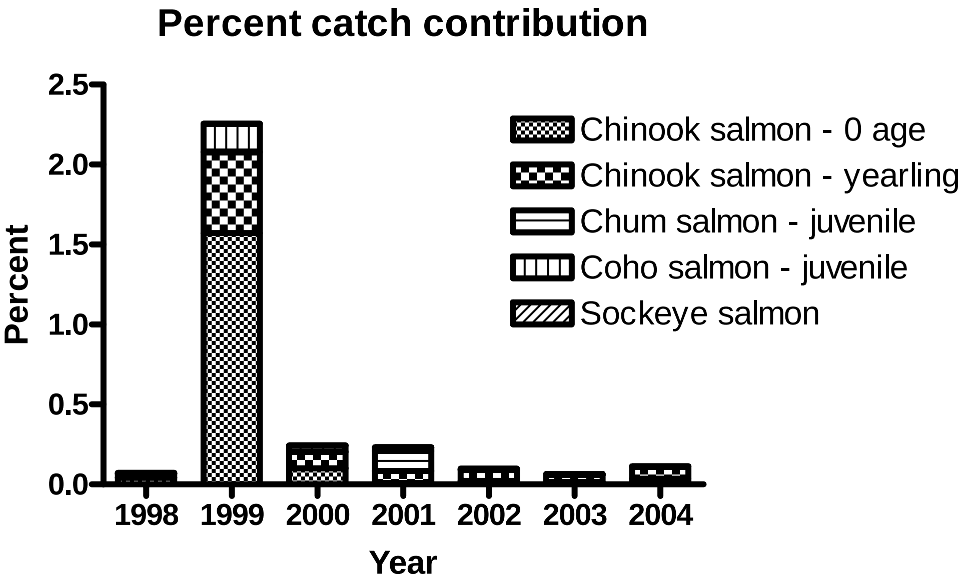


Figure 2.3. Percent of the total forage fish community composed by juvenile salmonids during surface trawling, 1999-2003. Juvenile salmon include Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*)

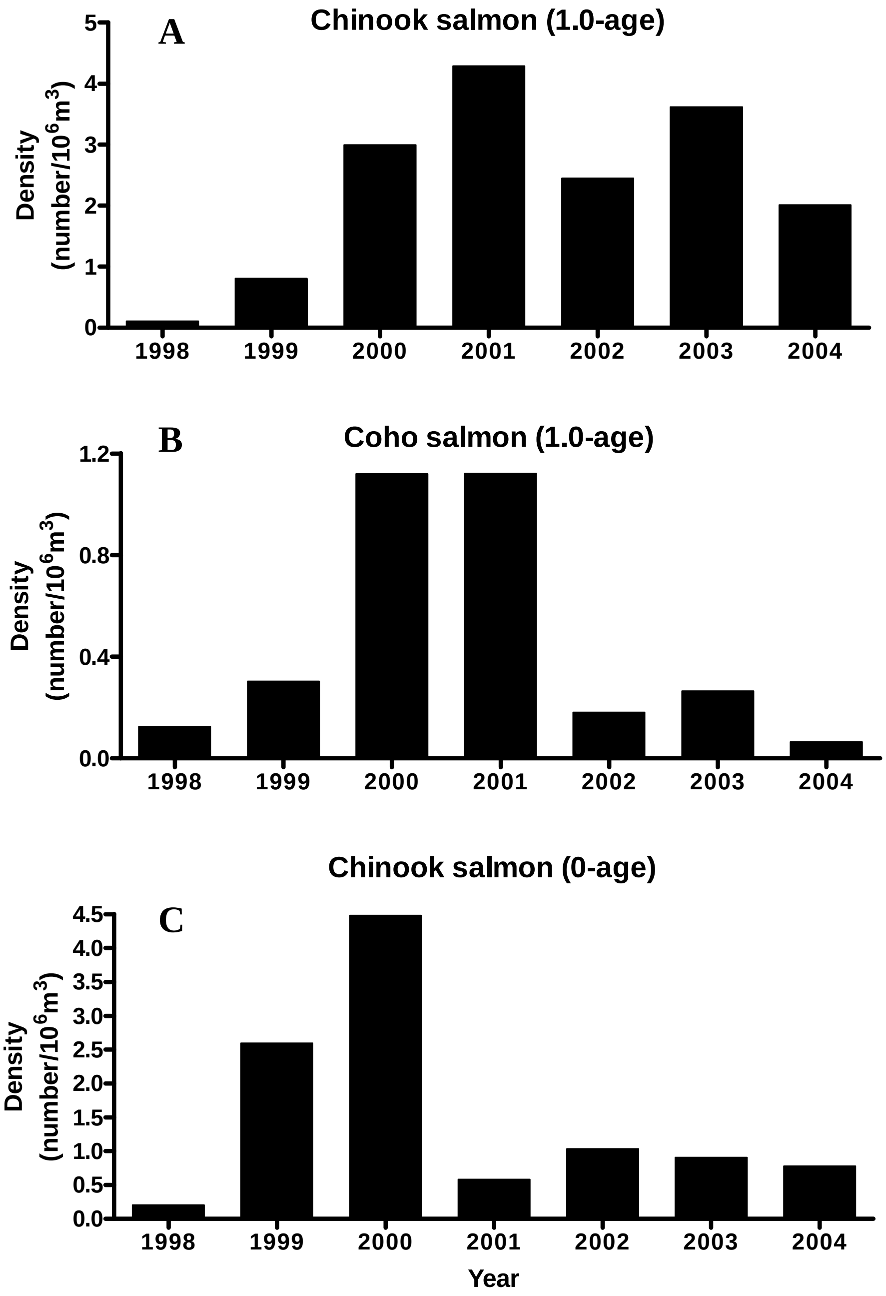


Figure 2.4. Annual average densities of juvenile Chinook (two age-classes) and coho salmon off the Columbia River, 1998 through 2004. Age classes of salmonids are shown in parenthesis after the common name, with years in fresh water represented as the number before the decimal, and years at sea the number after the decimal.

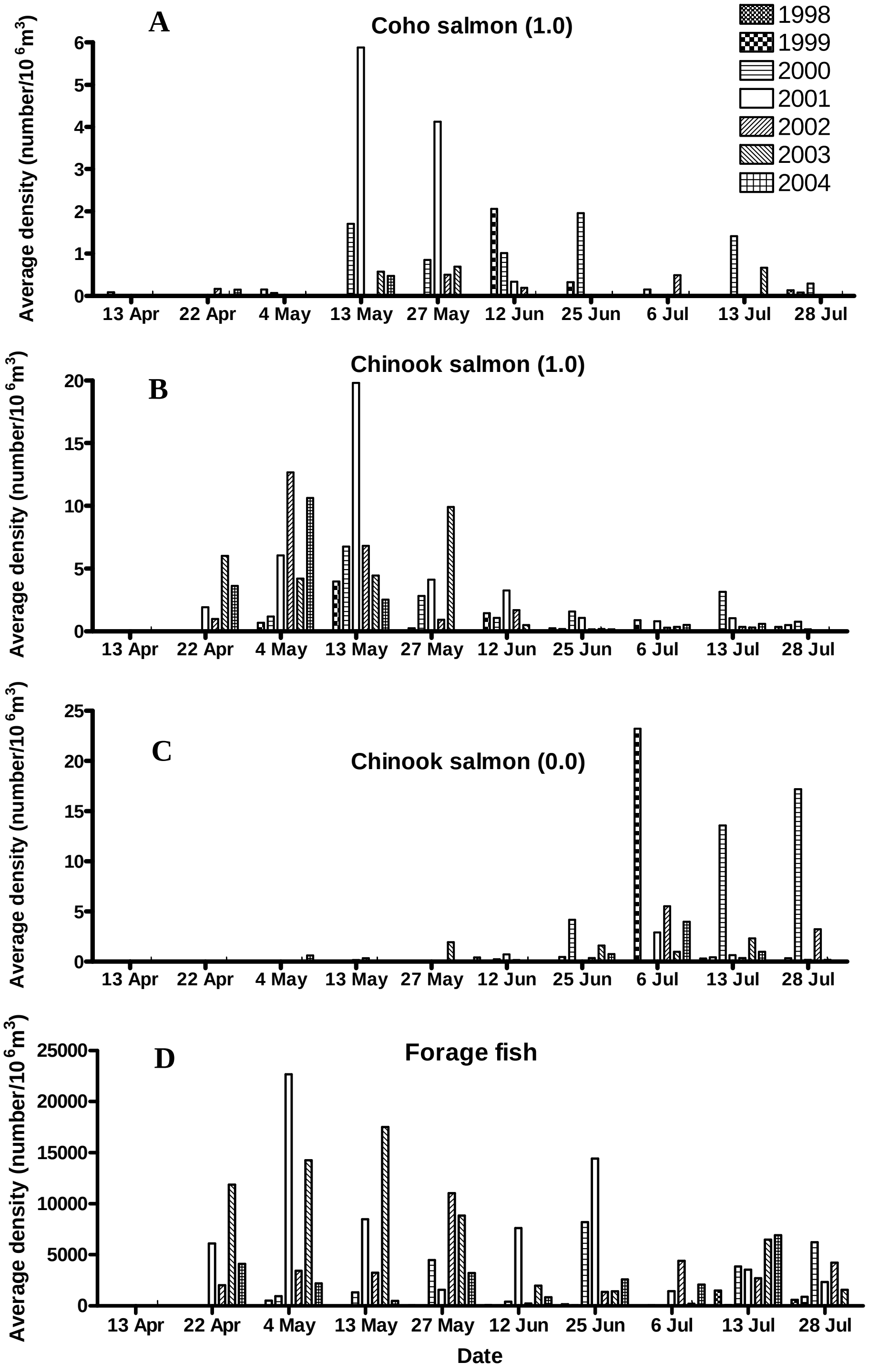


Figure 2.5. Average densities of Chinook salmon (two age classes), coho salmon, and forage fishes (northern anchovy, Pacific herring, Pacific sardine, and whitebait smelt) by survey date.

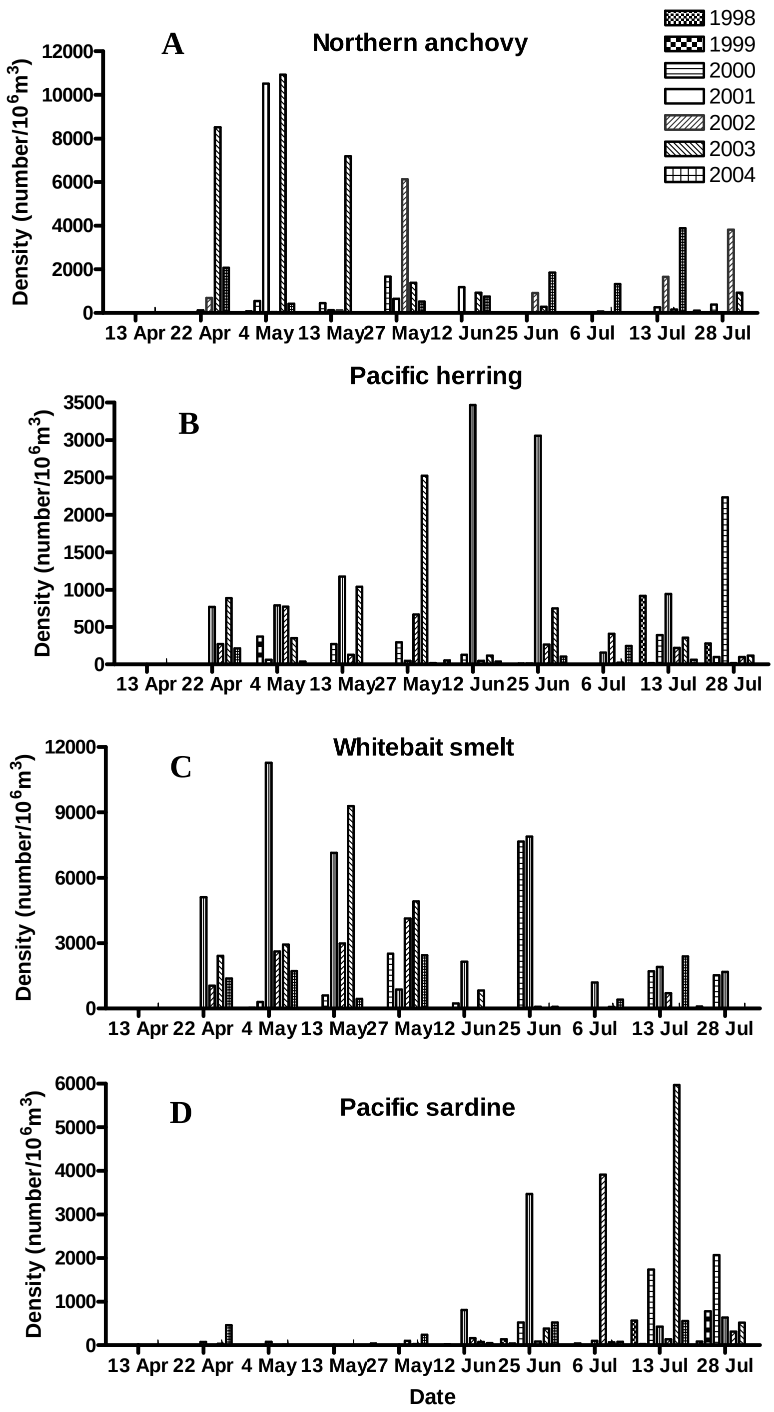


Figure 2.6. Average densities of northern anchovy, Pacific herring, whitebait smelt, and Pacific sardine by survey date.

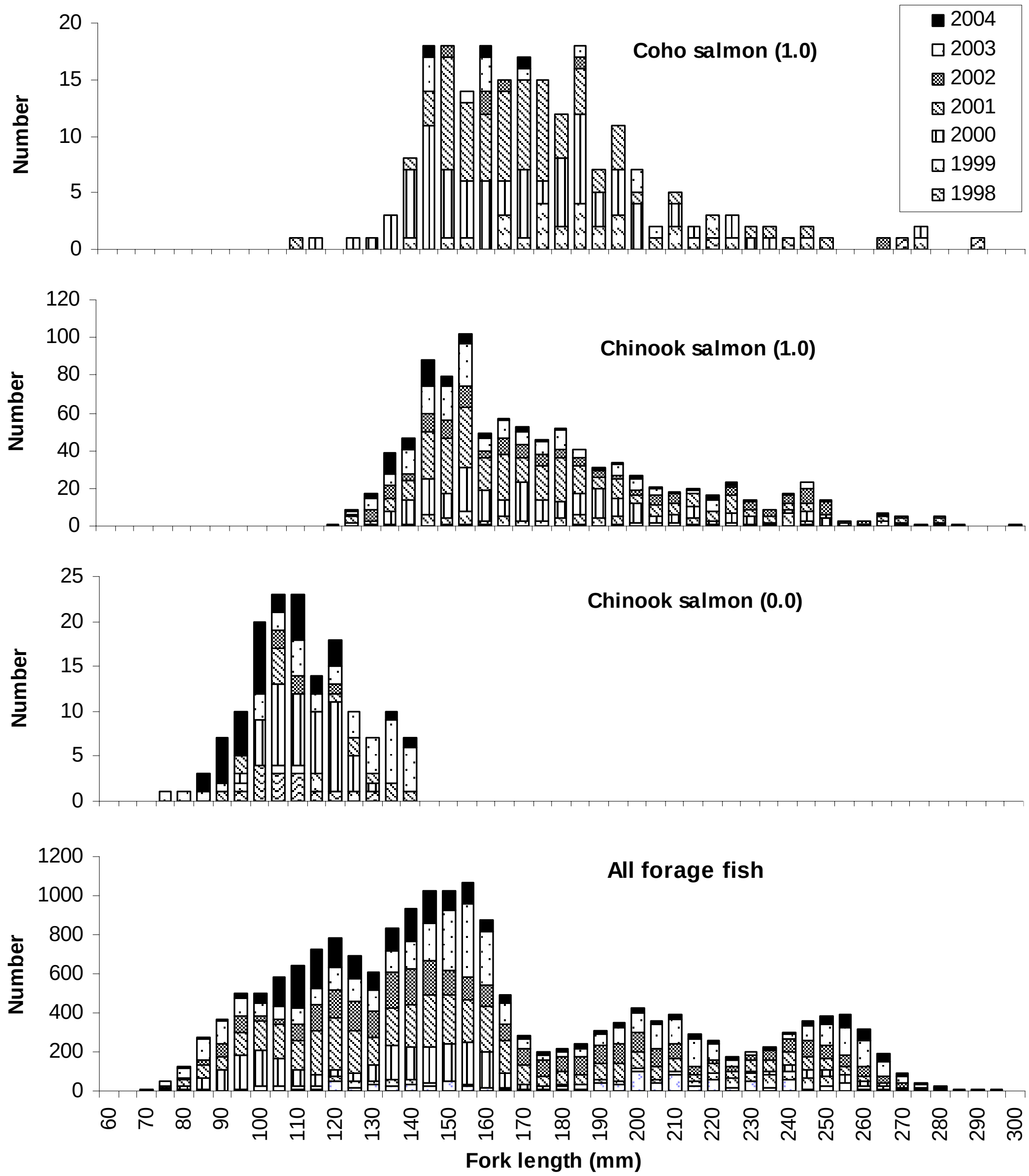


Figure 2.7. Annual May/June length frequency distributions of juvenile coho salmon, Chinook salmon (two age classes) and forage fishes off the Columbia River 1999-2004. Forage fishes were composed of northern anchovy, Pacific herring, whitebait smelt, and Pacific sardine. Age classes of salmonids are shown in parenthesis after the common name, with years in fresh water represented as the number before the decimal, and years at sea, the number after the decimal.

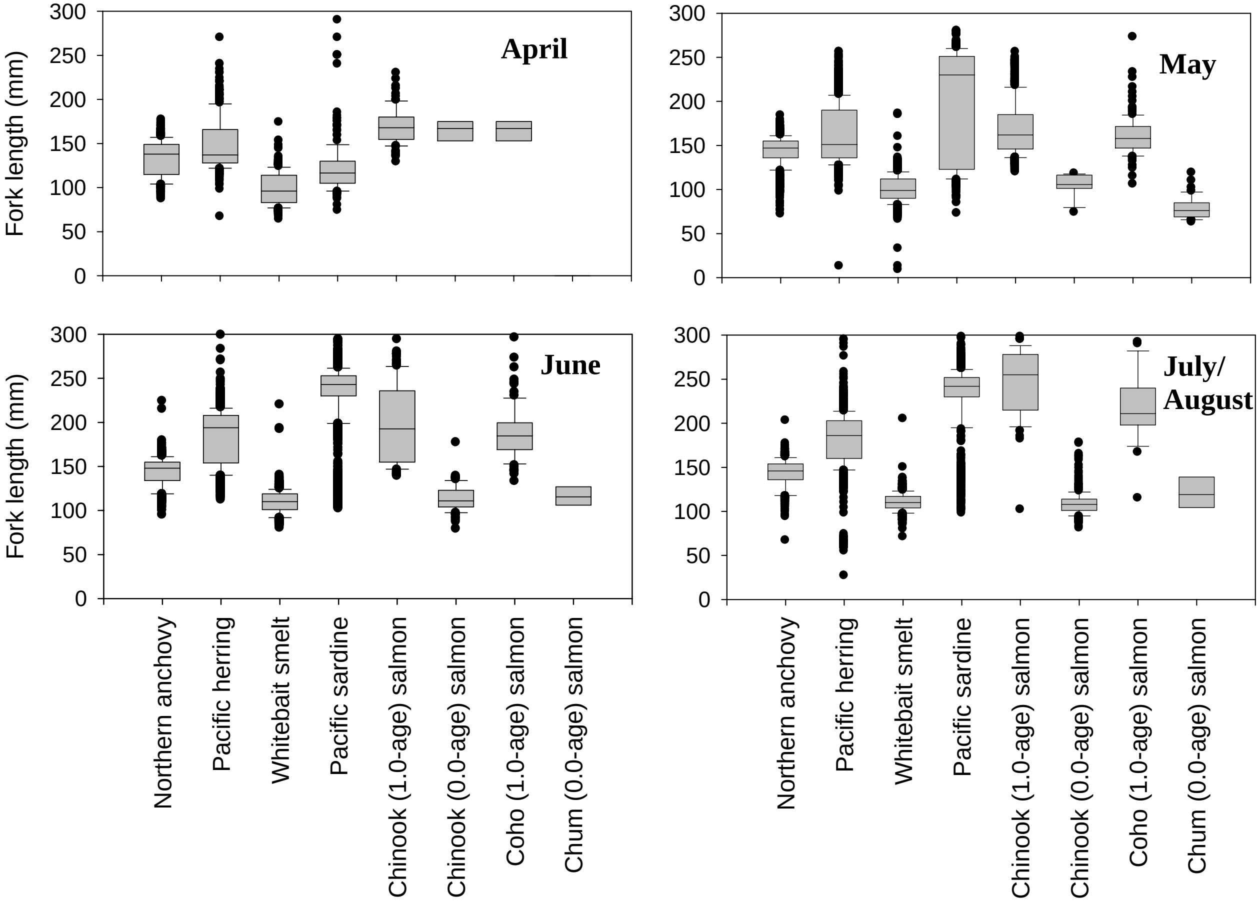


Figure 2.8. Box and whisker plots of fork lengths of forage fishes and salmonids by month collected off the Columbia River, 1999-2003. Whiskers of the box plots represent the 10th and 90th percentiles, with the line in the middle of the box representing the median. Dark circles above and below a box plot represent outlier values. Age classes of salmonids are shown in parentheses after the common name, with years in fresh water represented as the number before the decimal, and years at sea the number after the decimal.

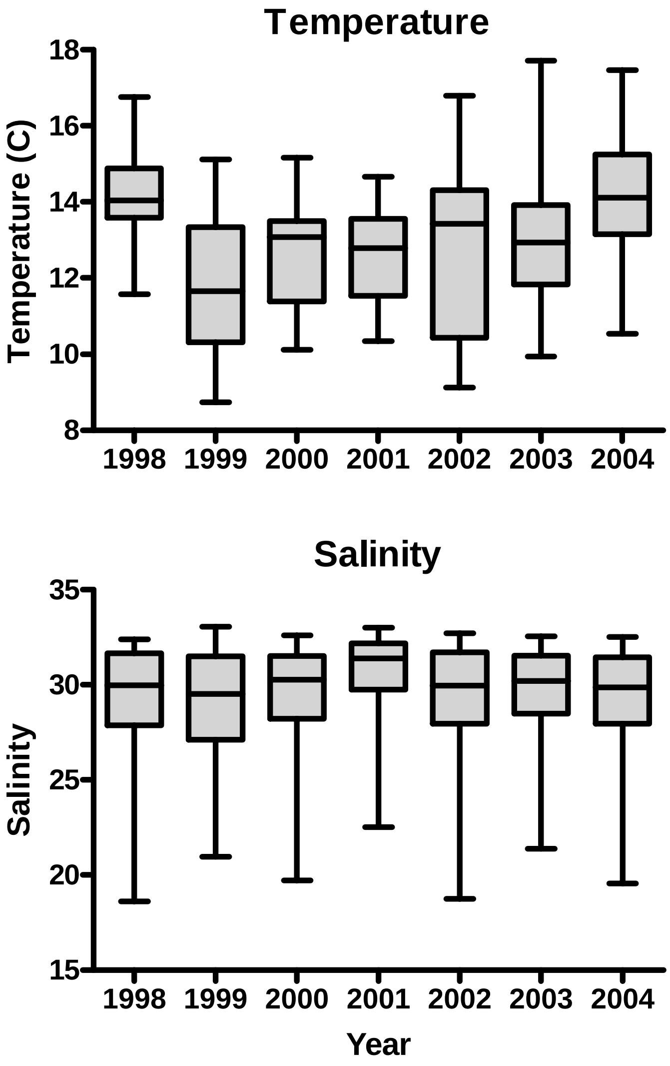


Figure 2.9. Box and whisker plots of April-July temperatures and salinities at 3-m depth off the Columbia River, 1998-2004.

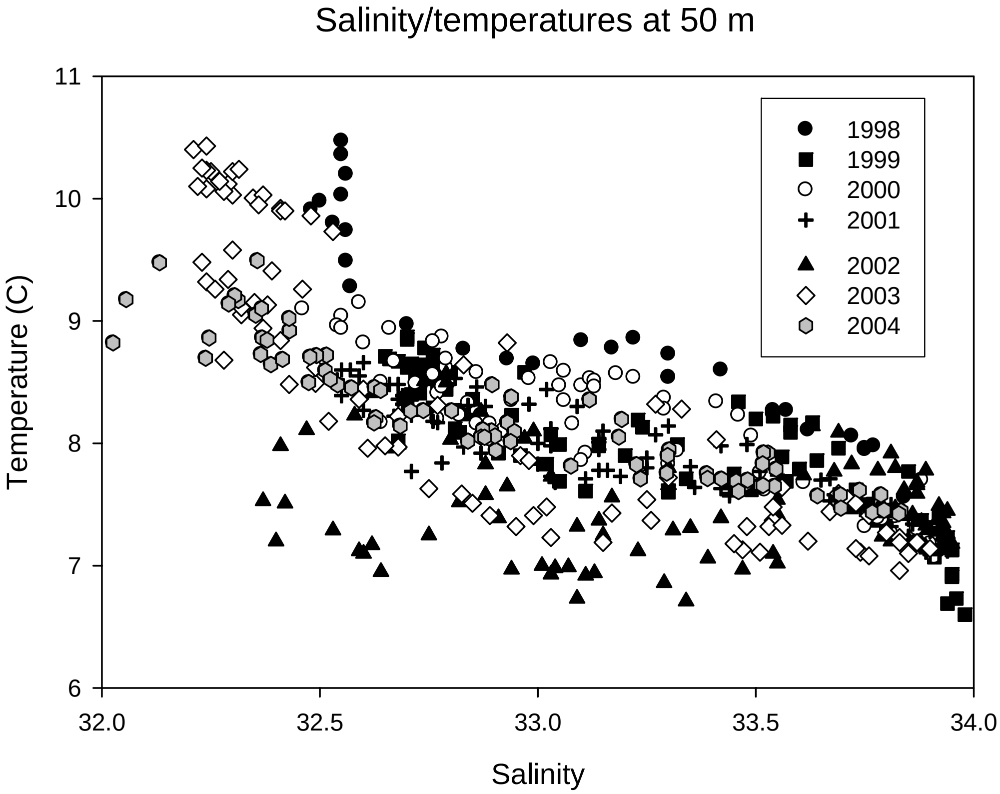


Figure 2.10. Salinity and temperatures at 50 m depth from all stations sampled from 1998-2004.

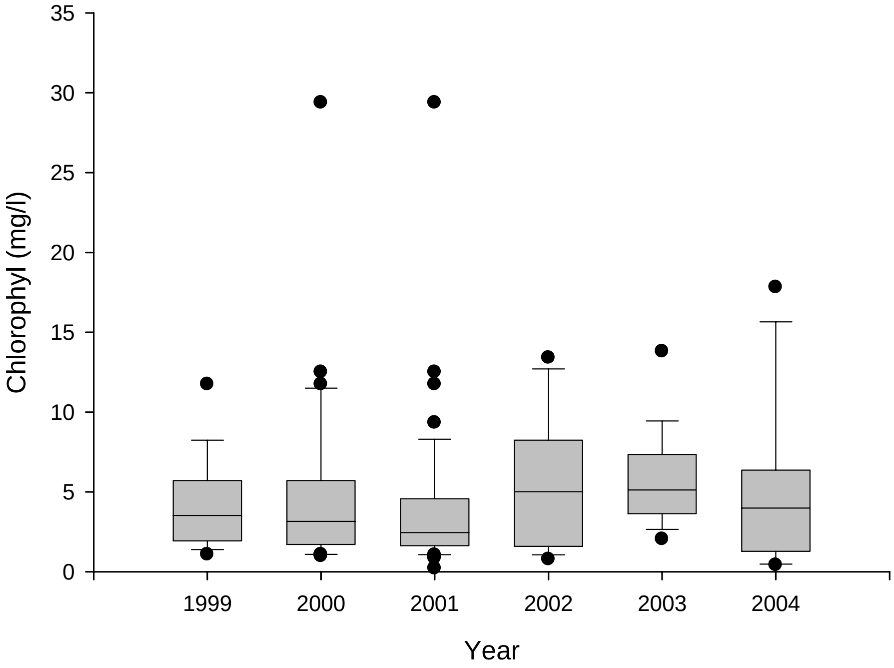


Figure 2.11. Box plot of chlorophyll *a* levels observed off the Columbia River from April-July 1998-2004.

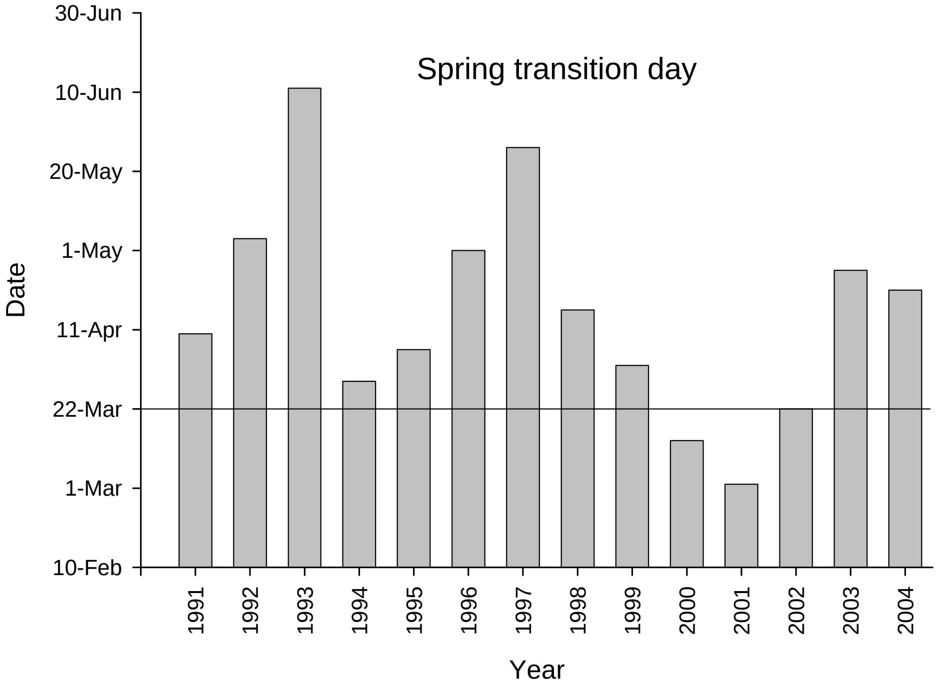
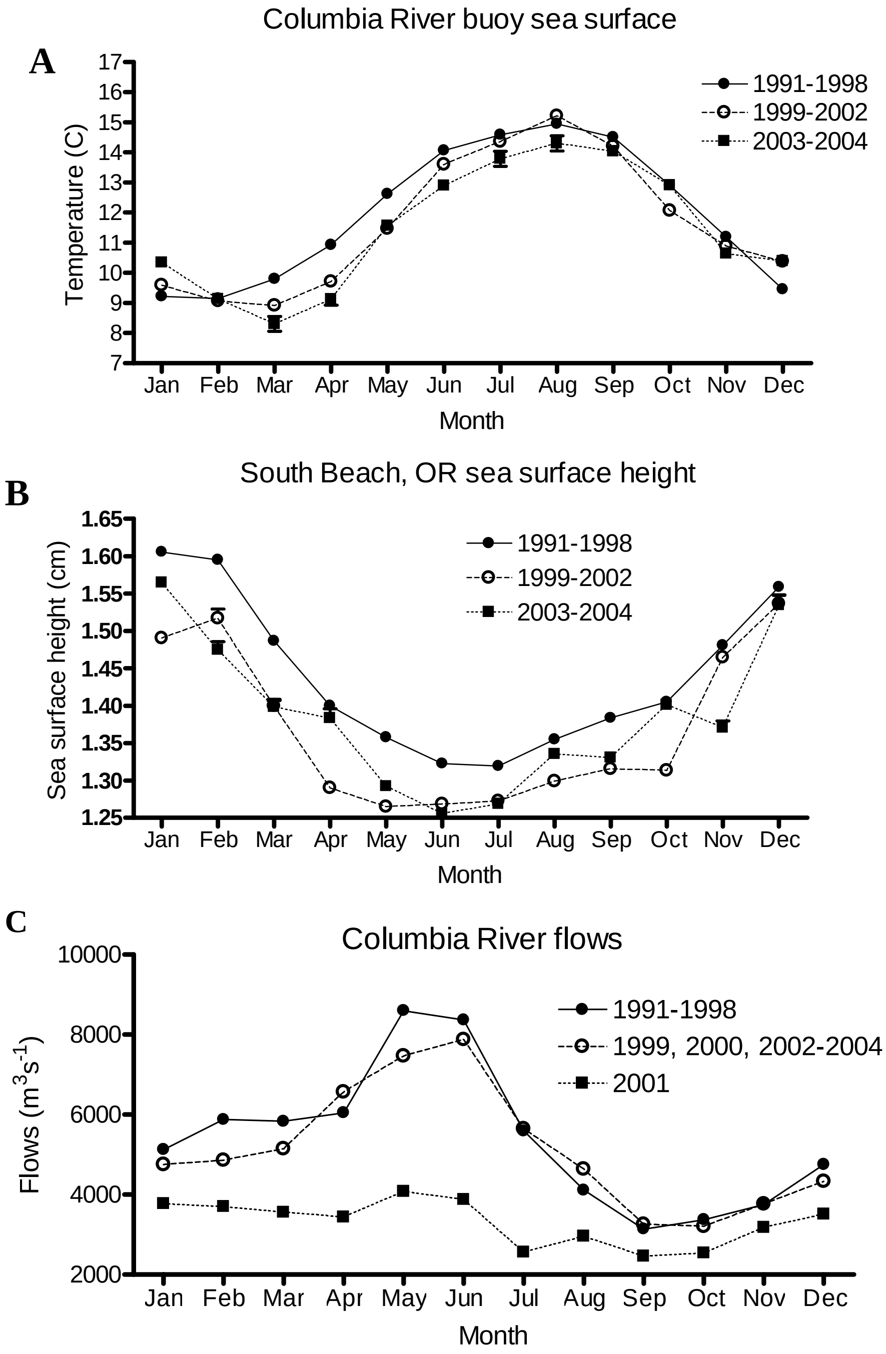


Figure 2.12. Date of the spring transition off the Pacific Northwest from 1991 to 2004 as defined by Logerwell et al. (2003).


Columbia River buoy sea surface

South Beach, OR sea surface height

Columbia River flows

Figure 2.13. Average monthly Columbia River buoy sea surface temperatures (A) and South Beach, OR sea surface heights (B) for three time periods: 1991-1998, 1999-2002, and 2003-2004. Also shown are average monthly Columbia River flows (C) for 1991-1998; 1999-2000, 2002-2004; and 2001.

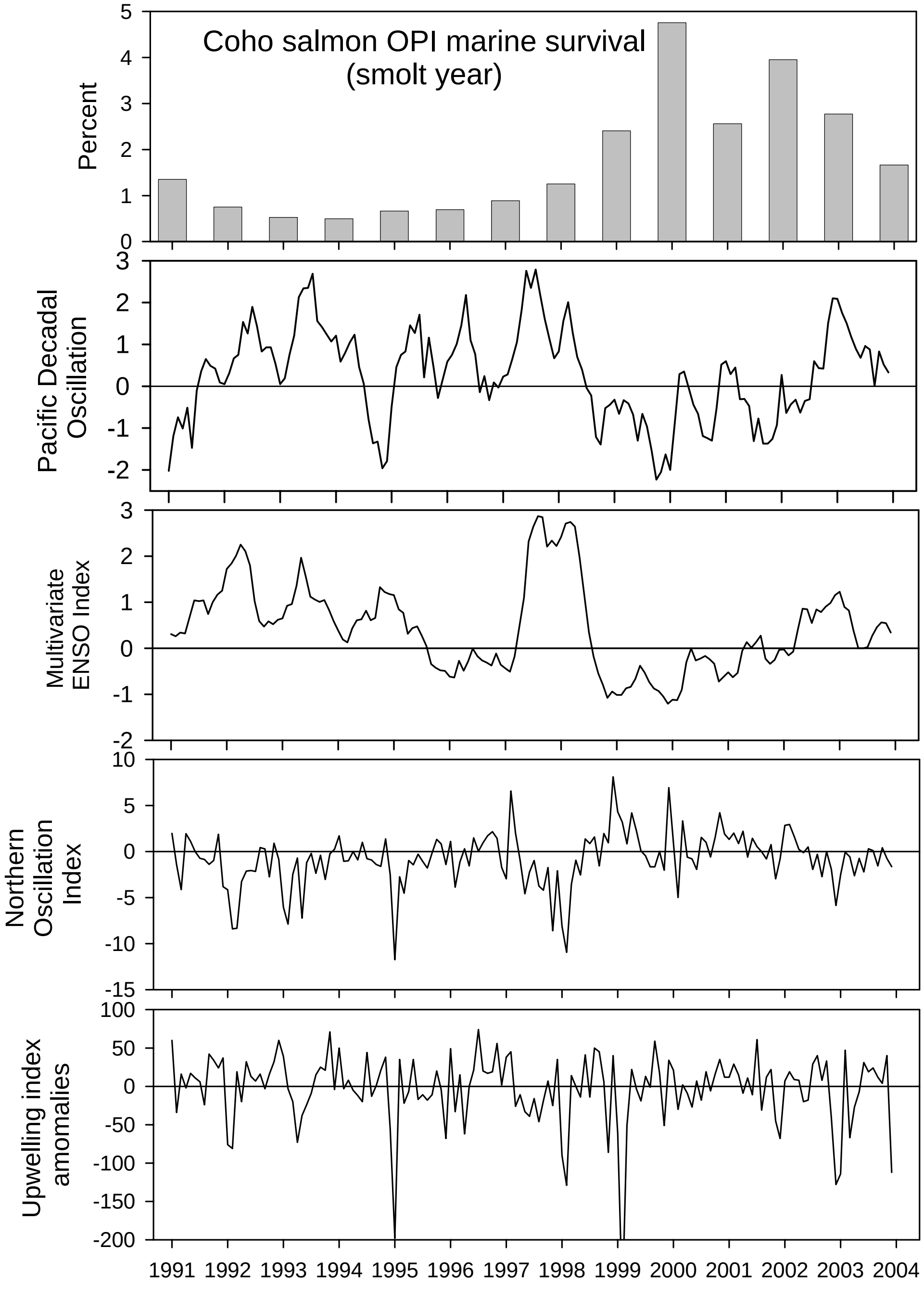


Figure 2.14. Oregon Production area Index (OPI) of hatchery coho salmon marine survival by year of ocean entry (A) and four indices of ocean conditions; the Pacific Decadal Oscillation index (B), Multivariate El Niño Southern Oscillation (ENSO) index (C),Northern Oscillation Index (D), and upwelling anomalies at 45ºN 125ºW (E).

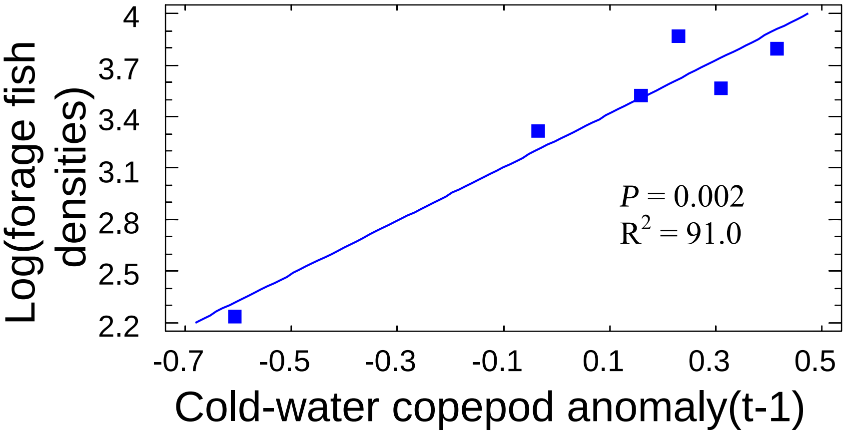


Figure 2. 15. The relationship between annual forage fish densities and cold-water copepod anomalies the previous year (t-1).

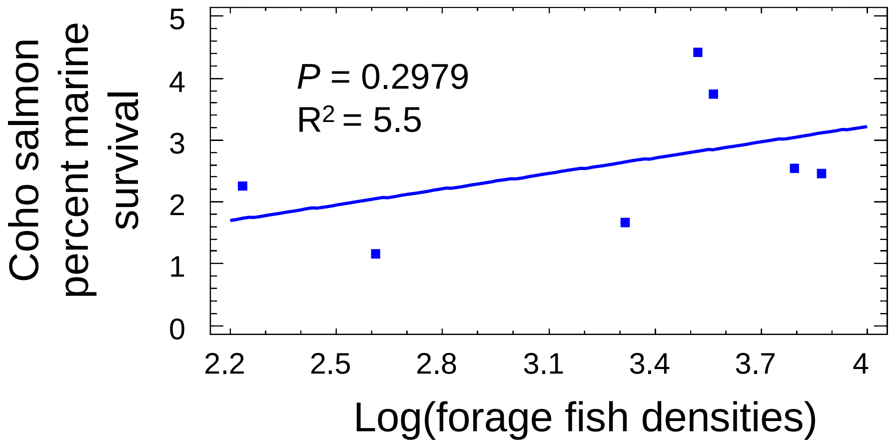


Figure 2. 16. The relationship between annual densities of forage fishes off the mouth of the Columbia River and hatchery coho salmon (*Oncorhynchus kisutch*) marine survival.

Chapter 3. Abundance and Distribution of Pelagic Piscivorous Fishes in the Columbia River Plume During Spring/Early Summer 1998-2003: Relationship to Oceanographic Conditions, Forage Fishes, and Juvenile Salmonids.

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Progress in Oceanography
Elsevier Inc.
Radarweg 29, Amsterdam 1043, The Netherlands
Volume 68(2006):1-26.

ABSTRACT

From 1998 to 2003, we observed large fluctuations in the abundance and distribution of four pelagic predatory (piscivorous) fishes off N Oregon/S Washington. Fluctuations in predatory fish species composition and abundance were strongly linked to the date of the spring transition and to ocean temperatures. Predatory fishes, forage fishes, and juvenile salmonids had distinct spatial distributions, with predators distributed primarily offshore and forage fish and salmonids onshore, but this varied depending on ocean conditions. We suggest that predatory and forage fish distributions respond to ocean temperatures, predator/prey interactions, and possibly turbidity. A shift in ocean conditions in 1999 decreased overall predator fish abundance in the Columbia River plume, particularly the abundance of Pacific hake. Marine survival of juvenile salmon started to increase in 1999, but forage fish densities increased in 2000, lagging by one year.

INTRODUCTION

Predation influences ecosystem structure (Pace et al. 1999; Shears and Babcock 2003), the abundance of fish stocks (Borgstad and Mehl 1997; Bax 1998; Tsou and Collie 2001) and is an important parameter to include in fish stock assessments (Hollowed et al. 2000). For example, Livingston and Jurado-Molina (2000) found that fish predation influenced recruitment of walleye pollock (*Theragra chalcogramma*) in the Bering Sea. In the Barents Sea, pelagic fish stocks fluctuate depending on shifting predation pressures

(Gjøsaeter 1995). The abundance of capelin (*Mallotus villosus*) stocks in the Northwest Atlantic also appears to be driven by changes in predation pressure (Carscadden et al. 2001). Swain and Sinclair (2000) found evidence that predation by Atlantic herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) affected the recruitment of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence.

Pacific hake (*Merluccius productus*) (also known as Pacific whiting) is the most abundant predatory (piscivorous) fish on the west coast of North America (Methot and Dorn 1995). Predation by Pacific hake affects the abundance of Pacific herring (*Clupea pallasii*) off Vancouver Island, Canada (Ware and McFarlane 1995) and pink shrimp (*Pandalus jordani)* off Oregon and Washington (Hannah 1995). Pacific hake have also been found to be major predators of juvenile salmon in Alberni Inlet and Barkley Sound, Canada (Beacham 1990).

Pacific hake migrate north in the spring/summer to feed off Oregon/Washington/British Columbia, and south in fall and winter to spawn off California (Dorn 1995). During spring, hake are generally found over the continental slope, but are reported to move onto the shelf in June (Methot and Dorn 1995). Hake show an age/size specific migrational pattern, with larger/older, usually female hake, migrating the farthest north (Dorn 1995; Methot and Dorn 1995; Ware and McFarlane 1995) and smaller, younger hake, migrating the least (Dorn 1995). Northern and southern migrations appear to be strongly affected by ocean temperatures (Dorn 1995) and perhaps food resources (Benson et al. 2002), with warm or cold spring temperatures, respectively, increasing or decreasing the number of hake migrating to Canadian waters

(Dorn 1995; Ware and McFarlane 1995). There is also evidence that when winter ocean temperatures are warm, many Pacific hake do not migrate south, but over winter and spawn off the Pacific Northwest and Canada (Hollowed 1992; Benson et al. 2002).

Other important coastal pelagic predatory fishes off Oregon/Washington include jack mackerel (*Trachurus symmetricus*), chub mackerel (*Scomber japonicus*), spiny dogfish (*Squalus acanthias*), and adult salmonids (Brodeur and Pearcy 1986). Very little is known about the migrational movement of chub and jack mackerel, except that they generally arrive in Pacific Northwest coastal waters in mid-summer (June; MacCall et al. 1980) and are more abundant during warm ocean years, such as El Niño years (Brodeur and Pearcy 1986; Pearcy and Schoener 1987). While no directed fishery for jack mackerel presently exists in the Pacific Northwest, it is often abundant and the primary bycatch in the Pacific hake fishery (Wiedoff et al. 2003). Spiny dogfish has a nearly worldwide distribution (Compagno 1984), and there is a Northeast Pacific population that ranges from northern California to Alaska (McFarlane and King 2003). The once-large Northeast Pacific fishery for spiny dogfish peaked in the 1940s (Hart 1973) but is relatively small now because of limited demand (PSMFC 2001). Spiny dogfish was harvested in the 1940s for its liver, which has high concentrations of vitamin A, but the development of synthetic vitamin A eliminated the market for shark livers.

There are primarily four species of forage fish that reside in the coastal zone off the Columbia River and the Pacific Northwest; northern anchovy (*Engraulis mordax*), Pacific herring, whitebait smelt (*Allosmerus elongatus*), and Pacific sardine (*Sardinops sagax*). Until the mid-1990s, Pacific sardine were rarely found off the Pacific Northwest, but they now support an important fishery (Emmett et al. 2005). These forage fishes are important prey for many species of large fish, seabirds, and marine mammals, but relatively little information has been published on their abundance and spatial/temporal distributions off Oregon/Washington (Brodeur and Pearcy 1986; Emmett and Brodeur 2000; Brodeur et al. 2005).

There were large changes in abundances of pelagic predatory and forage fishes off Oregon/Washington during the 1980s-1990s and concurrent fluctuations in marine survival of salmon (Emmett and Brodeur 2000). Starting in 1999, large increases in marine survival of salmon led to rebounding salmon stocks in the Northwest (Williams et al. 2005). This change in marine survival occurred simultaneously with a large shift in oceanographic conditions in the California Current Ecosystem (CCE) (Schwing et al. 2002; Peterson and Schwing 2003). Were there changes in the distribution and abundance of pelagic predators in the CCE as a result of this shift? If so, could these changes be responsible for the observed increase in marine survival of salmon? Here we identify changes in the abundance and distribution of the four most abundant pelagic predatory fishes off the Pacific Northwest from 1998 to 2003 and characterize the associated oceanographic conditions during this time. We also begin to explore if there is any relationship between predatory fish populations, forage fish populations and juvenile salmonid marine survival.

METHODS

Study area

The study area was located off the mouth of the Columbia River (Fig. 3.1) and in the northern portion of the CCE. This portion of the CCE has seasonally variable winds and currents, with northwest winds, southerly currents (California Current) and upwelling in the summer, and south winds, northerly flows (Davidson Current), and downwelling in winter (Hickey 1989; Hickey and Banas 2003). Upwelling strongly affects primary productivity and oceanographic conditions in the study region but is highly variable, and the effectiveness of northerly winds in generating it, the amount of deep cold water actually rising to the surface, can be limited if the thermocline is deep. The date of the spring transition, when upwelling begins, sea level drops, and nearshore surface currents become southerly, is an important parameter determining coastal ocean environmental conditions and ocean survival of coho salmon (*Oncorhynchus kisutch*) (Logerwell et al. 2003). The low-salinity Columbia River plume is a dominant feature of the study area and is usually located on the continental shelf (nearshore) off Washington during winter and beyond the shelf off Oregon during summer (Hickey and Banas 2003). Columbia River flows are highly regulated by dams, with peak flows much lower than historical levels (Sherwood et al. 1990); highest flows are generally in May/June and lowest flows in August/September.

Ocean temperatures, salinities, and densities at 50-m are good indicators of nutrient rich source water that surfaces when upwelling occurs. This water lies below the Columbia River plume and is influenced by upwelling intensity and large-scale fluctuations in the California Current (Hickey and Banas 2003). In 2002, these deep waters saw an intrusion of deep cold low oxygen subarctic water that originated in the North Pacific (Kosro 2003; Strub and James 2003). The influx of this nutrient rich water increased primary productivity (Wheeler et al. 2003), reduced dissolved oxygen levels, and caused mortality of bottom-dwelling fishes and crabs off central Oregon (Grantham 2004), and probably modified the movements of pelagic fishes.

Sampling

We conducted this study from 1998-2003 and will refer to it as the Predator Study. The first year (1998) was used principally to identify the appropriate gear type and sampling scheme to collect pelagic fishes near the surface. As a result, many different stations were sampled in 1998 (Fig. 3.1). During all years we sampled at night to take advantage of the diel vertically migratory behavior of pelagic fishes (Bailey et al. 1982; Blaxter and Holiday 1963) and because surface trawls are more effective at night due to less visual avoidance (Dotson and Griffith 1996).

In 1998 the fishing gear was deployed one or two times each night when the depth sounder indicated fish (undetermined species) were around the vessel and near the surface, as one of the initial study objectives was to identify whether our surface trawl gear fished effectively. Blind tows (no prior information about fishing conditions) were also conducted. We report 1998 data only from collections when a rope trawl was used (1 June 1998-on), as this was the fishing gear finally identified as most effective. Because the 1998 sampling scheme differed from that in 1999-2003 (different stations), calculated fish densities in 1998 may not be completely comparable to later years. While we did not have any May 1998 surface-trawl catch information, our subsurface trawl catches indicate that hake were in the study area (unpublished data). As such, fish densities were probably similar to what we observed in June 1998. Fish catches and oceanographic conditions differed widely between 1998 and 1999-2002. The 1998 data thus provided valuable contrasting information on fish/oceanographic relationships that we believe are important to include in this analysis. Finally, fish catch data from 2003 indicated that the 1998 data were not aberrant.

From 1999-2003 we sampled at pre-determined stations along two transect lines north and south of the mouth of the Columbia River (Fig. 3.1). 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. Sampling was conducted at night, approximately every 10 days from mid-April through July-early August from 1998 to 2003, for a total of 20 sampling days (10 sampling cruises per year). From each trawl, all fish species were identified, enumerated and measured, except when large catches occurred. For each large haul, a random sample of 30 individual fish from each species was measured, and a subsample (approximately 5-30 kg, depending on fish size) of each species was counted and weighed, and the remaining mass weighed. Total numbers of each species captured were then determined by adding the number in the subsample to the number calculated by dividing the mass weight of the species by the average weight/individual calculated from the subsample.

All salmon were separated into age classes, yearling (1.0-age), subyearling (0.0-age) and ($\geq$2-year-old-age) by length. Size of each age group varied monthly, so age was identified by length-frequency analysis and historical salmon size at age information (J. Fisher, Oregon State University, Corvallis, OR. pers. comm.). We used the salmon age nomenclature of Koo (1962) with number before the period indicating winters spent in freshwater after hatching and before migrating to sea, and the number after the period indicating winters spent in the ocean.

From 12 June 1998 through 2003, all samples were conducted with one gear type aboard a chartered commercial trawler. All surface trawling was conducted with a 264-rope trawl with 3-m foam-filled Lite doors, designed and built by NET Systems. This gear is also used to capture juvenile salmonids and associated fishes off southeast Alaska (Murphy et al. 1999) and California (MacFarlane et al. 2002). The trawl is 100-m long with a fishing mouth area 28-m wide and 12-m deep. The effective mouth area (336 m^2) was identified 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 (Krutzikowsky and Emmett 2005). Mesh size ranged 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 traveling approximately 2.9 knots (1.5 m s^{-1}) for 30 minutes. However, starting in 2001, trawl times were shortened to 15 minutes to reduce the very large catches of forage fishes. Fish catches were standardized by calculating densities [number $(10^6 m^3)^{-1}$] using the distance fished (geographic distance between beginning and end of trawl) multiplied by the effective mouth area.

Estimates of predator densities presented here must be considered as minimum estimates, particularly for very large predators such as adult salmon and sharks. Large predator fishes are fast swimmers that may evade trawl nets, and generally do so during daylight. For example, although the Columbia River has relatively large runs of adult salmonids, we captured very few. On one occasion we placed a video camera on the head rope during daylight trawling operations and saw large adult salmonids both enter and leave the net opening. Evidently adult salmonids can easily evade a surface trawl traveling at 1.5 m s^{-1}. Better estimates of very large and fast predatory fishes, such as adult salmonids, would require different sampling gear. Nevertheless, our nighttime surface trawling appeared to be effective at capturing Pacific hake, a relatively slow swimmer, and mackerel, a medium-speed swimmer. This rope trawl was originally designed to be capture fishes such as hake at mid-water depths but modified (foam filled doors and floats attached to head rope) to fish at the surface (Steve Patterson, NET Systems, Bainbridge Island, WA, pers. comm.). Mid-water trawls are also used to capture jack mackerel commercially (Arcos et al. 2001). Our catches of large dogfish shark may not be reliable, but are presented because they were commonly captured and we believe the data does represent relative abundance differences.

Our night-time surface trawling appears to be effective for forage fishes (Emmett et al. 2004; Krutzikowsky and Emmett 2005). Because of their small size (most averaged < 200 mm FL) and slower swimming speeds, forage fishes are easily captured by the net. The efficiency of the trawl for forage fish was verified by large catches of forage fishes once they became abundant. For example, we also caught large numbers of Pacific sardine/trawl when the commercial sardine purse-seine fishers did.

Juvenile salmon are similar in size to forage fishes, and the surface trawl effectively captures juvenile salmon, especially during day (Murphy et al. 1999; Orsi et al. 2000). The surface trawl is less effective at capturing juvenile salmon during night, possibly because of diel behavior (Krutzikowsky and Emmett 2005). However, the annual juvenile salmon density estimates provide consistent relative densities.

Annual trawl surveys could not be conducted on exactly the same dates each year due to weather and other factors. To allow annual comparisons, data were grouped by proximate calendar date. Dates of each sampling effort and how the data were grouped are shown in Table 3.1.

To identify the overlap in habitat use between predators, forage fishes, and juvenile salmonids, their distributions and species densities were compared as a function of distance from shore. Since nighttime sampling may under represent juvenile salmonid densities (Krutzikowsky and Emmett 2005), distributions of juvenile salmonids off Oregon/Washington from the NOAA Fisheries/Bonneville Power Administration (BPA) Columbia River Plume Study (June 1998-2003) are presented. The BPA Plume Study used the same surface trawl and protocol, but sampled during daylight hours on a series of transects ranging from Cape Flattery, WA to Newport, OR (Fig. 3.2) (Emmett and Brodeur 2000).

Physical measurements

Temperature and salinity profiles were collected at all trawl stations (from this study and the BPA Plume Study) by lowering a SeaBird SB-19 conductivity, temperature, and depth (CTD) probe to 100 m depth (or just off the bottom). Starting in 2002, a transmissiometer was attached to the CTD used in the BPA Plume Study to measure water clarity. Upwelling values and their anomalies at 45°N 125°W were obtained from NOAA/NMFS Pacific Fisheries Environmental Laboratory web site (http://www.pfeg.noaa.gov/). Annual dates for the spring transition, defined by when upwelling, northwest winds, and equator-ward currents begin seasonally, were identified by examining changes in daily plots of Oregon/Washington coastal upwelling winds and sea level height filtered at 10 and 90 days, (Logerwell et al. 2003; E. Logerwell, NOAA Fisheries, Seattle, WA, pers. comm.). Columbia River flows, which influence surface salinities within the study area, were obtained from US Geological Survey Beaver Army Terminal located near Quincy, Oregon (46°10'54" N, 123°10'58" W) (http://waterdata.usgs.gov/nwis/nwis).

Statistical analysis

A Kruskal-Wallis test was used to identify statistical differences in physical oceanographic features (Columbia River flows, ocean temperatures, ocean salinities, etc.) and fish densities (by species and combined) between years because these data were not normally distributed. Dunn's multiple comparison test identified which years were significantly different when a Kruskal-Wallis test identified differences among years. A 2 x 2 chi-square contingency test with Yates' correction was used to evaluate the relationship between the presences of predatory fishes and forage fishes and juvenile salmonids in the surface trawls.

A suite of multiple linear regression models were used to identify which physical and biological factors were related to the annual variation in average predatory/forage fish densities (all species combined and individually). Average fish densities were log transformed before analysis. Residuals were tested for normality using a chi-square goodness-of-fit statistic. Physical factors in the analysis included: date of the spring transition, Columbia River flow, ocean temperature, salinity, density, and distance from shore. Spring transition was measured in Julian days. An extra sum of squares F-test was used to evaluate the strength of relationship between species densities and distance from shore after accounting for the effect of year (Ramsey and Schafer 1997). We considered a $P < 0.05$ to indicate a significant relationship for all statistical tests.

A regression model was also used to identify the relationship between average May/June predator/forage fish densities and coho salmon marine survival in the Oregon

Production Index (OPI) area (PMFC 2005). Coho salmon OPI survival was calculated by dividing hatchery coho salmon adult and jack returns by number of smolts released.

RESULTS

Physical oceanographic conditions

Sea surface salinities and temperatures in our study area were strongly affected by Columbia River flow. For example, in June 1999, a month and year with average Columbia River flows (approximately 10,000 m^3s^{-1}; Sherwood et al. 1990), the Plume Study documented a low-salinity plume that spread both north and south along the Oregon and Washington coast (Fig. 3.2). The depth of this low-salinity/low-density water was generally < 20 m (Fig. 3.3) and depended not only on the amount of freshwater flow, but general oceanic conditions at that time (winds and currents). During 2001, a drought year, average Columbia River flow was about half the average during the other five years. Annual and monthly Columbia River flow differed significantly (Kruskal-Wallace, $P < 0.0001$), especially during the spring (April-June) (Fig. 3.4).

As expected, the seasonal pattern of northerly winds and annual upwelling showed a general increase from April to July and August (Fig. 3.5A). While we identified no annual upwelling differences from 1998 through 2003 (Kruskal-Wallace, $P = 0.504$) (overall median upwelling from April-August was 34 $m^3/s/1{,}000$ m of coastline), there were significant interannual differences within months (Table 3.2). For example, in April 2003 median upwelling was strongly negative (downwelling), whereas in all other Aprils, including 1998, a warm El Niño year, April upwelling was either near zero or positive. Upwelling in May 2000 was significantly less than in 2001 (Dunn's multiple range test, $P < 0.05$) (Table 3.2) and June 2003 had significantly higher upwelling than June 1999 (Dunn's multiple range test, $P < 0.05$). There were no interannual upwelling differences for July, but upwelling in August 2001 was lower than in either August 1998 or 2002 (Dunn's multiple range test, $P < 0.05$) (Table 3.2). There were also large variations in the date of the spring transition from 1998 to 2003, with 2000 and 2001 having very early transitions (early March) and 2003 having a very late transition date (April 24) (Fig. 3.5B).

Surface physical conditions fluctuated much more than those at depth. There were significant differences in annual sea surface (1-m) temperatures (SSTs), salinities (SSSs), and densities (SSDs) (Kruskal-Wallace test, $P < 0.0001$) during the study period (Fig. 3.6, Table 3.3), with differences in SSS related to Columbia River flow. For example, salinities were generally highest in 2001 when Columbia River flow was lowest.

Monthly SST, SSS, and SSD showed significant differences between years, with differences depending on the variable and year. For example, there were significant differences in monthly SSTs for all years (Kruskal-Wallace, $P < 0.0001$) but significant inter-annual differences in monthly SSSs were identified only for July (Kruskal-Wallace, $P < 0.0001$), with 2001 having higher salinities than 1999 and 2003. Monthly SSDs were significantly different among years (Kruskal-Wallace, $P < 0.0001$), and were correlated with surface temperatures, indicating that changes in temperature were driving water density differences.

Deep (50-m) water temperatures, salinities, and densities fluctuated significantly off Oregon/Washington from 1998 to 2003 (Kruskal-Wallace test, $P < 0.0001$; Fig. 3.7, Table 3.3), indicating fluctuating water masses during the study period. Much of the annual difference in temperatures at 50-m depth can be attributed to the high temperatures associated with the 1998 El Niño. However, in 2002 we observed an intrusion of cold, low-oxygen, Subarctic water that originated in the North Pacific (Fig. 3.7).

Monthly 50-m depth temperatures, salinities, and densities showed significant differences between years, but differences depended on the variable and year (Fig. 3.7). All monthly 50-m temperatures were significantly different (Kruskal-Wallace, $P < 0.0001$), with differences attributed to high temperatures in 1998 (all months) and 2003 (just April and May), and cold temperatures in 2002 (all months) (Dunn's multiple range test, $P < 0.05$). Significant differences in monthly 50-m salinities were only identified for April and May (Kruskal-Wallace, $P < 0.0001$). Monthly water densities were similar to salinities, with significant differences in April and May (Kruskal-Wallace, $P < 0.0001$), but not June and July. In summary, during the six-year study period, physical characteristics of 50-m water were most variable during the months of April and May.

Annual abundance of predators

Overall densities of the four predatory fishes off the Columbia River changed significantly during the six study years (Kruskal-Wallace, $P < 0.0001$) (Fig. 3.8). Highest average densities were observed in 1998 [$242(10^6 m^3)^{-1}$] and lowest in 1999 [$43(10^6 m^3)^{-1}$]. Pacific hake was the most abundant predator overall, but not for all years. In 2000 and 2001, both species of mackerel and spiny dogfish were more abundant than Pacific hake (Fig. 3.8).

Only two predatory species (Pacific hake and chub mackerel) showed significant between-year differences in density (Kruskal-Wallace, $P < 0.0001$) during the study period. Pacific hake showed the largest changes in annual average density, ranging from a high of 226.4 $(10^6 m^3)^{-1}$ in 1998 to a low of 1.6 $(10^6 m^3)^{-1}$ in 2000. In 2003, Pacific hake again became abundant with an annual average of 116.6 $(10^6 m^3)^{-1}$. Other predators had average annual densities much lower than that of Pacific hake. While spiny dogfish had high average annual densities, with 33.8 $(10^6 m^3)^{-1}$ and 37.6 $(10^6 m^3)^{-1}$ in 2000 and 2001, respectively, densities averaged <3 $(10^6 m^3)^{-1}$ during other years. Annual catches of spiny dogfish were not significantly different (Kruskal-Wallace, $P = 0.319$), because catches were generally low (except for two extremely large catches). Highest average annual abundance of jack mackerel was 23 $(10^6 m^3)^{-1}$ in 2001, but densities averaged < 17 $(10^6 m^3)^{-1}$ during all other years, although differences in annual densities were not significant (Kruskal-Wallace, $P = 0.456$). Chub mackerel were most abundant in 1998

[10.9 $(10^6 m^3)^{-1}$] and least abundant in 2002 [0.10 $(10^6 m^3)^{-1}$], with annual densities significantly different (Kruskal-Wallace, $P < 0.0001$).

Generally, when Pacific hake were abundant, other predators were not (Fig. 3.8). For example, lowest densities of jack mackerel and spiny dogfish occurred in 1998 and 2003, when Pacific hake were most abundant. During years when Pacific hake had relatively low densities (2000-2001), spiny dogfish and jack mackerel had their highest densities.

Predators also showed large biweekly variations in density (Fig. 3.9). In 1998, for example, Pacific hake had its highest densities around 28 May (our first survey), and although hake densities varied widely, they remained relatively high through July (Fig. 3.9). In 2003, Pacific hake was again abundant, and densities showed a pattern similar to 1998, becoming relatively high in late May and remaining high through July, although, unlike 1998, Pacific hake densities in 2003 were highest in early July. Both mackerel species showed a general pattern of very low numbers in April and May, increases in June, and highest densities in July (Fig. 3.9). Chub and jack mackerel had their highest densities of the entire study period during mid-July 2003 [29.9 $(10^6 m^3)^{-1}$] and late-July 2001 [110.6 $(10^6 m^3)^{-1}$], respectively. Spiny dogfish densities showed three peaks during different years: early-July 2000, mid-June 2001, and mid-May 2002 (Fig. 3.9). However, these high densities can be attributed to single large catches of small spiny dogfish off Willapa Bay. Length/frequency analysis (not shown) revealed that most spiny dogfish catches during these cruise dates were composed of small juveniles, indicating that Willapa Bay is probably a spiny dogfish birthing area. Ignoring the very large catches of juvenile spiny dogfish in July 2000 and June 2001, overall densities of spiny dogfish were low [$\leq 15\ (10^6 m^3)^{-1}$] during all years and sampling dates.

Forage fishes

Forage fish were not abundant during 1998 and 1999, but were very abundant from 2000 through 2003 (Fig. 3.10). Large variations in density were seen in all four forage fish species except Pacific sardine, but only northern anchovy increased from year-to-year from 1998-2003. Pacific herring and whitebait smelt densities were highest in 2001, and Pacific sardine in 2003. Densities of northern anchovy, Pacific herring, and whitebait smelt were significantly different between years (Kruskal-Wallace, $P < 0.05$), but densities of Pacific sardine were not (Kruskal-Wallace, $P = 0.0604$).

There was a strong seasonal component to forage fish densities. For example, northern anchovy and whitebait smelt densities were generally highest during late April and May, and then decreased as the summer progressed. Pacific sardine was most abundant in late June and July (Fig. 3.11). In 2003, both northern anchovy and whitebait smelt were abundant in May, but we caught few in June or July when, perhaps not coincidentally, densities of predatory fishes (Pacific hake and mackerel) were highest (Fig. 3.9). Peak densities of Pacific herring did not follow any specific trend, with time periods of peak abundance varying among years (Fig. 3.11). Overall, highest densities of Pacific herring were observed in June (Fig. 3.11).

Juvenile salmonids

Densities of juvenile salmonids captured in the Predator Study varied widely (Fig. 3.12A), and all salmon showed significant density differences between years (Kruskal-Wallace, $P < 0.05$). Highest average juvenile salmon densities occurred in 2001, when many juvenile chum and 1.0-age Chinook salmon were captured. Juvenile coho salmon were found at very low annual densities except in 2000 and 2001. Sockeye salmon was rarely captured; densities of juvenile steelhead (*O. mykiss*) and cutthroat (*O. clarkii*) were so low they are not shown in Figure 3.12A.

Juvenile salmon showed two seasonal peaks in abundance, one in May and another in July/August, although neither peak was evident every year (Fig. 3.12B). Generally, the peak in May reflected the migration of yearling (1.0-age) Chinook and coho salmon smolts and juvenile chum salmon. The July/August peak primarily reflected the migration of subyearling (0.0-age) Chinook salmon.

Spatial distribution of predatory fishes, forage fishes, and juvenile salmonids

The spatial distribution of the four predatory fishes differed by species and by year (Fig. 3.13). For example, Pacific hake were abundant nearshore (0-10 km) during 1998, a year with a late spring transition and with the warmest temperatures at the sea-surface and 50-m depth (Fig. 3.6 and 3.7). In 1999, a relatively cold year, hake were not very abundant and were mainly caught offshore (40-50 km). In 2003, another warm year, Pacific hake were again distributed nearshore, within 10-20 km of the coast (Fig. 3.13).

Jack mackerel and chub mackerel had similar spatial distributions; they were most abundant at 30-40 and 20-30 km from shore, respectively; few were captured nearshore (< 10 km) or far offshore (50-60 km) (Fig. 3.13). Spatial abundance for both species appeared to change annually, with peak abundance closer to shore during warm years and farther offshore during cold years. For example, during 1998, a warm year, chub mackerel was caught within 10 km of the coast but its highest average densities were 20-30 km offshore. In 1999, a cold year, chub mackerel was captured no closer than 20 km from the coast, and peak densities were 30-40 km offshore.

Spiny dogfish distribution was primarily nearshore, with first and second highest densities found less than 10 km and 10-20 km from shore, respectively (Fig. 3.13). High nearshore densities in 2000 and 2001 were strongly skewed by single large catches of small juveniles just off Willapa Bay, but their overall distribution was still nearshore; very few spiny dogfish were captured between 40 and 60 km from shore.

Catches of most forage fishes showed significant inshore/offshore trends. All but sardine had highest densities nearshore and very low densities offshore (Fig. 3.14); no forage fishes were caught at the station farthest offshore (50-60 km), which was beyond the continental shelf (Fig. 3.14). Northern anchovy showed a high affinity for the very nearshore environment after accounting for year by comparing a linear regression model with and without a year variable (extra sum of squares F-test, $F = 11.43$, $P < 0.001$); highest densities during all years were < 10 or 10-20 km from shore (Fig. 3.14).

Northern anchovy densities dropped quickly beyond 20 km from the coast, with very few captured 40-50 km from shore. Pacific herring also showed a preference for nearshore water, with highest densities 0-30 km offshore and very low densities farther offshore, but this relationship was not significant after accounting for year (F = 1.638, *P* = 0.1737) (Fig. 3.14). While highest herring density was observed within 10 km of the coast in 2003, highest densities during other years were 20-30 km (2001) or 10-20 km from the coast (2000). Very few Pacific herring were captured over the slope, 40-60 km off the coast. Whitebait smelt densities were significantly related to distance from shore (F = 6.45, *P* = 0.0169), with highest densities 10-20 km from the coast during all years (Fig. 3.14); few were captured beyond 30 km and none 40-60 km from shore. Pacific sardine were distributed differently than the other forage fishes. There was clearly no relationship between sardine densities and distance from shore after accounting for year (F = 0.1512, *P* = 0.9872). For example, in 2000 most sardine were captured within 20 km of the coast, but in 2001 highest densities were 40-50 km from the coast (Fig. 3.14).

Juvenile salmon captured during the Predator Study (nighttime catches) showed distribution patterns that varied widely depending on species and year (Fig. 3.15). In general, most juvenile salmon species/and age-classes had high densities nearshore, but no salmon species/age-class had densities that were significantly related to distance from shore after accounting for year (extra sum of squares F-test, *P* > 0.05). Highest densities of juvenile coho salmon in 2000 were 40-50 km from shore. Both 0.0-age Chinook and chum salmon showed weak negative relationship between distance offshore and density. This was observed for densities of 0.0-age Chinook salmon for 1999 and 2000, but not for other years. Nearly all juvenile chum salmon captured were taken in 2001, so it was unclear whether this nearshore distribution pattern re-occurred annually. Finally, 1.0-age Chinook salmon densities showed no clear relation to distance offshore, with similar densities found both offshore and nearshore during most years. Most of the juvenile salmon captured during the Predator Study were undoubtedly recent migrants from the Columbia River. As such, their marine distribution was influenced by the shape, direction, and strength of the Columbia River plume.

June data from the Oregon/Washington coast-wide BPA Plume Study (daytime catches) provide juvenile salmonid coastal distributions away from the Columbia River. These data show onshore/offshore distribution patterns similar those from the Predator Study for 0.0-age Chinook salmon, but not for other salmonids species/age groups. For example, 0.0-age Chinook salmon densities were highest nearshore (1-20 km), and this relationship was significant after accounting for year (F = 8.52, $P = 0.0067$) (Fig. 3.16). Unlike the Predator Study catches, chum salmon densities from the Plume Study were highest 40-50 km offshore (Fig. 3.16) but this relationship was not significant (F = 2.464, $P = 0.1273$). Yearling (1.0-age) Chinook salmon in the Plume Study showed a significant relationship between density and distance from shore (F = 4.83, $P = 0.0364$), with densities highest between 10-30 km nearshore and gradually decreasing to zero at 60 km offshore. Finally, coho salmon in the Plume Study were most abundant from 10 to 50 km offshore, and not related to distance from shore (F = 2.68, $P = 0.1123$).

Predator densities, oceanography, forage fish and juvenile salmonids

Annual average Pacific hake densities were highest closest to shore (Fig. 3.9), when the spring transition was late (Fig. 3.5A) and spring (April-May) temperatures were warmest at the 50-m depth, which was in 1998 and 2003 (Fig. 3.7A). As a result, annual average Pacific hake densities were strongly related to the spring transition (GLM, $P = 0.028$, adjusted $R^2 = 67.36\%$) (Fig. 3.17). High hake catches in May/June occurred in 1998 and 2003, years with a late spring transition.

Annual jack mackerel densities were highest when the spring transition was early (Fig. 3.17), but this relationship was not statistically significant (GLM, $P = 0.0729$, $R^2=49.2\%$). Jack mackerel densities were directly opposite Pacific hake densities, and highest during cool ocean years (1999-2002). Annual chub mackerel densities were not related to the spring transition or any other physical or biological variables (GLM, $P > 0.10$). Spiny dogfish densities were generally very low and showed no relationship with oceanographic conditions.

We found no statistical relationship between predatory fish abundance and forage fish abundance (GLM, $P > 0.05$). However, seasonal abundance of predatory fishes appears to be inversely related to forage fish abundance. For example, both whitebait smelt and northern anchovy were generally most abundant in early spring (May), while predatory fishes usually arrived later (June and July) (Fig. 3.9). After the arrival of predatory fishes, particularly Pacific hake in late May 2003, abundance of northern anchovy and whitebait smelt declined dramatically. This was most evident for whitebait smelt, which were abundant in May 2003 but virtually disappeared from our catches by late June-July 2003. Examination of Pacific hake stomach contents at sea indicated they were feeding on whitebait smelt and anchovy in 2003.

Annual densities of Pacific hake (Fig. 3.8) generally trended opposite to those of juvenile salmonids (Fig. 3.12), but it was unclear whether Pacific hake abundance directly affected juvenile salmonid abundance. Statistical analysis indicated a possibly negative relationship between juvenile salmonid densities and Pacific hake densities (GLM, $P = 0.064$, $R^2 = 52.14\%$) but this was not significant. However, there was a significant negative relationship between annual average May/June densities of hake and OPI coho salmon percent survival (GLM, $P = 0.030$, $R^2 = 57.01\%$) (Fig. 3.18).

Analysis of presence/absence of juvenile salmonids versus predator and forage fishes sampled by trawl indicated strong interactions between species (Table 3.4). With the exception of spiny dogfish, when predators occurred in a trawl, salmonids usually did not (chi-square, $P < 0.05$). Conversely, there was a positive interaction (i.e., species co-occurred more than expected) between the occurrence of juvenile salmonids and northern anchovy, Pacific herring, and whitebait smelt (chi-square, $P < 0.05$). There was no relationship between the occurrence of juvenile salmonid and Pacific sardine in the catches (chi-square, $P = 0.396$).

DISCUSSION

This and other studies (Brodeur and Pearcy 1986; Emmett and Brodeur 2000) show that the abundance and distribution of large pelagic predatory fishes off Oregon and Washington fluctuates widely, both annually and seasonally. These changes in predatory fish abundance and distribution appear to be strongly linked to the date of the spring transition, as well as to changes in ocean temperature (Brodeur and Pearcy 1986; Dorn 1995; Ware and McFarlane 1995) and prey abundance (Benson et al. 2002). Warmer ocean temperatures (at depth and the surface) and the date of the spring transition influenced the movement of Pacific hake and probably jack mackerel in Northwest waters.

Our catches indicated Pacific hake were distributed similarly to the coastal distribution of hake identified by NMFS triennial acoustic surveys (Helser et al. 2004). These surveys found hake to be relatively abundant in the Columbia River region in 1998 and 2003, but not in 2001 (Helser et al. 2004). Our low hake catches in 2001 appears to have been related to both reduced Pacific hake stock size, and slower hake migration to the north because of cooler ocean temperatures and slower northerly currents.

The Pacific hake population in 2003 was estimated to be between 2.7 and 4.2 million tons (Helser et al. 2004). With such a large biomass, hake movement and feeding habits undoubtedly affect other biological resources in the California Current ecosystem (Jay 1996), including Pacific herring off British Columbia, Canada (Ware and McFarlane

1995), pink shrimp off Oregon (Hannah 1995), and probably anchovy and whitebait smelt off Oregon/Washington (Predator Study).

One reason we conducted our sampling at night was that we suspected interactions among predators (particularly hake), forage fish, and juvenile salmonids would be most evident at night. Juvenile salmonids off Oregon do not appear to migrate vertically, but remain near the surface (Pearcy and Fisher 1988; Emmett et al. 2004). They are thus more likely to interact with diel migrating predatory and forage fishes at night. Preliminary stomach analyses indicated that hake, mackerel, and spiny dogfish, feed actively at night, with euphausiids and forage fishes the primary prey. Alton and Nelson (1970) concluded that Pacific hake feeds primarily between sunset and sunrise, but Livingston (1983) found feeding during both day and night. Rexstad and Pikitch (1985) found evidence that hake eat more at night, but their data may have been influenced by an El Niño (possibly altered food web). We believe that hake eat during both the day and night, migrating vertically to follow prey (euphausiids and forage fish) and feeding at night if prey are abundant.

Ongoing stomach analyses have identified few juvenile salmonids in any predator stomachs. As noted by Holtby et al. (1990) in British Columbia waters, the scarcity of salmonids relative to forage fish would make it unlikely that salmon would constitute a significant fraction of Pacific hake diet. However, even if juvenile salmon are incidental prey, hake biomass is sufficiently large to cause substantial juvenile salmonid mortality. The significant negative relationship between hake densities and coho salmon marine survival supports the hypothesis that predation when salmon first enter the ocean is a major source of salmon marine mortality. However, other factors appear correlated with hake densities, such as sea surface temperature and cold-water copepods (Peterson and Schwing 2003).

The presence of Pacific hake and other predators in a trawl was negatively related to the presence of salmon smolts and forage fishes, indicating that predators could be altering the distributions of these fishes. Large piscivorous fishes feed most effectively in clear, non-turbid water, while planktivorous fish feeding is relatively unaffected by turbidity except at very high levels (De Robertis et al. 2003). As such, we suspect that ocean turbidity may play a critical role in the onshore/offshore distributions and interactions among predators, salmonids, and forage fish. Predatory fishes, such as Pacific hake, are generally found farther offshore (Fig. 3.13) in low turbidity (high transmissivity) waters (Fig. 3.19), while most salmonid and forage fish species are found primarily inshore (Figs. 14-16) in higher turbidity (low transmissivity) waters. In 2000 and 2001, when hake densities were very low, both Pacific herring and whitebait smelt were distributed farther from shore, perhaps because these areas offered less predation pressure and more turbid ocean conditions.

Our intensive field sampling was designed to identify when pelagic predators and forage fishes first become abundant off the Columbia River. Our data indicate that hake move into nearshore waters during warm spring (weak upwelling) and clear (low primary production and low turbidity) years (1998 and 2003) (Emmett, pers. obs). Methot and Dorn (1995) noted that hake usually move onto the shelf in June. Our data indicate that in years when the ocean is warm in spring, especially at depth, hake will move onto the

Oregon/Washington shelf by late May, which is also the peak migrational period of yearling salmonids leaving the Northwest coastal rivers. May is also when forage fishes peaked in abundance. We hypothesize that the spring migration of juvenile salmon from the Columbia River is a life history strategy to minimize marine predation. Migrating juvenile salmon can minimize marine predation by arriving to the ocean before predators become abundant and when alternative prey (forage fishes) are abundant.

There was evidently a shift in oceanographic conditions off Oregon/Washington in 1999. This shift caused changes in the zooplankton species composition and abundance (Peterson and Schwing 2003), and marine survival of salmon (Williams et al. 2005). Our data indicate that the composition and abundance of predatory fish species changed in 1999, and that of forage fishes changed by 2000. The distributions and densities of Pacific hake and jack mackerel were much different after 1998. However, in 2003, ocean conditions were similar to those of 1998: the spring transition was late, spring ocean temperatures were warm, and Pacific hake were again relatively abundant on the shelf. While predatory fish densities and distributions were similar in 1998 and 2003, forage fish densities were not. We believe this was because predatory fishes are long-lived and migrate to the study area (except dogfish) during the spring and summer, while forage fishes (except sardine) are primarily local spawners. As such, predators can immediately shift their population distributions with changing ocean conditions, while the short-lived forage fishes must respond by changing recruitment patterns. Forage fish population abundances showed a 1-year lag between changed oceanographic condition/predator densities (1999) and increasing densities (2000). Because of their different life history strategies, forage fish appear to respond differently than predatory fishes to the fluctuating oceanographic climatic conditions.

Northwest coastal ocean temperatures, primary productivity, and ocean currents are linked, and all affect the distributions and abundances of fishes in the Columbia River plume. Warmer ocean temperatures at 50-m depth in spring indicate a late spring transition and either continued northerly transport (Davidson current) or slow southerly transport. As Dorn (1995) showed, during years with a warm spring Pacific hake are transported more quickly to the north because northerly currents are stronger: conversely, during cooler spring years, transport is slower due to strong southerly currents. Coastal current meter data (Kosro 2003) and altimetry data (Strub and James 2003) collected during most of our study period support this hypothesis. During 2000 and 2002, spring coastal currents off Oregon were anomalously equatorward, and hake densities were low; in 1998 and 2003 currents were more northward (M. Kosro, Oregon State University, pers. comm.), and hake densities on the shelf were high.

Using purse seines during daylight hours, Brodeur and Pearcy (1986) observed wide fluctuations in the abundance of pelagic nekton species off Oregon/Washington from 1979 to 1984, concurrent with relatively small changes in ocean temperatures. They found chub mackerel was the dominant predatory fish during the warm ocean conditions of 1983-1984, not Pacific hake as we observed in 1998 and 2003. However, diel-migrating fishes such as hake would be underrepresented in their daylight catches. We suspect that lower densities of chub mackerel were observed in 1998 and 2003 because the west coast chub mackerel population is much lower now than in the 1980s

(California Dept. Fish Game 2002). Nevertheless, similar to our study, Brodeur and Pearcy (1986) also observed higher predator fish catches (mackerel and hake) and lower forage nekton catches during warmer ocean conditions.

Rebounding Northwest salmonid runs appear to have begun with the high marine survival of juvenile salmonids that entered the ocean in 1999 (coho salmon OPI index; Williams et al. 2005). That year, overall predatory fish abundance off Oregon and Washington, particularly Pacific hake during May and June, were considerably lower than in 1998, suggesting that reduced predator fish abundance may be related to increased salmonid survival. Holtby et al. (1990) concluded that growth of age-1 coho salmon and fluctuations in predation intensity (number of predators) accounted for the annual variations in coho marine survival of salmon on the west side of Vancouver Island, Canada. Fisher and Pearcy (1988) and Pearcy (1992) observed that low marine survival of Oregon coho salmon was not due to food shortages and slow growth in the ocean, but hypothesized that years with poor marine survival of salmon related to increased marine mortality caused by predators switching to salmon when their preferred prey were scarce. Our data support this hypothesis; when predator numbers decreased, marine survival of salmon increased. We also observed a coincidently large increase in forage fish or "alternative" prey abundance since 2000. If alternative prey are important (Fisher and Pearcy 1988; Pearcy 1992), then marine survival of salmon for outmigrant smolts in 2003 (a warm year with many predators) will decline, but not to the extremely low levels observed during most of the 1990s because, while predators were numerous, alternative prey (forage fish) remained abundant. Future adult salmon returns should verify or refute this hypothesis.

In conclusion, the effects of climate variability on the ocean fisheries resources are considerable (Cushing 1982; Beamish 1995; Ware 1995; Ware and McFarlane 1995; Mantua et al. 1997; McGowan et al. 1998; Anderson and Piatt 1999; Beamish et al. 1999; Hare et al. 1999; McFarlane et al. 2000; Zhang et al. 2000; Hollowed et al. 2001; Benson et al. 2002; Field and Francis 2002). Our research indicates that large scale oceanographic forcing affects the movements and abundance of predatory fishes around the Columbia River plume. These predatory fishes appear to affect in turn the abundance and distribution (inshore/offshore) of forage fishes. While it is still unclear how these fish predator/fish prey interactions affect marine survival of juvenile salmonids, circumstantial evidence suggests that these interactions are an important factor. Non-salmonid predatory and forage fishes numerically dominate the pelagic nearshore fish community in the northern California Current. Only long-term observational studies will provide the data needed to assess how species interactions affect predatory and forage fish abundances and the role these fishes play in marine survival of salmonids. This knowledge will be critically important if we are to properly manage Northwest coastal fisheries, including salmonids, during oceanic climate shifts.

ACKNOWLEDGEMENTS

We thank the many people who assisted with gathering the data presented here. The field work was completed with the assistance of J. Fisher, T. Miller, C. Morgan, L. Feinberg, J. Lamb, T. Auth, L. Stamatiou, J. Phillips, B. Sandford, W. Muir, and L. Weitkamp. Summer students who helped with field and lab work included, J. Douglas, C. Cochran, L. Davis, E. Locke and J Muir. Drs. W. Pearcy, R. Brodeur, and E. Casillas provided excellent comments of earlier drafts of this manuscript. Finally, this work could not have been accomplished with out the hard work of Captain D. Parker and the crew of the F/V Sea Eagle. This research was financially supported by NOAA Fisheries and the Bonneville Power Administration.

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Table 3.1. Dates of sampling each year and the grouping dates used to show seasonal differences in abundance.

Grouping date	Year					
	1998	1999	2000	2001	2002	2003
15 Apr		15-Apr				
23 Apr		23-Apr		26-Apr	24-Apr	24-Apr
5 May		5-May	30-Apr	8-May	3-May	3-May
14 May		14-May	11-May, 18-May	18-May	14-May	14-May
28 May	1-Jun	28-May	30-May	29-May	24-May	24-May, 5 June
13 Jun	13-Jun	13-Jun	14-Jun	8-Jun	15-Jun	14-Jun
26 Jun	28-Jun	26-Jun	29-Jun	30-Jun	27-Jun	27-Jun
7 Jul		7-Jul	11-Jul	11-Jul	10-Jul	10-Jul
15 Jul	13-Jul	15-Jul	22-Jul	20-Jul	23-Jul	23-Jul
28 Jul	30-Jul	28-Jul		31-Jul	2-Aug	2-Aug
28 Jul	12-Aug					

Table 3.2. Median monthly upwelling values at 45ºN, 125ºW from 1998-2003 and significant differences (Kruskal-Wallace test) among years. Significant annual differences identified by Dunns multiple comparison test ($p < 0.05$).

		Year						
Month	***P* value**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**Significant annual differences**
April	0.0002	11.5	43.0	-4.5	5.0	26.5	-23.5	2003 < 1999 and 2002
May	0.0661	15.0	27.0	5.0	44.0	15.0	28.0	2000 < 2001
June	0.0033	46.5	19.5	63.0	28.5	24.5	55.0	1999 < 2003
July	0.0455	47.0	44.0	44.0	75.0	56.0	70.0	None found
August	0.0087	56.0	24.0	51.0	30.0	50.0	52.0	2001 < 1998 and 2002

Table 3.3. Annual median temperatures, salinities, and densities at 1-m and 50-m depths off the Columbia River 1998-2003 and significant differences (Kruskal-Wallace test) among years. Significant annual differences identified by Dunn's multiple comparison test ($P < 0.05$).

Depth (m)	**Parameter**	***P* value**	**Year**						**Significant annual differences**
			1998	**1999**	**2000**	**2001**	**2002**	**2003**	
1	Temperature	< 0.0001	14.01	11.84	13.27	12.91	13.57	13.1	1998 > all other years; 1999 < 2002 and 2003
1	Salinity	0.0036	29.68	28.18	29.2	30.29	29.43	29.62	1999 < 2001
1	Density (sigma-theta)	0.003	21.94	21.24	21.99	22.82	22.05	22.3	1998 and 1999 < 2001
50	Temperature	< 0.0001	8.73	8.05	8.33	7.81	7.42	8.22	1998 > 1999, 2001, 2002, 2003; 1999 > 2002; 2000 > 2001, 2002; 2001 > 2002; 2002 < 2003
50	Salinity	< 0.0001	33.17	33.22	33.08	33.16	33.35	32.75	2003 < 1999, 2000, 2001, 2002
50	Density (sigma-theta)	< 0.0001	25.72	25.86	25.71	25.86	26.1	25.47	1998 < 2002; 2000 < 2002; 2003 < 1999, 2001, 2002

Table 3.4. Percent surface trawls with and without juvenile salmonids and other fishes along with statistical differences (chi-square test, with Yates correction) between the occurrence of juvenile salmonids and other fishes in trawls. Relationship variable indicates whether predator or forage fish species occurrences were significantly negative (i.e.,< expected) or positive (i.e., > expected), or there was no relationship.

	Pacific hake	Chub mackerel	Jack mackerel	Spiny dogfish	Northern anchovy	Pacific herring	Whitebait smelt	Pacific sardine
With juvenile salmonids	11.87%	4.68%	7.69%	10.87%	20.74%	31.61%	21.57%	17.22%
Without juvenile salmonids	22.07%	11.70%	16.05%	10.37%	19.57%	27.59%	13.71%	23.75%
Chi-Square	10.3	11.02	10.1	2.74	7.86	28.06	36.35	0.72
P-Value	0.0013	0.0009	0.0015	0.0980	0.0051	0.0000	0.0000	0.3960
Relationship	Negative	Negative	Negative	No	Positive	Positive	Positive	No

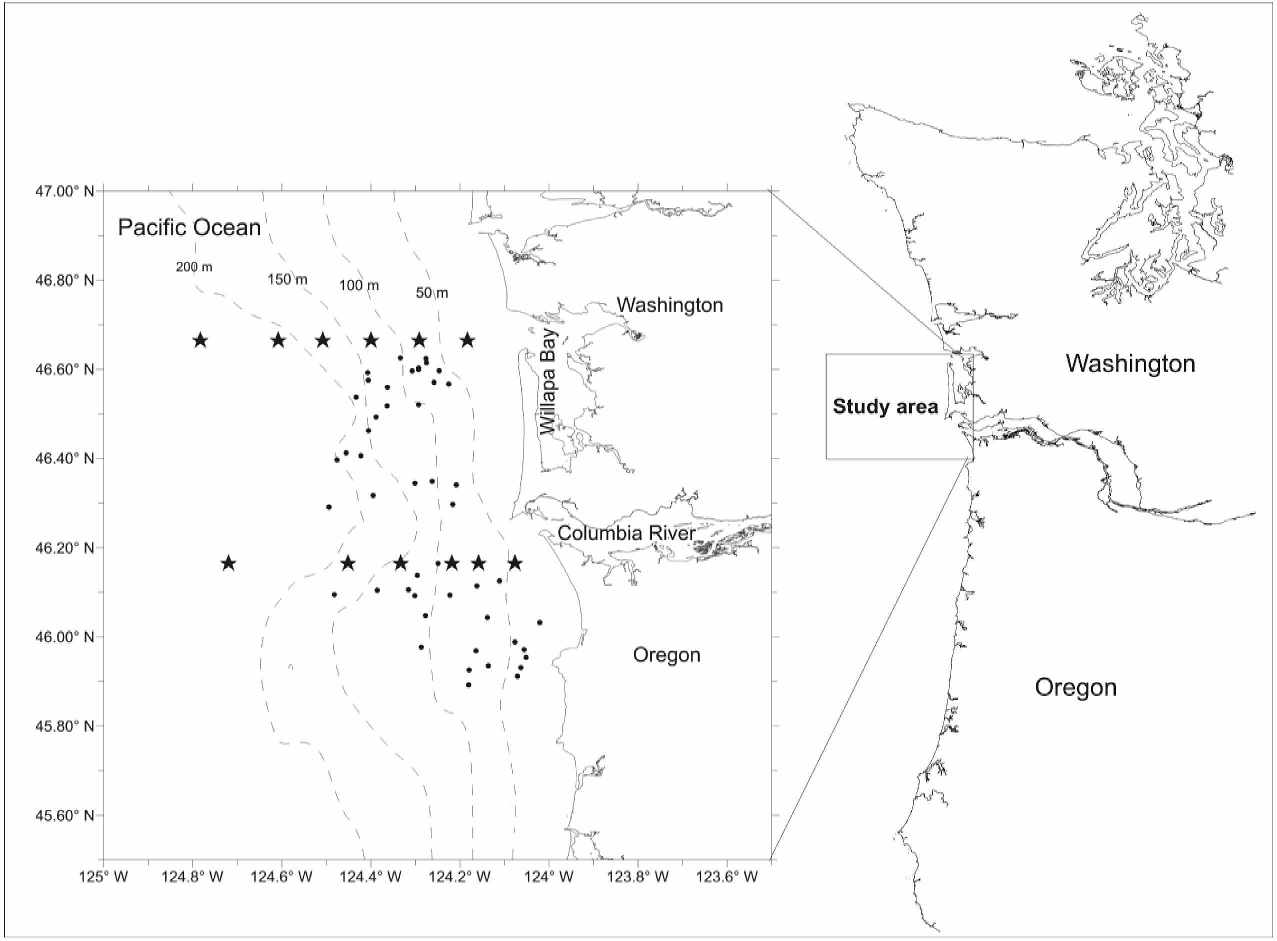


Figure 3.1. Location of surface trawl stations sampled during spring/early summer 1998 (●) and 1999-2003 (★) off the mouth of the Columbia River.

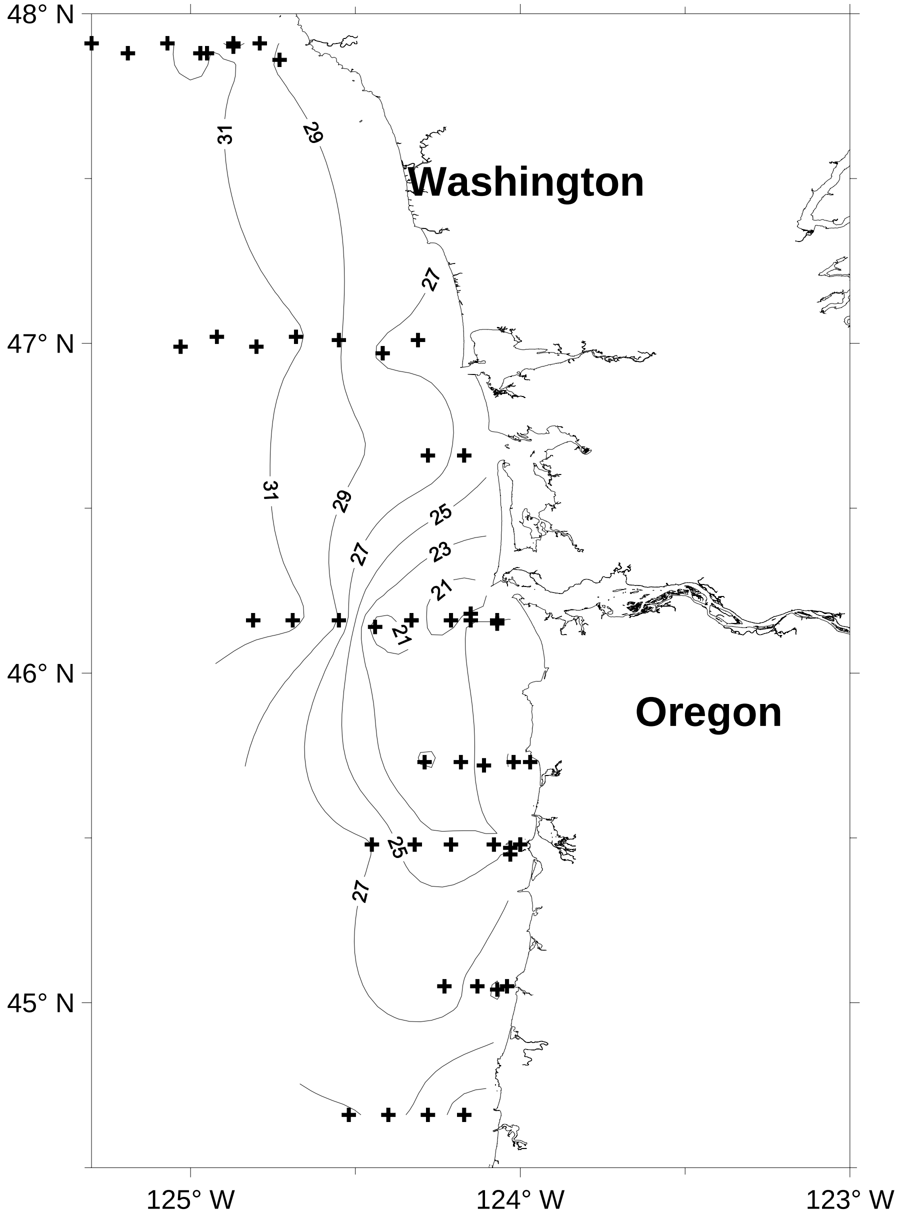


Figure 3.2. Location (✚) of daytime surface trawl stations sampled during June 1999 by BPA Plume Study. Surface salinity isopycnals are also shown.

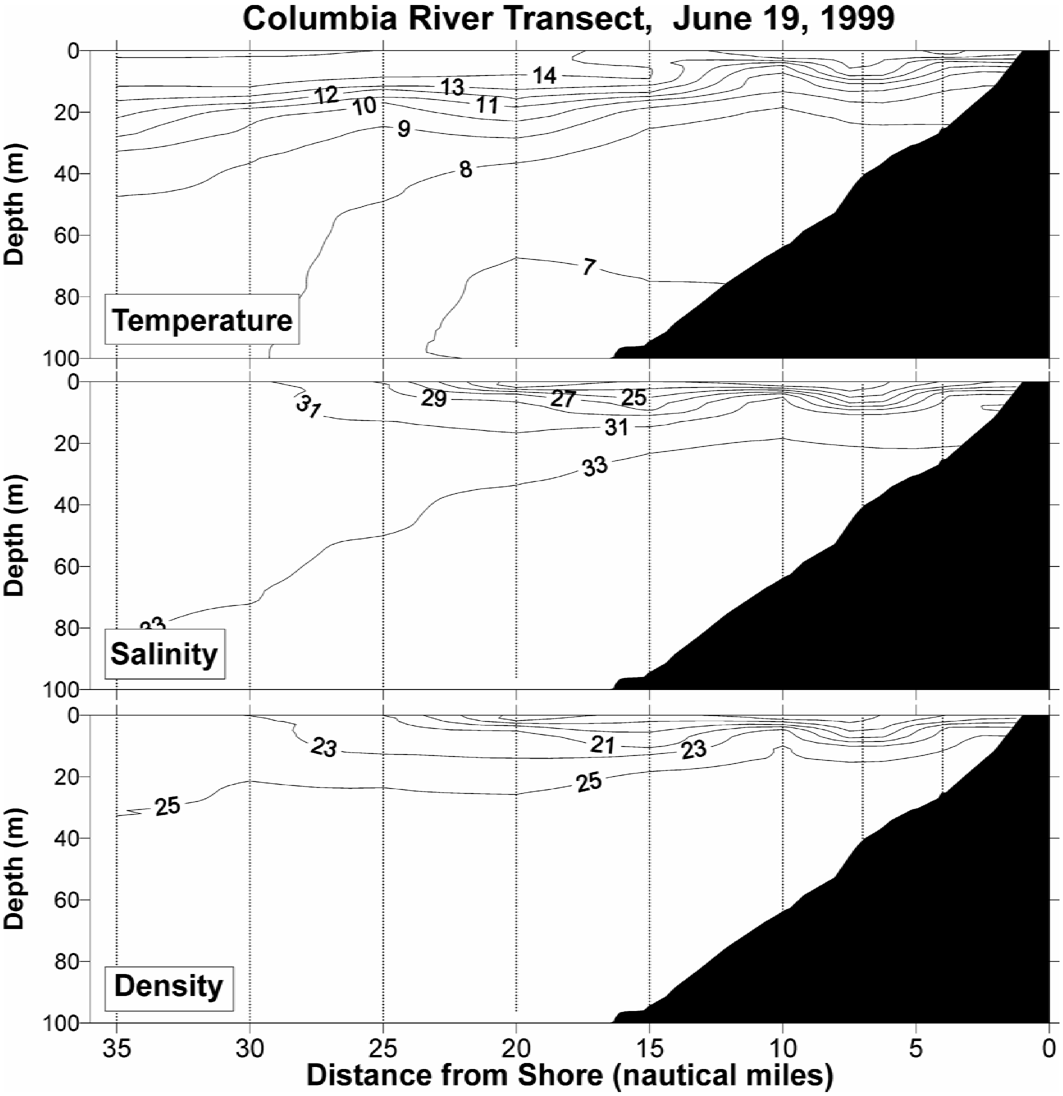


Figure 3.3. Depth contours of temperature, salinity, and density on a coastal transect just south of the Columbia River, 19 June 1999.

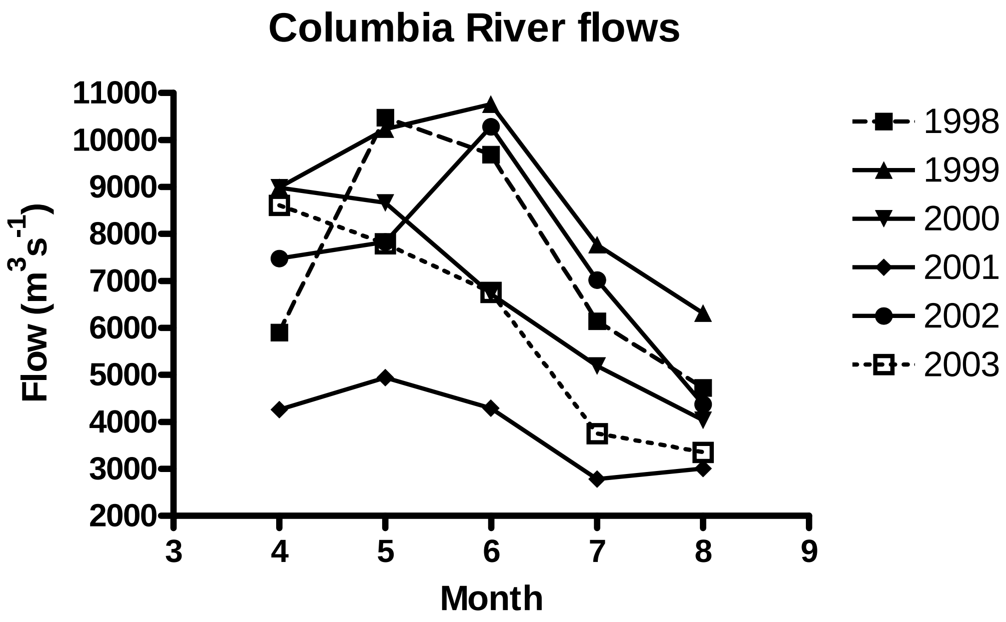


Figure 3.4. Average monthly Columbia River flows from April through August 1998-2003.

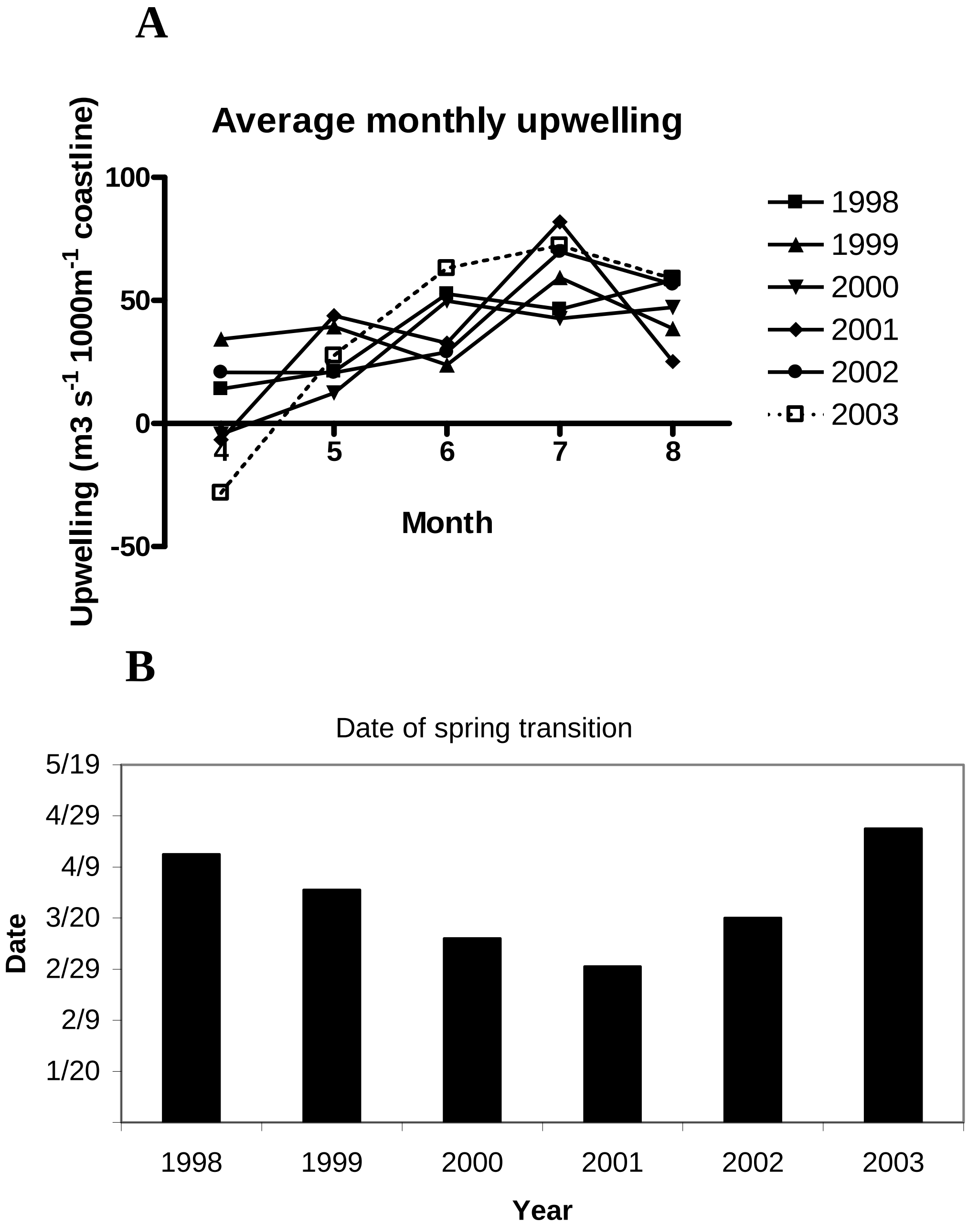


Figure 3.5. Average monthly upwelling from April through August at 45° N 125° W (A), and day of the spring transition off Oregon/Washington (B), 1998-2003.

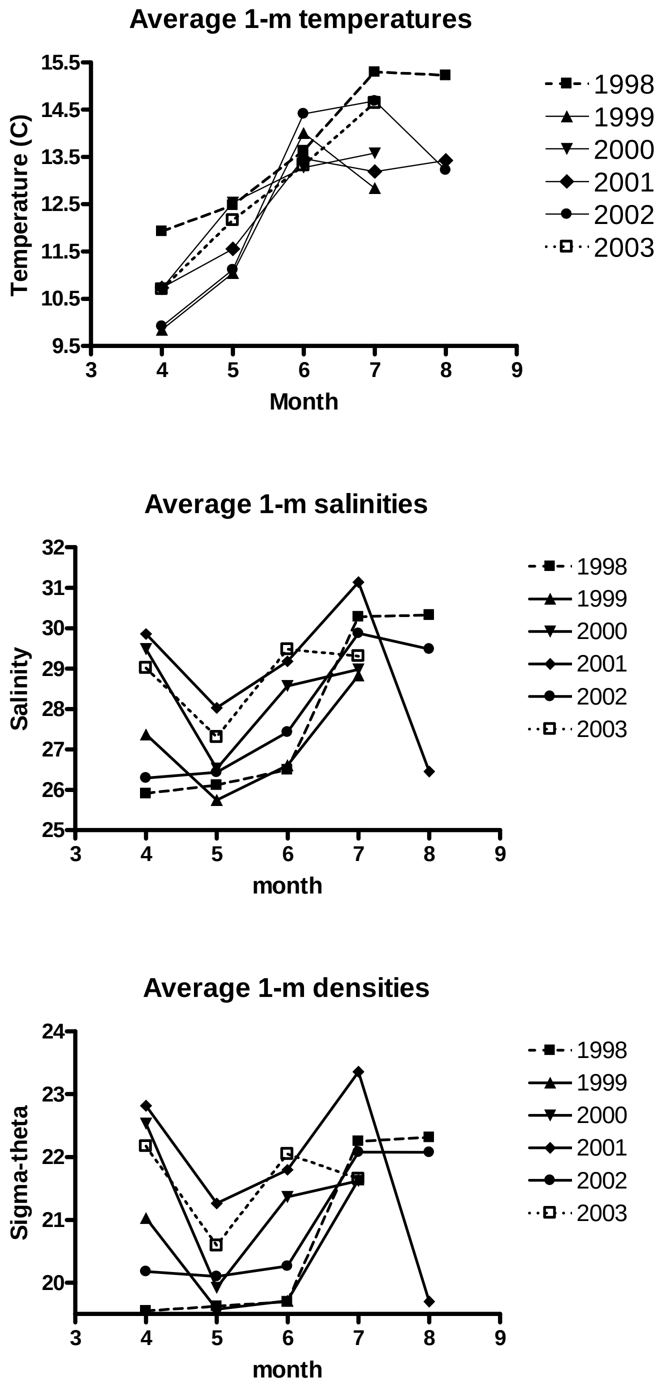


Figure 3.6. Average temperatures, salinities and densities at 1-m depth off the Columbia River, April-August, 1998-2003.

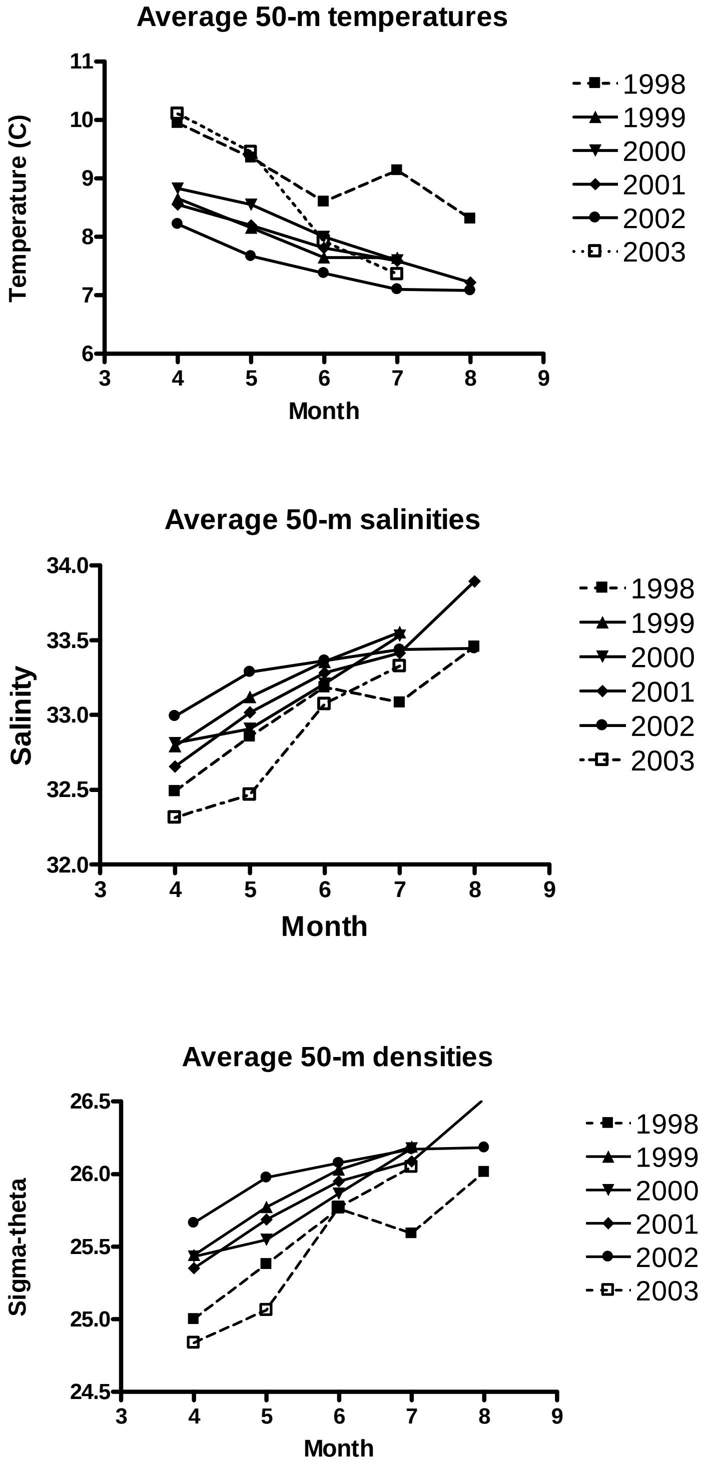


Figure 3.7. Average temperatures, salinities and densities at 50-m depth off the Columbia River, April-August, 1998-2003.

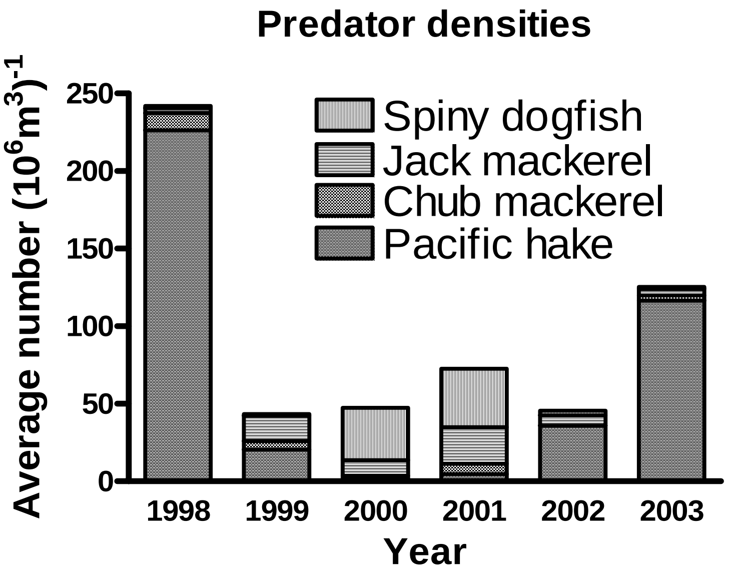


Figure 3.8. Average annual densities of four pelagic predatory fishes collected at night by surface trawls off the Columbia River during spring/early summer 1998-2003.

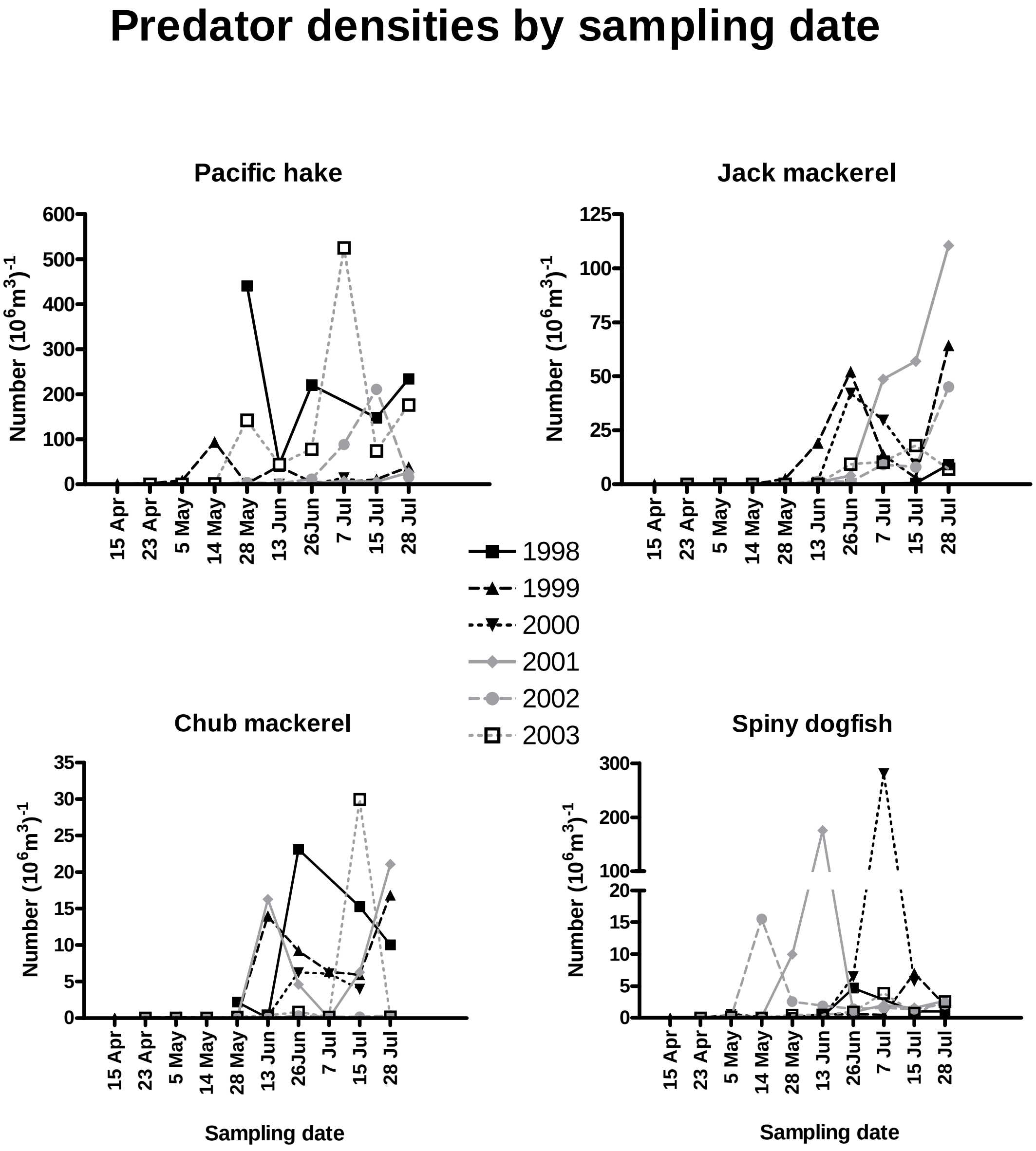


Figure 3.9. Average densities of four predatory fishes collected at night by surface trawls off the Columbia River by sampling date, 1998-2003.

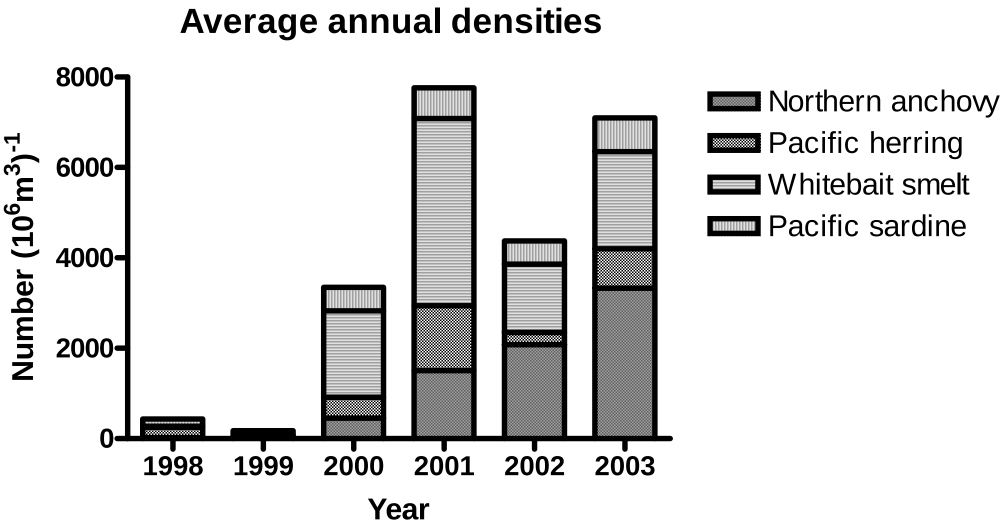


Figure 3.10. Annual average densities of forage fish captured at night by surface trawls off the Columbia River, 1998-2003.

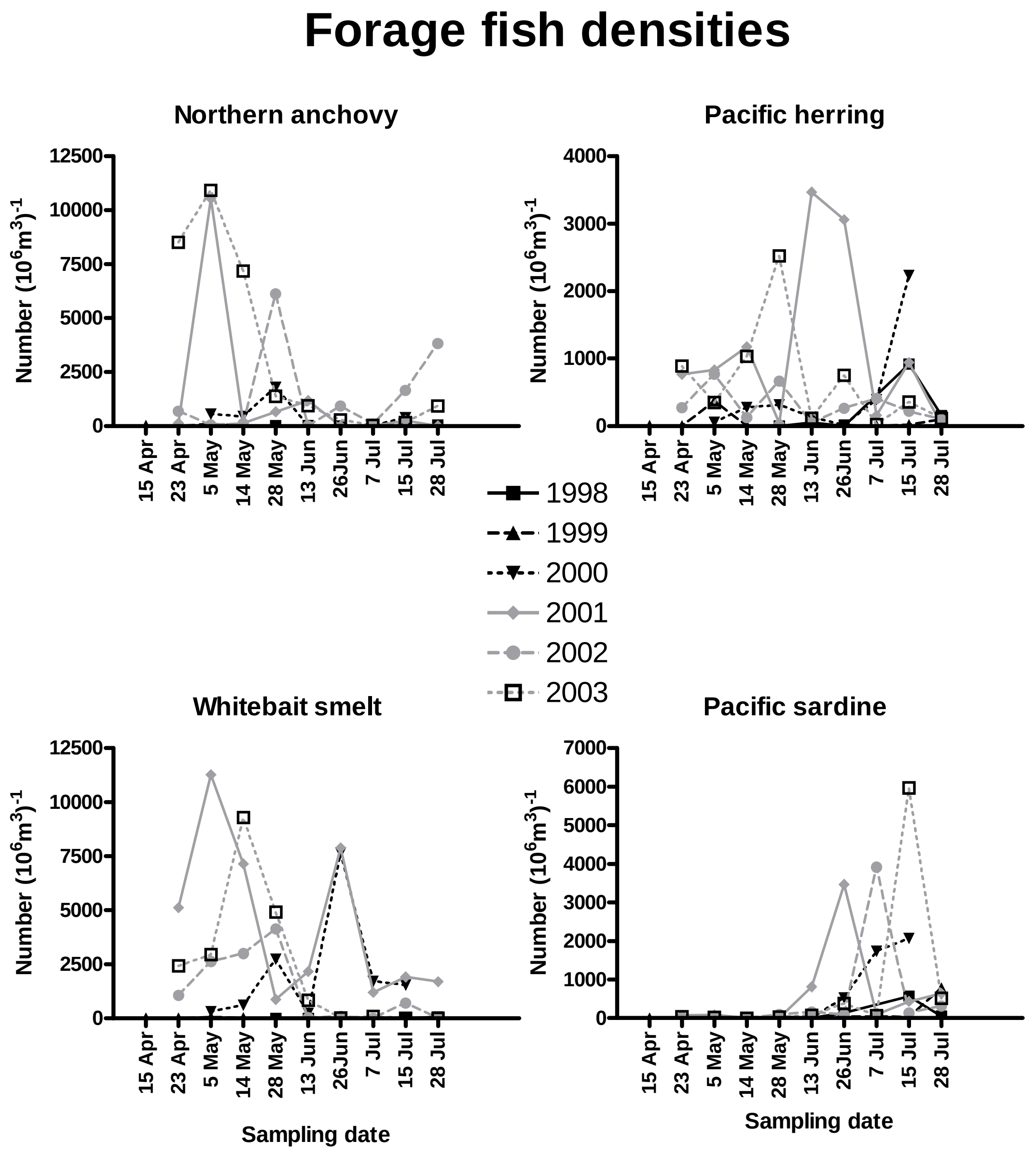
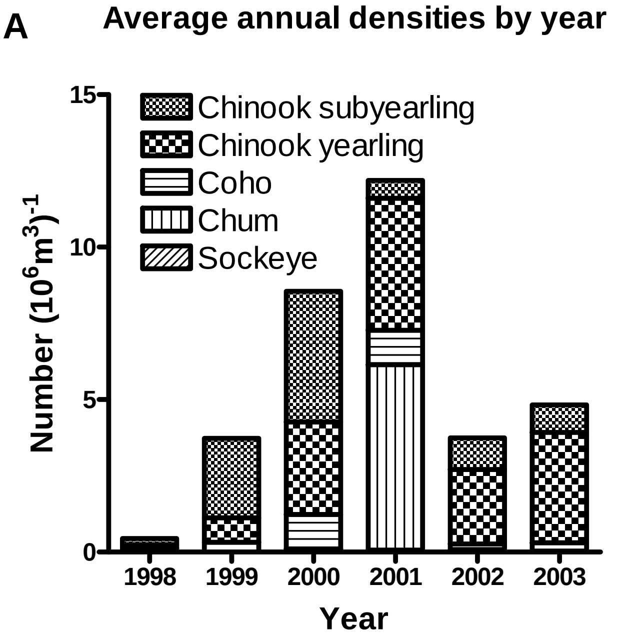


Figure 3.11. Average densities of four forage fish species collected at night by surface trawls off the Columbia River by sampling date, 1998-2003.



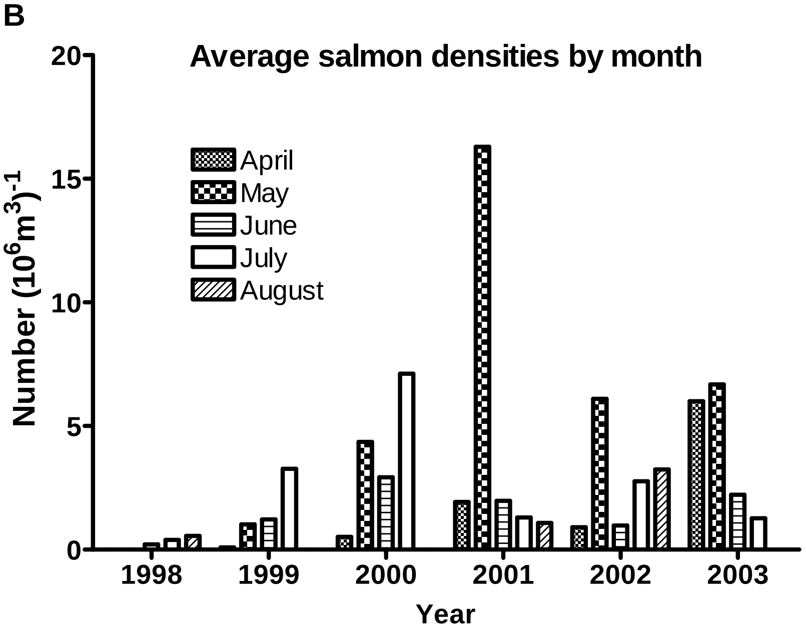


Figure 3.12. Average annual densities of juvenile salmonids captured at night by surface trawls off the Columbia River, 1998-2003 (A). Average densities of juvenile salmonids captured by surface trawls off the Columbia River by month, 1998-2003 (B).

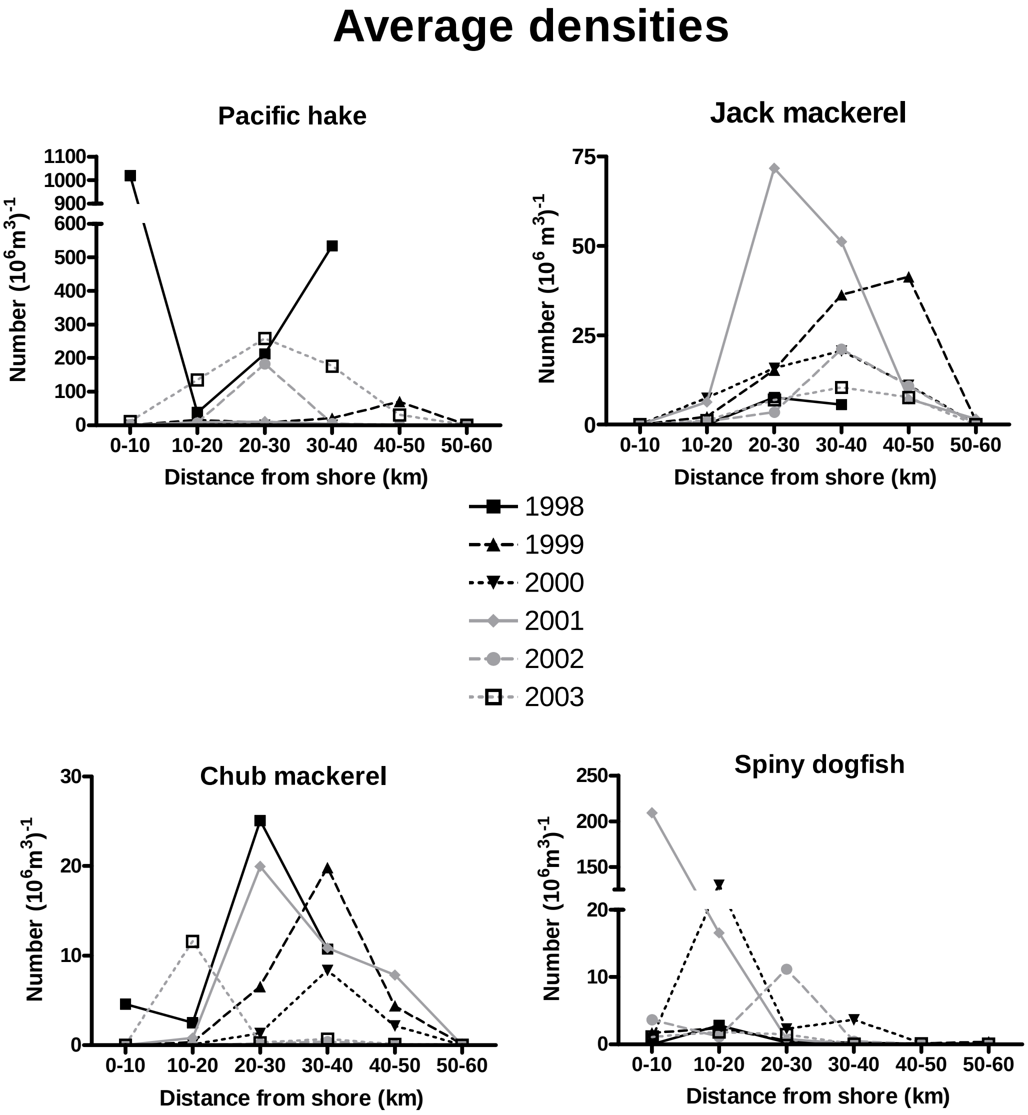


Figure 3.13. Average annual densities of four predatory fishes collected at night by surface trawls off the Columbia River at different distances from shore, 1998-2003.

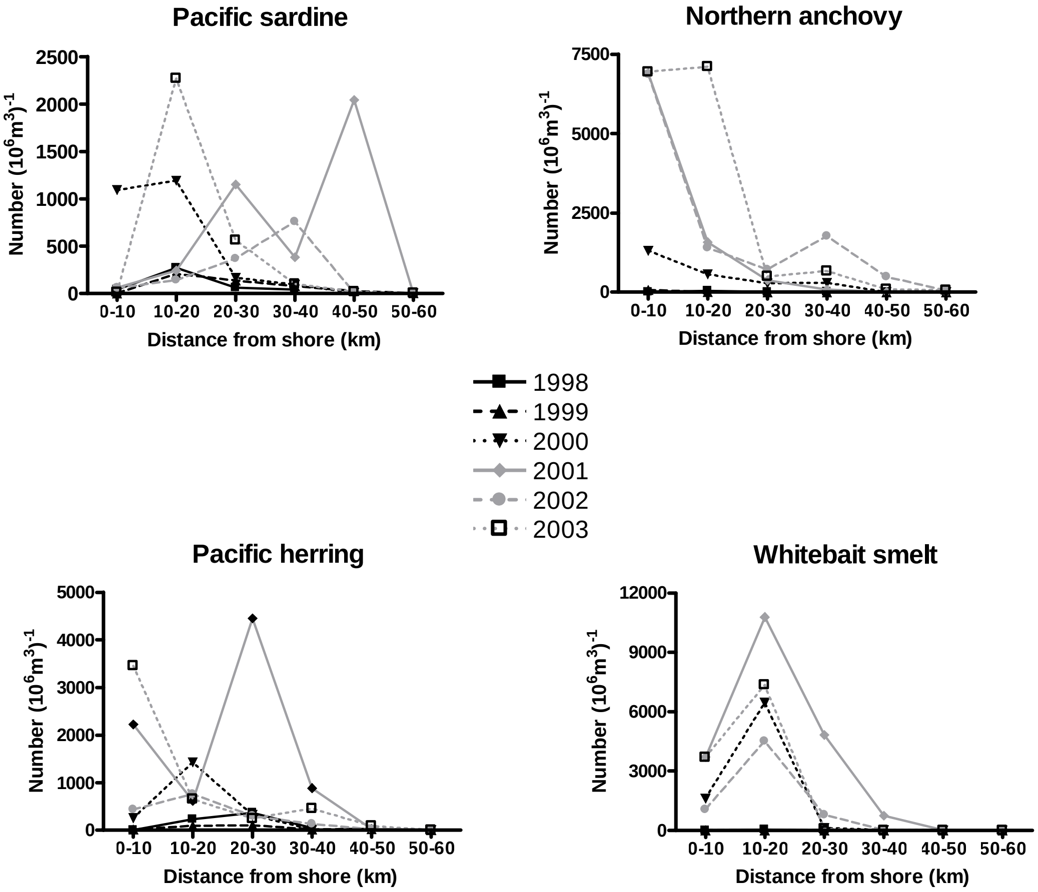


Figure 3.14. Average annual densities of four forage fishes collected at night by surface trawls off the Columbia River at different distances from shore, 1998-2003.

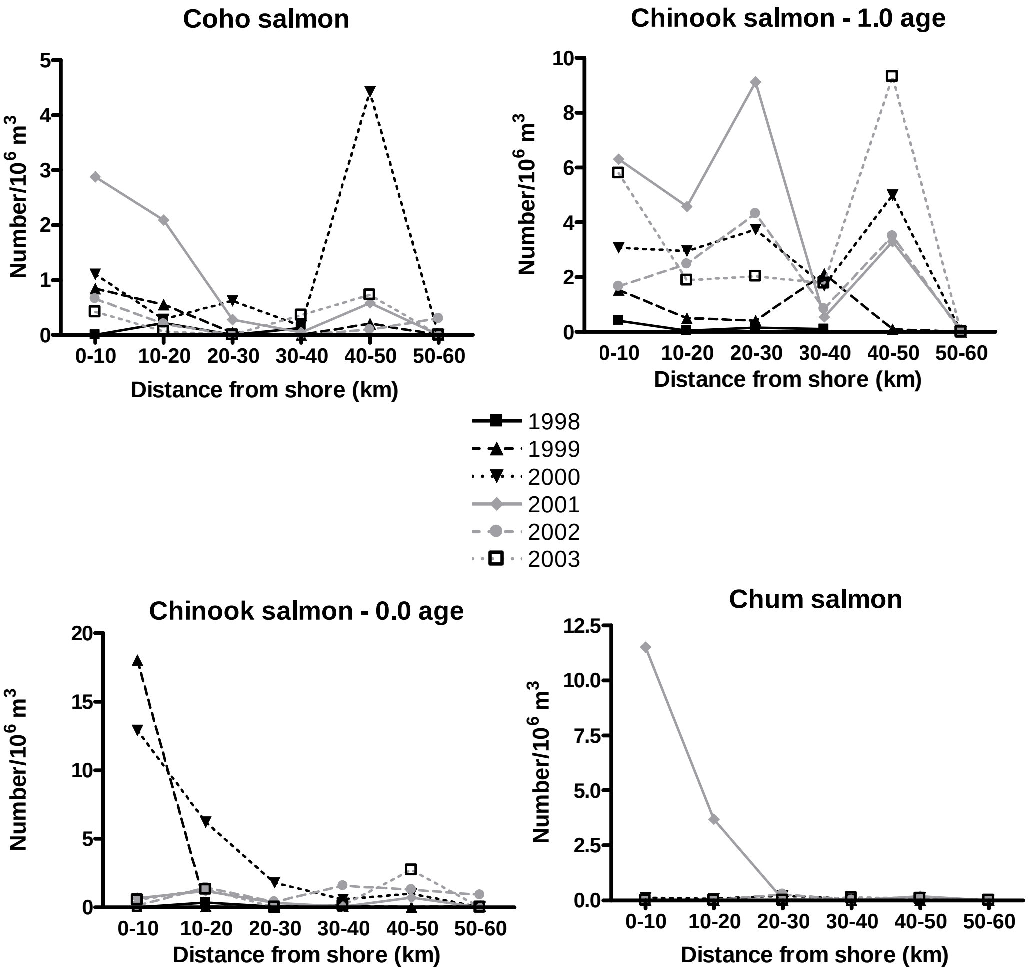


Figure 3.15. Average annual densities of juvenile salmonids collected at night by surface trawls off the Columbia River, 1998-2003.

Plume Study

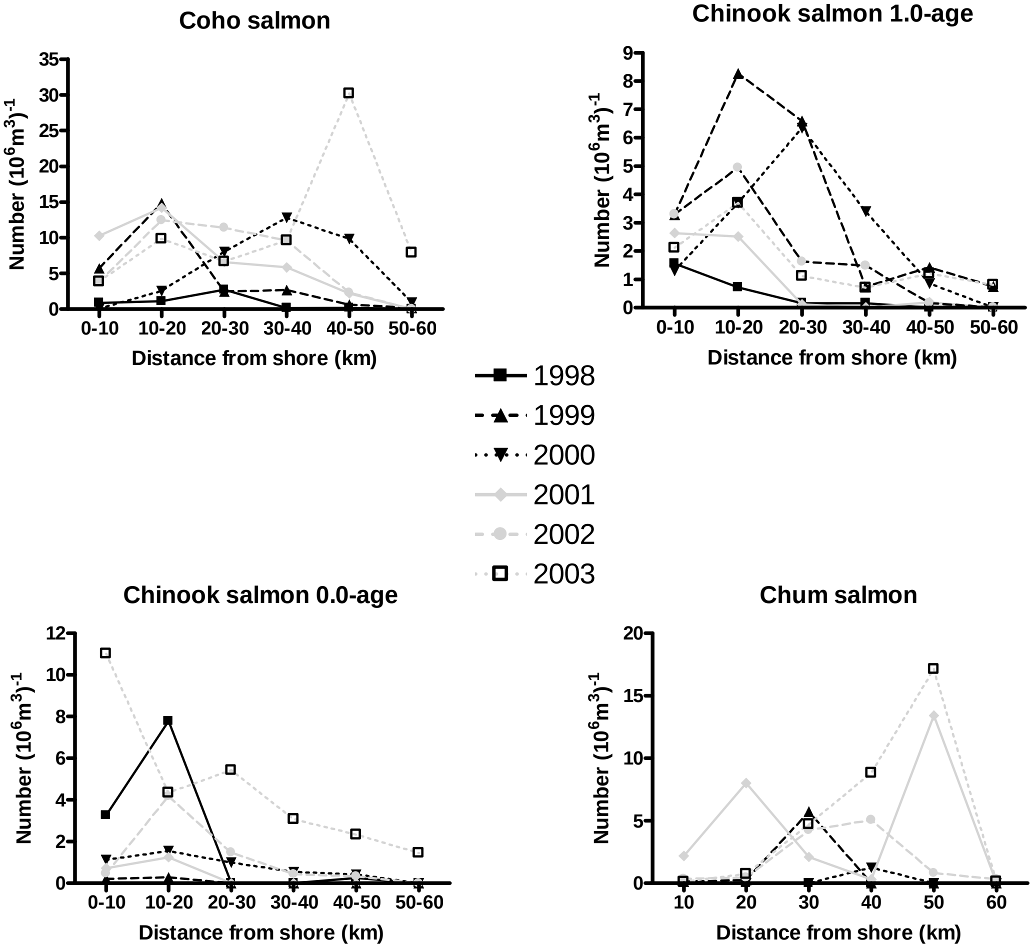
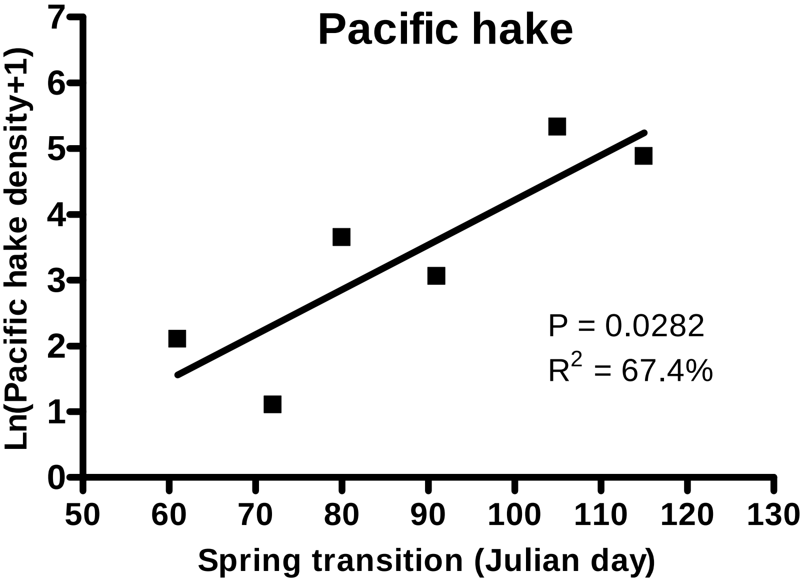


Figure 3.16. Average annual densities of juvenile salmonids collected during BPA Plume study (daylight) by surface trawls in June off the Oregon/Washington coast at different distances from shore, 1998-2003.



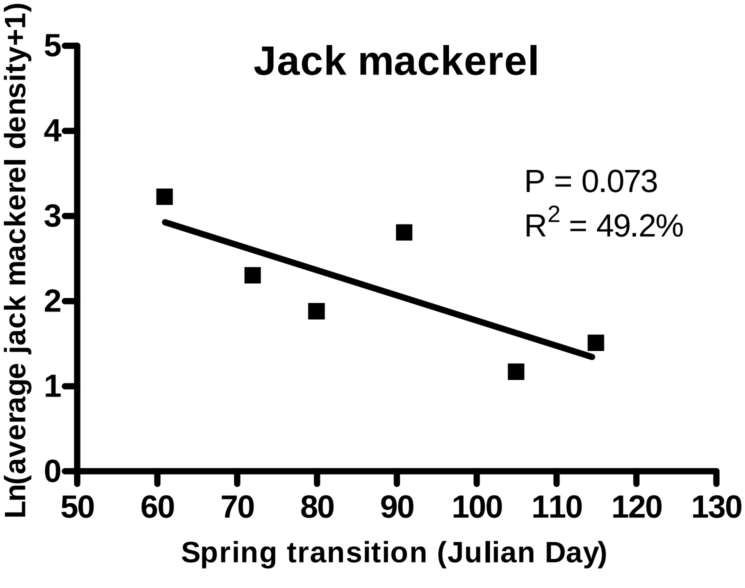


Figure 3.17. Relationship between annual Pacific hake (*Merluccius productus*) and jack mackerel (*Trachurus symmetricus*) densities identified by surface trawling at night off the Columbia River, 1998-2003, and date of the spring transition.

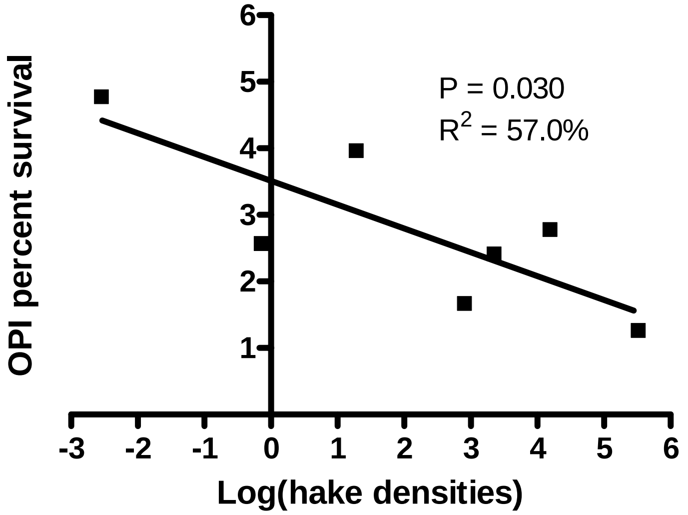


Figure 3.18. Relationship between average May/June densities of Pacific hake (*Merluccius productus*) caught off the mouth of the Columbia River, 1998-2004, and coho salmon (*Oncorhynchus kisutch*) OPI percent marine survival.

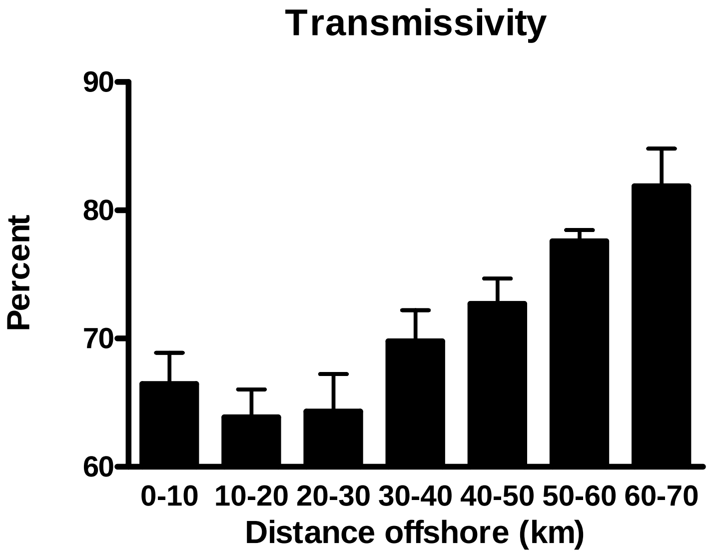


Figure 3.19. Average surface (1-m depth) percent transmissivity (water clarity) observed at BPA Plume Study surface trawling stations off Oregon/Washington by distance from shore, 2002-2003.

Chapter 4. Nocturnal Feeding of Pacific Hake (*Merluccius productus*) and Jack Mackerel (*Trachurus symmetricus*) off the Mouth of the Columbia River, 1998-2004.

Robert L. Emmett and Gregory K. Krutzikowsky

In Review
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ABSTRACT

Predation by piscivorous marine fishes has been hypothesized to be a primary source of marine mortality for Pacific Northwest juvenile salmon. From spring-summer 1998-2004, we collected predator and prey fishes (forage and juvenile salmonids) at the surface at night off the mouth of the Columbia River. Pacific hake (*Merluccius productus*) appeared to feed most intensively during cool ocean years (2001 and 2002), and less intensively during 1998, a warm year. Euphausiids and fishes were the most commonly eaten prey for both species. Hake and jack mackerel (*Trachurus symmetricus*) appeared to show some diet selectivity, eating some fish, including salmonids, in a higher proportion than found in the environment. Both Pacific hake and jack mackerel ate juvenile salmonids, but at very low amounts. After considering population size in the study area, these two predators do not appear to be responsible for the death of large numbers of Columbia River juvenile salmon smolts. However, our estimates of the number of salmonids eaten by hake and mackerel could be very low. More work needs to be done to identify and quantify salmon predation off the Pacific Northwest.

INTRODUCTION

The coastal zone where the Columbia River meets the Pacific Ocean is a very dynamic environment with very strong currents and large fronts (Hickey and Banas 2003; De Robertis et al. 2005; Morgan et al. 2005), and where each year, approximately 100 million juvenile salmon smolts originating from the Columbia River first encounter the marine environment. This habitat is also where much of the marine mortality of juvenile salmon (*Oncorhynchus* spp.) is thought to occur, with predation suspected to be the primary source of this mortality (Pearcy 1992; Beamish and Mahnken 2001). To examine this hypothesis, we initiated a study in 1998 to identify the abundance and document the feeding habits of large predatory fishes off the Columbia River.

The movement and feeding patterns of predatory fishes are known to affect fish prey resources (Carpenter and Kitchell 1993; Ware and McFarlane 1995; Bax 1998; Tsou and Collie 2001; Hunt and Stabeno 2002; Worm and Myers 2003). Nevertheless, an extensive analysis of pelagic fish food habits off Oregon/Washington in the 1980s (Brodeur et al. 1987) found only black rockfish (*Sebastes melanops*) and searun cutthroat trout (*O. clarkii*) eating salmon smolts off Oregon/Washington. Since these predatory species were not abundant, their feeding would likely account for relatively little juvenile salmon mortality.

We suspected that few instances of juvenile salmonid predation were observed by Brodeur et al. (1987) because nearly all their purse seine sampling occurred during daylight. Many large predatory fishes undertake diel vertical migrations; staying deep during the day but approaching the surface at night. Diel movement in fishes, particularly among clupeids (Blaxter and Holliday 1963) and hakes (Pitcher and Alheit 1995), is common, and thought to be related to both reduced predation and an increase in prey availability (Clark and Levy 1988; Bozzano et al. 2005). Juvenile salmonids off the Columbia River, on the other hand, do not appear to undertake diel migrations, but remain near the surface (Emmett et al. 2004). By sampling fishes at night at the surface, we were able to observe the interactions of diel migrating predators with surface oriented juvenile salmonids, as well as diel migrating forage fishes, which may act as alternative prey.

During our sampling, only two predatory fishes [Pacific hake (*Merluccius productus*) and jack mackerel (*Trachurus symmetricus*)] were abundant enough to possibly affect juvenile salmonid abundance (Emmett et al. 2006). Pacific hake is the most abundant predatory fish along the US Pacific Coast (Methot and Dorn 1995). While their present population biomass is lower than the recent peak abundance during 1987, it is still estimated to be 2.6 to 4.0 million mt (Helser et al. 2004). Pacific hake normally migrate to the Pacific Northwest (Oregon/Washington/British Columbia, Canada) waters in the spring/summer to feed and return to southern California waters in winter to spawn (Bailey et al. 1982; Dorn 1995). Hake feeding habits have been relatively well studied (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986; Brodeur et al. 1987; Tanasichuk et al. 1991; Buckley and Livingston 1997; Tanasichuk 1999; Nelson 2004) but none of these studies collected hake at the surface at night. Furthermore, while the ecological consequences of hake feeding, movements, and migrations on other fishery resources has been relatively well documented in Canadian waters, particularly the decline in Pacific herring (*Clupea pallasii*) abundance (Ware and McFarlane 1995, Robinson and Ware 1999, Benson et al. 2002), studies in United States waters (Francis 1983; Livingston and Bailey 1985; Rexstad and Pikitch 1986; Jay 1996; Buckley and Livingston 1997) have not been very conclusive. However, Hannah (1995) did find that

Pacific hake predation influences the abundance of pink shrimp (*Pandalus jordani*) off Oregon.

Jack mackerel is perhaps the second most abundant large pelagic predatory fish on the Pacific coast (MacCall et al. 1980; MacCall and Stauffer 1983), and was the second most abundant large pelagic fish off Oregon in 1983 and 1984 (Brodeur and Pearcy 1986; Emmett and Brodeur 2000). Little is known about their migratory behavior, but juveniles are generally abundant off California, and adults are regularly found from the Gulf of California to Alaska (Blunt 1969; MacCall and Stauffer 1983). There are currently no regular estimates of jack mackerel biomass off the West Coast, but in 1983, their spawning biomass was estimated to be 0.64 to 1.3 million mt off southern California, with perhaps the same biomass outside this area (MacCall and Stauffer 1983). While no directed commercial fishery currently exists for jack mackerel off Oregon, they are the most common by-catch in the commercial Pacific hake fishery off Oregon (Wiedoff et al. 2003).

Jack mackerel off Oregon/Washington eat primarily euphausiids (mostly *Thysanoessa spinifera* and *Euphausia pacifica*), other crustaceans, and small fishes, but the importance of any particular prey varies annually (Brodeur et al. 1987). For example, juvenile northern anchovy (*Engraulis mordax*) were important jack mackerel prey in 1982, but not in 1983 and 1984. Euphausiids are usually the most important prey in spring and summer, and fish in fall (Brodeur et al. 1987). Carlisle (1971) found that jack mackerel off California fed mainly on euphausiids by weight, but copepods and pteropods were important by number. Other species of *Trachurus* spp. appear to feed similarly, with euphausiids the primary prey, and fish eaten more often as mackerel become larger (Pillar and Brange 1998; Šantić et al. 2005). Diel feeding behavior of *Trachurus* spp. varies geographically. Off Chile, *Trachurus murphyi* feeds mostly at night (Bertrand et al. 2004), as does *Trachurus trachurus* in the Adriatic Sea (Jardas et al. 2004), but off South Africa, *Trachurus capensis* feeds primarily during daylight (Pillar and Brange 1998).

While our primary goal was to determine if large predatory fishes were eating juvenile salmonids, this study also provided information on the nocturnal pelagic marine food web off the Pacific Northwest, data that are rarely collected. This type of information is valuable when developing regional multispecies ecosystem models and ecosystem management plans. This study also provides information on how fish feeding habits can be used to document ecosystem changes (Hanson and Chouinard 2002; Link 2004) and indicate the recruitment processes of prey species (Mills et al. in press). However, the overall goal of this paper is to present the nocturnal feeding habits of two large marine predatory fishes and discuss their relationship to Northwest fishery resources, particularly juvenile salmon.

METHODS

All fishes for this study were collected by contracting a commercial fishing vessel and trawling at night. Once captured, fishes were processed (identified, measured, counted, and stomachs removed) on deck at sea. Final stomach analysis was conducted in the laboratory.

Study area

The study area, located just off and north of the mouth of the Columbia River (Fig. 4.1), is a very dynamic physical environment with abundant natural resources. Important commercial fisheries in the area include Pacific salmon (*Oncorhynchus* spp.), Pacific sardine (*Sardinops sagax*), flatfishes, and Dungeness crab (*Cancer magister*). Detailed biological and physical oceanographic information about the area can be found in Pruter and Alverson (1972), Hickey (1989), and Hickey and Banas (2003), therefore only a brief synopsis is presented here.

The study area is strongly affected by three physical factors: ocean currents, including tides, upwelling, and Columbia River flows. Ocean currents are generally southerly (California Current) in the spring and summer, and northerly (Davidson Current) in the winter. Upwelling occurs during spring and summer when winds are northwesterly. Downwelling occurs during winter when winds are southwesterly. Upwelling is normally not continuous, but sporadic, with periods of strong upwelling usually followed by a couple of days of relaxation. Columbia River flows usually peak in May/June when snow in interior basins melts. Columbia River juvenile yearling salmon smolt migration peaks in May, and subyearling salmon smolt migration generally peaks in June-July.

Fish sampling

All stomach collections were made from 1998 through 2004 at approximately 10-day intervals from late April through July or early August. Although 10 surveys were attempted each year, in 1998 and 2004 nine surveys were conducted, and in 2000 only eight, because of weather or mechanical malfunction.

For all but 3 of the 67 cruises, we used a 264-rope trawl. From June 1998-on, the 264-rope trawl and 3-m foam filled doors built by NET Systems were used because this gear was found to be the most effective at fishing at the surface. The 264-net is 100-m long and has a fishing mouth opening of approximately 28-m wide by 12-m deep (Emmett et al. 2004). Trawl 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 #4 rope trawl had similar mesh sizes to those of the 264-rope trawl. All trawl net tows were made at the surface, except during May 1998 when they were ~ 5 m below the surface. The net was towed 137 m (75 fathoms) behind a chartered commercial fishing vessel traveling approximately 3 knots (1.5 m s^{-1}). The trawl was towed for 30 minutes. However this was often shortened to 15 minutes from 2001-2004 because of extremely large tows of forage fish. All trawling was conducted at night when diel migrating predators would interact most with surface oriented juvenile salmonids (Emmett et al. 2004) and when pelagic trawling for many fishes is most effective (Dotson and Griffith 1996; Krutzikowsky and Emmett 2005).

In 1998 a variety of stations (Fig. 4.1) were sampled every 10 days because we wanted to verify that the fishing gear worked effectively, and that predator and forage fishes had a wide distribution in the study area. From 1999-2004, twelve designated stations along two transects were sampled each survey (Fig. 4.1).

The first 30 individuals of every species collected during each haul were identified and measured and the remainder counted. However, when large catches of a species were caught (generally > 200), the catch was subsampled; lengths of the first 30 individuals were measured, and at least one random basket of that species was counted and weighed, and then the remainder of that species weighed. The total number of that species per haul was then calculated.

Minimum estimates of predator and forage fish densities (number/10^6m^3) were determined by dividing the number of fish caught by the distance trawled times the mouth area of the trawl (336 m^2). Net catching efficiency was assumed to be 1. Distance fished was calculated by computing the distance between the beginning and ending trawl locations using the geographic positioning system. Densities of salmon species were calculated by age-class, which was identified by length (Dawley et al. 1986). We use the salmon age convention of Koo (1962) with the number before the period to indicate winters in fresh water and the number after the period indicating winters spent in the ocean. Densities of young-of-the-year (YOY) Pacific hake and rockfishes (*Sebastes* spp.) were calculated separately from older age classes. YOY were easily separated from older age-classes because all were <100 mm long. Monthly densities of Pacific hake, jack mackerel and forage fishes were calculated using the delta-distribution method

(Pennington 1996). The delta-distribution is appropriate for a species that shows a very patchy distribution (relatively few large catches and some zero catches). The delta-distribution method uses a lognormal model for the non-zero fish catches to estimate population mean and variance and adjusts these values for the proportion of tows with zero catches (Pennington 1996).

Stomach analysis

Since the primary objective of this study was to identify if Pacific hake or jack mackerel were feeding on salmon smolts, which occurred rarely, we attempted to analyze as many stomachs as possible. This was accomplished by analyzing stomachs both *quantitatively* and q*ualitatively*. Stomachs selected for *quantitativ*e analysis were dissected from the fish, placed in labeled muslin bags and then into a bucket containing a 10% formalin solution. From 1998 through 2003 stomachs from the first 30 Pacific hake or jack mackerel identified and measured per haul were removed and saved for quantitative stomach analysis. Qualitative stomach analysis consisted of cutting open and examining fish stomachs at sea. If fish were found in the stomach, we recorded the haul number, species, and length of the predator and placed the stomach in a muslin bag and preserved it in formalin for quantitative analysis. If a stomach did not contain fish, general identification of what the stomach contained was recorded (e.g., euphausiids, shrimp, and digested material). From 1998 through 2003 qualitative stomach analysis was performed on as many predatory fish as time allowed between sampling efforts (i.e., before the next haul), approximately 15 minutes. In 2004, all stomachs were analyzed semi-quantitatively at sea; stomachs were opened, prey were identified to general taxa, and fish prey were identified to species, counted, and measured. All stomachs from fishes that appeared to be net feeding (i.e., fish showing in the mouth or clearly just eaten) were not included in these analyses.

In the laboratory, stomachs were first soaked in freshwater and then their contents were analyzed. Fish prey were identified to the lowest possible taxonomic level, measured (TL, mm), and weighed (0.001 g). For 25% of all stomachs collected, non-fish prey taxa were identified to lowest taxonomic level possible, counted, measured (first 30 of a prey species, body length, mm) and weighed (0.001 g). For the remaining stomachs, non-fish prey items were identified to family and weighed.

Fishes preserved in formaldehyde shrink below their live lengths. As such, total lengths of fish eaten were increased by 4% (Parker 1963). To allow comparisons between fish prey lengths and juvenile salmon lengths, juvenile coho and Chinook salmon fork lengths were converted to total lengths using the formulas described by Ramseyer (1995).

Data analysis

To accurately represent the diets of hake and mackerel populations' off the Columbia River it was necessary to account for differences in catches per haul. As such, all measures of diet (percent empty, frequency of occurrence, etc.) were calculated by haul and then weighted by multiplying these data by the percent of the entire catch that each haul represented, and then summed. For example, if Haul A had 20% empty stomachs and represented 10% of the entire catch and Haul B had 50% empty stomach but represented 90% of the catch for that month, then the percent empty for that month was calculated as (0.2 x 0.1)+(0.5 x 0.9) = 0.47 (47% empty) .

A Kruskal-Wallis Test (a nonparametric analysis of variance) was used to identify differences in percent empty stomachs between years and between months. When a significant difference was observed per time period ($P < 0.05$), Dunn's Multiple Range Test (a pair-wise comparison test) was used to identify which year or month differed. Linear regression was used to identify the relationship between percent empty stomachs and predator abundance, and a Kruskal-Wallis test was used to identify annual and monthly differences in predator sizes. Predator densities and percent empty data were log and arcsine transformed, respectively, before analysis. A Mann-Whitney test was used to compare medians lengths of euphausiids eaten by Pacific hake and mackerel.

The frequency of occurrence (FO) of each prey species or prey category was calculated for each month/year by dividing the number of times a prey category occurred by the total number of stomachs that contained food. Again, these data were weighted by catch per haul.

To identify if hake and jack mackerel were feeding selectively on specific fish species (i.e., eating a fish prey either with greater or less frequency than it was found locally in the environment), we compared the numerical percentage of a fish species in the diet with the numerical percentage of that fish species in the hauls that captured hake or jack mackerel. The “selectivity” metric we used was the log of the odds ratio (LOR) (Gabriel 1978, Schabetsberger et al. 2003). The LOR is symmetrical around 0 (no selectivity, a prey type was eaten in the same proportion as it occurred in the local surroundings) and ranges from 0 to + ∞ (positive prey selection), and 0 to - ∞ (negative prey selection):

$$\mathrm{LOR} = \ln\left(\frac{d_i(100\text{-}e_i)}{e_i(100\text{-}d_i)}\right)$$

where d_i and e_i are the numerical percentages of fish taxon i in the predator diet and local surroundings, respectively. As stated earlier, the LOR values were calculated by month by summing diet and catch data from each individual haul after these data were weighted (multiplied) by the percent predator catch each haul represented per month. Positive selective feeding occurs when prey are found at a higher percentage in a fish’s diet than in observed in the catch (i.e. local environment). Negative selective feeding takes place when a prey is more abundant in the catch than in a predator’s diet.

RESULTS

Predator sizes

The size of predators may affect their ability to feed on specific prey items, with larger fish generally able to consume larger prey. Median standard length of Pacific hake examined for stomach analysis was significantly different between years (Kruskal-Wallis, $P < 0.001$) (Fig. 4.2). Pacific hake in 1998 were significantly smaller than all other years, and during 2000 and 2001 larger, than all other years (Dunn's Multiple Comparison's Test, $P < 0.01$). However, median Pacific hake lengths from 1999, 2003 and 2004 were found to be similar (Fig. 4.2). Median jack mackerel size also differed significantly between years (Kruskal-Wallis, $P< 0.001$) (Fig. 4.2); jack mackerel in 1998-1999 were significantly smaller than all other years, and jack mackerel in 2003 were larger than other years (Dunn's multiple range test, $P< 0.05$).

Number of stomachs examined

We examined a total of 5,320 Pacific hake and 2,082 jack mackerel stomachs for this study (Tables 4.1 and 4.2). The most stomachs of Pacific hake collected and analyzed, and also the highest catches, were in 1998 (2,722) and the fewest in 2000 (49), with the number of stomachs analyzed distributed similarly to the number of hake caught. The highest catches and largest number of jack mackerel stomachs taken were in 1999 (496); the fewest were in 2004 (115).

Percent empty

One of our research questions was do predatory fish feed at night? We also wanted to identify any annual or monthly variations in feeding. As such, it was important to document the percentage and variation of empty stomachs by species and year/month. There were substantial annual and monthly differences in the percentage of empty stomachs. Both Pacific hake and jack mackerel had their highest overall percent empty stomachs in 1998, 65% and 86%, respectively (Fig. 4.3), and their fewest in 2000, 6% and 32%, respectively. In April and May 1998, we may have over-estimated the percent of empty Pacific hake stomachs because fishes were not collected at the surface but at mid-depth (sampling gear issue). Nevertheless, 1998 appeared to be a poor feeding year (high percent empty) for both Pacific hake and mackerel, and 1999 and 2000 relatively good feeding years (low percent empty). Both 2001 and 2002 appeared to be relative good feeding years for Pacific hake (<40% empty) but not for jack mackerel (> 66% empty). Jack mackerel had higher percent empty stomachs than Pacific hake both annually and monthly (Fig. 4.3).

The percent of empty stomachs varied widely for both species by month and year, but only Pacific hake showed significant annual differences, with 1998 > 1999 (Kruskal-Wallis, $P = 0.05$). On a monthly basis, Pacific hake had significantly more empty stomachs in June (Kruskal-Wallis test, $P = 0.0003$, Dunn's Multiple Range Test, $P < 0.05$) than in the other months. Jack mackerel percent empty stomachs showed no significant annual differences (Kruskal-Wallis, $P = 0.063$) but there were fewer empty stomachs in June than in other months (Kruskal-Wallis, $P = 0.0007$, Dunn's Multiple Range Test, $P < 0.05$).

There was a significant positive linear relationship ($P < 0.001$, $R^2 = 54.6$) between Pacific hake monthly densities and the percent of empty stomachs, indicating a possible density dependent relationship between hake densities and their ability to feed. The addition of monthly forage fish densities (prey abundance) in a multiple regression model did not improve the simple regression model (extra sum of squares F-test, P = 0.29). There was no relationship between jack mackerel monthly densities and the percent of empty stomachs (*P* = 0.5047).

The percent empty stomach information was averaged into discrete time bins for both predatory fish species. Both Pacific hake and jack mackerel showed declining percent number of empty stomachs from early evening to early morning (Fig. 4.4). This indicated that both species were actively feeding during the night.

Stomach contents

The frequency of occurrence (FO) of prey consumed by Pacific hake and jack mackerel are shown in Tables 4.1 and 4.2, respectively. Euphausiids (primarily *Thysanoessa spinifera*, and *Euphausia pacifica*) were the prey items occurring most frequently in Pacific hake and jack mackerel stomachs. We did not identify all euphausiids to species in all stomachs. As such, *T. spinifera* and *E. pacifica* are reported as separate taxa categories, they were not also included in Euphausiids in Tables 4.1 and 4.2. Euphausiids were most commonly eaten in 1999 and 2000, when they were found in nearly all Pacific hake stomachs that contained food. Fishes were the second most frequent prey found in Pacific hake and jack mackerel during most years. However, decapods (primarily crab megalopae and zoea) were also important prey, especially for jack mackerel from 1999-2003 (Table 4.2). Fishes were most frequently found in Pacific hake stomachs in 2001 (52%) and 2002 (43%), years when Pacific hake were relatively large in size (Fig. 4.2) but not abundant. The FO of fishes in jack mackerel stomachs ranged widely, from 0% (1998) to 81.5% (2004) (Table 4.2).

Pacific hake consumed a large variety of prey items in 1998 (62), but only eight different taxa in 2000, probably related to the few hake captured and stomachs analyzed in 2000. Jack mackerel consumed a large number of taxa in 1999 (45) and few in 1998. For both predator species, the number of prey taxa increased with increased number of stomachs sampled. We suspect that the increase in prey taxa was related to the increased opportunity of predators to consume different taxa at larger sample sizes.

Many of the fishes found in Pacific hake stomachs were partially digested and not identifiable to species (Table 4.1). However, of the identifiable fishes, northern anchovy had a higher FO than any other fish prey. Northern anchovy were found in 21.8% of Pacific hake stomachs in both 2002 and 2004. Other important fish prey for Pacific hake included: whitebait smelt (*Allosmerus elongatus*), Pacific herring (*Clupea pallasii*), and Pacific sardine. In the sampled Pacific hake stomachs there were only five salmon, all of which were juvenile Chinook salmon (*Oncorhynchus tshawytscha*); four were 0.0-age and one 1.0-age. Chinook salmon were found in Pacific hake stomachs in 1998, 2003, and 2004; with a FO of 0.2%, 0.2%, and 0.5%, respectively. Hake cannibalism occurred in 1998 and 2004, but was limited (Table 4.1).

Jack mackerel only ate a large number of fishes in 2004 (FO 81%) (Table 4.2). During other years, the FO of fishes was less ≤ 13%. Nevertheless, jack mackerel consumed a wide variety of fish species (Table 4.2). In 2004, jack mackerel ate a large number of young-of-the year (YOY) Pacific hake (FO of 31.6%). A few YOY Pacific hake were also eaten in July 2003. We found YOY hake in stomahcs only during two cruises in 2004, late July and the early August. Jack mackerel also ate a large number of northern anchovy (FO of 30.3%) in 2004. During other years, important jack mackerel fish prey included Osmeridae (in 1999 and 2001), juvenile rockfishes (YOY *Sebastes* spp.) (2000 and 2004), and Pacific sand lance (*Ammodytes hexapterus*) (2002). Two 0.0-age Chinook salmon were found in jack mackerel stomachs, one in 2003 and 2004, a FO of 0.6% and 1.3%, respectively.

Salmon eaten

A total of 5 juvenile Chinook salmon were found in Pacific hake and 2 jack mackerel stomachs. No other salmonid species were found in the stomachs examined. The Chinook salmon eaten ranged from 85 to 135 mm FL, and all but one was < 109 mm FL, or 0.0-age (Table 4.3). Pacific hake that ate salmon averaged 410 mm standard length (SL) and ranged from 376 to 439 SL. The two Jack mackerel which ate salmon were larger fish, 490 and 545 mm fork length (FL). Two salmon were eaten in 1998 and 2003, and three in 2004. One salmon was eaten in May, two in June and four in July. They were found in stomachs collected at both nearshore locations (10 km) and offshore locations (46.3 km).

Euphausiid lengths

Both Pacific hake and jack mackerel ate a wide range of sizes (length) of euphausiids annually (Fig. 4.5). Pacific hake consistently ate *E. pacifica* and *T. spinifera* that were larger on average than those that the jack mackerel consumed (Mann-Whitney, $P < 0.001$) (Fig. 4.5). Pacific hake also usually ate smaller size ranges of both euphausiids than did the jack mackerel. During the most recent years Pacific hake fed mostly on large *E. pacifica*, but this was not true for *T. spinifera* (Fig. 4.5). This may have been related to availability of small *E. pacifica*, but we did not collect any information on euphausiid abundance.

Prey fish lengths

The size of fish eaten by Pacific hake appeared to have an almost normal distribution ranging from 19 to 343 mm TL, with a mean length of 107 mm TL (Fig. 4.6). For jack mackerel, in contrast, the distribution of fish prey lengths was bimodal and had a smaller size range (2 to 208 mm) (Fig. 4.6). Overall, Pacific hake ate significantly larger fish than jack mackerel (Mann-Whitney, $P < 0.0001$).

Total lengths of coho and 1.0-age Chinook salmon captured were generally larger than the fish eaten by hake and mackerel (Fig. 4.6). However, length frequency distributions were skewed to the right indicating a possible loss of smaller individuals. Juvenile coho and 1.0-age Chinook salmon that migrate out of the Columbia River average 150 mm FL (Dawley et al. 1986) or approximately 165 mm TL. Subyearling (0.0-age) Chinook salmon captured in the trawls had a similar length distribution to fishes found in hake stomachs (Fig. 4.6). This may explain why 0.0-age Chinook salmon comprised the majority of salmon eaten by hake and mackerel.

Large hake ate both small and large fishes. However, the maximum length of fish eaten by Pacific hake increased with hake size (regression, $P < 0.0001$, $R^2 = 23.0$) (Fig. 4.7). The maximum sized fish eaten by a 400 mm (SL) Pacific hake averaged 110 mm (TL) (±4.48 mm), whereas a 600 mm (SL) Pacific hake consumed a maximum sized fish of 184 mm (TL) (±9.43 mm).

Jack mackerel also ate a very wide size range of fishes (Fig. 4.7). However, there was no relationship between maximum size of fish eaten and mackerel size (regression, $P = 0.090$, $R^2 = 3.37$). The largest fish consumed was 208 mm (TL), but was unidentifiable to species.

Selection of fish prey

During all years, there were many instances when prey fishes observed in hauls were not also observed in the stomachs of Pacific hake captured in the same hauls (Table 4.4). For example, American shad (*Alosa sapidissima*) commonly occurred in surface hauls most years but was never found in any Pacific hake stomachs. Conversely, there were many fishes observed in Pacific hake stomachs that did not appear in the hauls. Pacific sand lance, for example, were observed in the Pacific hake stomachs in 1999 and 2002 but not in any hauls. Nevertheless, when a fish species was prevalent in the environment, it was usually observed in Pacific hake stomachs, but rarely in the same proportion as in the local environment, implying that hake fed, or the net fished, selectively. For example, while northern anchovy was common in hauls and in Pacific hake stomachs, it was usually eaten by hake in a larger numerical proportion than found in the local environment; in the hauls). Hake positively selected northern anchovy during most months (14 out of 20), and they were strongly positively selected (LOR = 13.12) in May 2004. Other fish prey that hake seemed to prefer included whitebait smelt, eulachon (*Thaleichthys pacificus*), and YOY rockfishes (*Sebastes* spp.) (Table 4.4). Hake had strong positive selection for YOY rockfishes in June 1998, July 2000, June 2003, and June and July 2004. Adult hake showed positive selection for YOY hake in August 2004, but negative selected YOY hake in August 1998 and July 2004.

Pacific hake nearly always showed negative selection for Pacific herring and Pacific sardine. There were negative LOR's in 21 out of 25 months for Pacific herring, and 22 out of 23 months for Pacific sardine. Hake by and large showed negative selection for all juvenile salmonids during most months and years, except juvenile Chinook salmon during June 1998, May 2003, and July 2004.

Over the seven-year study period the diet of hake changed as fish prey (northern anchovy, whitebait smelt, and Pacific herring) became more abundant in the environment, as evidenced by the increasing prevalence in hauls. Linear regression analysis indicated there was a strong positive relationship between average monthly densities of northern anchovy in the local environment and the percent (by number) in the Pacific hake diet ($P = 0.002$, $R^2 = 47.8$), indicating that, in general, Pacific hake ate northern anchovy more frequently when they became more abundant. Pacific hake also ate Pacific herring ($P = 0.0091$, $R^2 = 24.8$) and whitebait smelt ($P = 0.0236$, $R^2 = 18.4$) more frequently when they were more abundant in the local environment. These data indicate that hake diets are positive indicators for the local abundance of some prey species and could potentially be used as a stock abundance indicator.

Jack mackerel were much less piscivorous than Pacific hake, and there were many fish species that were observed in the environment that were rarely found in jack mackerel stomachs. This included American shad, Pacific herring, Pacific sardine (found only in 2004), 1.0-age Chinook salmon, juvenile coho salmon, longfin smelt (*Spirinchus thaleichthys*), night smelt (*Spirinchus starksi*), eulachon, Pacific tomcod (*Microgadus proximus*) (only found in 2003), lingcod (*Ophiodon elongatus*) Agonidae, and sanddabs (*Citharichthys* spp.) (only in 2000) (Table 4.5). Jack mackerel had positive selection for YOY rockfishes, especially in 2000 and 2004. They also had strong positive selection for YOY Pacific hake in July and August 2004. Other strongly selected fishes included Osmeridae (smelts), Myctophidae, and Pleuronectiformes (larval flatfish).

Jack mackerel generally did not show positive selection for forage fishes (anchovy, herring, or smelt). There was a negative LOR for anchovy in 11 of 13 months, and a negative LOR for whitebait smelt in 8 of 9 months (Table 4.5). Jack mackerel regularly showed negative selection for juvenile salmon during most years and months, but positive selection for 0.0-age Chinook salmon in July 2003 and 2004.

As with Pacific hake, there was a positive linear relationship between whitebait smelt densities in the local environment and their percent number in jack mackerel diets

($P = 0.0125$, $R^2 = 46.5$). However, there was no relationship between any other forage fish (herring, sardine, or anchovy) densities and percent by number in the mackerel diet (all $P > 0.05$).

DISCUSSION

Most previous diet studies of Pacific hake and jack mackerel off Oregon have been conducted primarily during daylight and from fish collected at depth (Livingston 1983; Buckley and Livingston 1997; Jay 1996). There have been questions whether Pacific hake are primarily nocturnal feeders (Alton and Nelson 1970; Outram and Haegele 1972; Livingston 1983; Rexstad and Pikitch 1986; Tanasichuk et al. 1991; Buckley and Livingston 1997). Livingston (1983) found that hake feed primarily during daytime or crepuscular periods. Our data support the argument that both species feed during both day (previous studies) and night (Fig. 4.4). Pacific hake appear to be better night feeders (lower percent empty) than jack mackerel. Our data indicate that to properly quantify feeding habits of diel migrating fishes it is important to observe nocturnal surface feeding habits. Trawling at the surface at night has the added benefit of effectively sampling diel migrating forage fishes, something that is usually unavailable from other sampling efforts. Past studies may have underestimated prey consumption by Pacific hake by not considering near-surface night feeding.

Jack mackerel had consistently higher percentages of empty stomachs than Pacific hake. Brodeur et al. (1987) found similar percentage empty stomachs from daytime samples, and a wide variation of primary prey, depending on the year. We suspect that jack mackerel are highly dependent on prey patches and have much faster digestion rates than Pacific hake.

Salmon comprised a very small portion of Pacific hake and jack mackerel diets. This was not surprising, given that juvenile salmon compose only a very small percentage of the small fish or forage fishes in the study area (Emmett et al. 2006). Nevertheless, when salmonids did occur in the diet, the calculated LOR values indicated that juvenile salmonids were selected more frequently than would be expected from their prevalence in the local environment. However, these results may reflect the fact that surface trawls underestimate the abundance of juvenile salmonids at night (Krutzikowsky and Emmett 2005). Alternatively, it could indicate that juvenile salmonids are more susceptible prey than other fishes. Forage fish species (anchovy, herring, smelt) school and diel vertically migrate, whereas juvenile salmonids do not (Emmett et al. 2004). It does appear that hake and jack mackerel ate primarily 0.0-age Chinook salmon, as opposed to other salmonids, because subyearling Chinook salmon enter the ocean at a relatively small size (usually ≤ 120 mm FL) and later in the summer, compared to 1.0-age Chinook and coho salmon, which average approximately 150 mm FL at ocean entry (Dawley et al. 1986; Fisher and Pearcy 1988; 1995). We suspect that no coho salmon were observed to be eaten by either predator because they are relatively large smolts, they move out of the study area quickly, or because coho salmon appear to move close to the surface at night (Krutzikowsky and Emmett 2005), which would reduce their availability to subsurface predators. Once coho salmon reached a relative large size, approximately 170 mm TL, they would be large enough that few hake would be large enough to eat them.

If we multiply the average percentage of Pacific hake or jack mackerel stomachs containing salmon by the estimated abundance of of Pacific hake or jack mackerel populations in the study area expanded over 30 days, we can calculate a minimum estimate of the number of Chinook salmon eaten by these two predators per month in the study area. For Pacific hake we derived the following estimates for the number of juvenile salmon eaten: $1.7\text{x}10^6$ in June 1998, $8.6\text{x}10^5$ in May 2003, and $4.\text{x}10^6$ in July 2004. For jack mackerel the estimates were $7.9\text{x}10^4$ in July 2003 and $7.3\text{x}10^4$ in July 2004. The larger estimated numbers consumed by Pacific hake reflects their much larger population size. These estimates of juvenile salmonids eaten by Pacific hake and jack mackerel in the study area are relatively small compared to the number of smolts leaving Oregon/Washington rivers. Approximately 100 million salmon smolts (roughly half are 0-age Chinook salmon) leave the Columbia River annually (D. Marsh, NOAA Fisheries, Seattle, WA, pers. comm.). Thus, the percent of Columbia River juvenile salmon annually consumed by hake and jack mackerel appears to be low. However, our estimates of Pacific hake and jack mackerel abundance, and thus predation, are probably low. Our study area (and thus Pacific hake and mackerel population estimates) comprised only a very small portion of juvenile salmonid habitat in the Northwest. Furthermore, we considered only the area around the Columbia River, but other areas, especially north along the Washington shelf, may have high predator densities. We also assumed a net efficiency of 1, which is probably not true for either species. If net efficiency was50% (i.e.,half the fish in front of the net were actually caught), then our population and predation levels would double.

The food habit data indicate that Pacific hake and jack mackerel may not be a major source of juvenile salmon marine mortality off the Columbia River during most years. However, there is a relatively strong negative relationship between Pacific hake densities off the Columbia River and juvenile salmon marine survival (Emmett et al. 2006), suggesting that hake predation on salmonids may be important. It is possible that this study did not accurately measure hake and mackerel predation well during this study. For example, if hake and mackerel are finding and feeding on patches or concentrations of salmonids, and we did not sample at those areas/times, we could have missed a significant portion of the salmonid predation that was occurring.

We suspect that fish predation on salmon may be higher during warm years, when euphausiid abundance is probably lower of Oregon/Washington (Tanasichuk 1999, 2002; Mackas et al. 2001, 2004; Brinton and Townsend 2003). Future research should collect stomachs from predatory fishes in marine areas where juvenile salmon are known to congregate and should also document euphausiid abundance. There are also other large fish predators, such as the Humboldt squid (*Dosicdicus gigas*) (Cosgrove 2005), known to be common off the Northwest during warm periods but not effectively captured by our surface trawl. Additional sampling techniques should be used to collect other juvenile salmonid predators in the marine environment (e.g., gillnet, hook and line, purse seine and paired trawl).

Predators are known to reduce prey resources, especially when prey resources are low (Krebs 1978). In Canadian waters, Pacific hake feeding significantly reduced Pacific herring population abundance (Ware and McFarlane 1995). Our data indicates that Pacific hake may also affect the abundance of northern anchovy, whitebait smelt, and possibly Pacific herring off Oregon/Washington. Pacific hake had positive selection for anchovy and whitebait smelt during most months and years. In 1998, when Pacific hake densities in the study area were very large, anchovy and smelt and other forage fish populations were extremely low, but Pacific hake still consumed relatively large numbers of anchovy. We estimate that in May 1998 alone, Pacific hake consumed over 3.5×10^8 northern anchovy in the study area. In 1999, however, Pacific hake densities were low and they consumed few anchovy, and one year later anchovy densities increased. By 2003, after three years of low Pacific hake and jack mackerel predation pressure, anchovy and other forage fishes increased by about two orders of magnitude (Emmett et al. 2006). In spring 2003, Pacific hake again became abundant and northern anchovy densities quickly declined that summer (Chapter 2). A similar decline in northern anchovy and forage fish abundance took place when Pacific mackerel (*Scomber japonicus*) and jack mackerel became abundant off Oregon in 1983-1984 (Emmett and Brodeur 2000). These were also years of poor salmon ocean survival, supporting Pearcy's (1992) hypothesis that forage fish play an important role for juvenile salmonids by acting as alternative prey. Avian predation on juvenile salmonids in the Columbia River estuary also tends to decline as forage fishes become more abundant (D. Lyons and D. Roby, Oregon State University, Dept. Fish Wildl., pers. comm.).

The feeding selectivity analysis indicated that Pacific hake and jack mackerel are selective fish feeders, eating certain fish prey either at much greater or much lower frequencies than their prevalence in the local environment. However, our analysis assumed that the surface trawl catches adequately reflected what hake and jack mackerel saw as available prey. This is assumption is probably not completely true. First, the trawl probably does not catch all sizes of fishes with equal efficiency, and secondly, turbidity and light are known to strongly affect predatory fish reaction distances (Mazur and Beauchamp 1991; De Robertis et al. 2003). Unfortunately, we were unable to address these factors during our study.

Pacific hake off Canada and the Columbia River consume primarily adult euphausiids. In Canada, the consumption of euphausiids by hake was not found to have a measurable effect on the euphausiid populations (Tanasichuk 1999, 2002). However, Tanasichuk (2002) noted that if Pacific hake and Pacific herring diets were combined, euphausiid populations could have been significantly reduced by their feeding. In our study area, besides finding euphausiids in Pacific hake stomachs, we also found euphausiids in the stomachs of jack and chub mackerel (*Scomber japonicus*), Pacific herring, northern anchovy, Pacific sardine, and whitebait smelt (R. Emmett, pers. obs.). Unfortunately we did not undertake systematic food habit studies of all these species, nor did we sample the euphausiid populations. However, we suspect the combined effect of lower ocean productivity and increased fish predation during the 1998 El Niño and the warm, poor upwelling years (2003 and 2004) could have decreased euphausiid abundance. The decrease in euphausiids has large ecosystem consequences, one of which is to encourage Pacific hake and jack mackerel to move nearshore where they are more likely to feed on fishes (Benson et al. 2002). During the El Niño year of 1998, hake showed a relatively high percentage of empty stomachs and percent fish prey consumed compared to other years (Fig. 4.3). Nelson (2004) also found that Pacific hake fed poorly in 1998.

Besides being predators, Pacific hake and jack mackerel may also be food competitors with juvenile salmonids, as euphausiids and small fishes are also important prey for juvenile salmonids off Oregon (Peterson et al. 1982; Emmett et al. 1986; Brodeur and Pearcy 1990; Schabetsberger et al. 2003). High densities of Pacific hake, as we observed 1998, 2003 and 2004, may have not only increased predation rates on salmonids directly, but also indirectly, by reducing salmonid food supply and thus growth rates, ultimately lengthening the time the salmonids are vulnerable to size-selective predators. As stated earlier, juvenile salmonids differ from forage fishes in that they do not diel vertically migrate (Emmett et al. 2004) but have a life history strategy of "outgrowing" predation by actively feeding during daylight hours (Schabetsberger et al. 2003; Railsback et al. 2005).

While still in dispute, there are studies indicating that marine predators can control the abundance of prey populations and community structure (Pace et al. 1999; Worm and Myers 2003). We were unable to directly show that predation by Pacific hake and jack mackerel caused any appreciable decrease in the euphausiid and forage fish populations off the Columbia River region. This would have required additional information on euphausiid and forage fish population dynamics. Nevertheless, the large changes in forage fish densities off Oregon observed from 1998 through 2003 (Emmett et al. 2006) appear to be correlated, at least in part, to fluctuations in predatory fish densities. The abundance of forage fishes and euphausiids in the Pacific Northwest undoubtedly affects upper trophic levels in the northern California Current ecosystem. Future research should attempt to collect simultaneous information on the abundance and feeding habits of Pacific hake and jack mackerel for a series of 24 hour periods, collecting fish and prey from their daytime, deep-water habitat, to their surface, night time, habitats. These data would provide valuable information on the total amount of prey consumed and if fishes and can exercise “top-down” control of forage fish and euphausiids populations.

Mills et al. (in press) found that top predator avian diets are useful indicators of rockfish (*Sebastes* spp.) recruitment off California. We suggest that adult hake and jack mackerel nocturnal diets are useful indicators of rockfish and hake recruitment (i.e., the abundance of 0-age individuals) off Oregon. The occurrence of YOY Pacific hake in jack mackerel stomachs (2004) and adult Pacific hake stomachs (1998 and 2004) provided independent confirmation that Pacific hake spawned and recruited off Oregon during those years, since it is unlikely that juveniles of this size could have been transported this far north from the normal spawning grounds off southern California. The occurrence of YOY *Sebastes* spp. in jack mackerel stomachs (1999, 2000 and 2004) indicated that rockfish recruitment was relatively good during those years. However, it is also possible that survival of *Sebastes* spp. larvae can be hindered by pelagic fish feeding, as gadids were in the Georges Bank ecosystem (Garrison et al. 2000), or herring on the west coast of Canada (Ware and McFarlane 1995). Since nearly all Pacific Northwest commercially important fishes have pelagic life stages, future research should attempt to identify if the feeding of pelagic fishes affects recruitment processes of other fishes. This could be accomplished by establishing a long-term pelagic fish abundance/stomach analysis program. Data from the stomach analysis program could be used in a multispecies virtual population analysis model (Livingston and Jurado-Molina 2000; Tsou and Collie 2001) to estimate the effects of predation on recruitment of Pacific Northwest fishes and euphausiids.

CONCLUSIONS

The nocturnal feeding of two fishes, Pacific hake and jack mackerel, varied significantly both within and among years (1998-2004) off the Columbia River. Pacific hake ate mostly euphausiids, but fishes were very important, especially during warm ocean years (1998, 2003, and 2004). Pacific hake were highly selective for northern anchovy, whitebait smelt, small rockfish, and small juvenile salmonids. Jack mackerel also ate mostly euphausiids, but fishes were important in 2004. Primary fish prey for jack mackerel were northern anchovy, small Pacific hake, Pacific sardine, and whitebait smelt. Both Pacific hake and jack mackerel rarely ate juvenile salmonids, but because of their large population sizes, they could consume many juvenile salmonids, thus adding to overall juvenile salmonid marine mortality. However, predation by Pacific hake and jack mackerel on juvenile salmon appears to account for only a few percent of the juvenile salmon marine mortality off the Columbia River. Additional research needs to be conducted in other coastal areas where predation impacts on juvenile salmon by predatory fishes may be more significant as juvenile salmon move from the turbid Columbia river plume environment to usually less turbid coastal waters.

ACKNOWLEDGEMENTS

We thank the many people who assisted with gathering the data presented here. The field work could not have been completed without the always able assistance of Paul Bentley. Field work was completed with the assistance of J. Fisher, T. Miller, C. Morgan, L. Feinberg, J. Lamb, T. Auth, L. Stamatiou, J. Phillips, B. Sandford, W. Muir, and L. Weitkamp. Summer students who helped with field and lab work included, J. Douglas, C. Cochran, L. Davis, E. Locke and J. Muir. Dr. David Sampson provided many constructive comments and suggestions. This work would not have been accomplished with out the hard work of Captains D. Parker and R. Williams and the crews of the F/V Sea Eagle and F/V Piky, respectively. Earlier drafts of this paper were improved with reviews by Drs. R. Brodeur, E. Casillas, and D. Sampson. This research was financially supported by NOAA Fisheries and the Bonneville Power Administration.

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Table 4.1. Percent frequency of occurrence of prey found in Pacific hake, *Merluccius productus*, collected off the Columbia River 1998-2004. N = number of stomachs with food. YOY indicates young-of-the-year.

Year	1998	1999	2000	2001	2002	2003	2004
Number of stomachs analyzed	2693	449	49	193	360	1083	493
N	1121	357	46	135	230	813	404
Plant material	0.4			0.7			
Unidentified invertebrates	25.6						
Velella velella							0.2
Annelida	0.9						
Polychaeta	0.9						
Gastropoda		0.8					
Olivella spp.	0.9						
Cephalopoda	0.3	1.1			0.9		
Loligo sp.	0.2					0.2	
Crustacea	2.2	1.1		9.6	0.4	0.1	
Copepoda	0.2						
Calanoida	0.9						
Mysidae	11.8	1.7		3.0		0.2	
Archaeomysis grebnitzkii	0.9						
Neomysis spp.	0.9						
Neomysis kadiakensis	0.9			0.7			
Neomysis rayii	1.2						
Cumacea	4.7	1.7	2.2			0.2	
Isopoda	1.1						
Gnorimosphaeroma oregonensis	0.9						
Idoteidae	0.2						
Synidotea spp.	0.2						
Synidotea bicuspida	0.9						
Amphipoda	0.3					0.1	
Gammaridea	0.9	0.3					
Hyperiidea	0.9	1.4					
Hyperoche sp.	0.9						
Parathemisto pacifica	0.2	0.3					
Caprellidea	0.9						
Euphausiidae	36.3	95.6	93.5	65.9	59.4	66.3	75.0
Euphausia pacifica	3.2	15.8	4.3	11.1	0.9	0.4	0.2
Thysanoessa spinifera	4.7	18.9	17.4	14.8	0.4	0.1	
Decapoda	0.2	0.3				0.1	
Caridea	0.4	0.3		0.7	0.4	0.2	0.2
Pandalidae		0.3			0.4		
Pandalus spp.				0.7			
Pandalus jordani					3.6		
Crangonidae	2.3	1.9		3.0	0.4		
Crangon	0.4	0.6					0.7
Crangon alba	0.2	0.6					
Crangon stylirostris	0.9	0.3					

Table 4.1. Continued.

	1998	1999	2000	2001	2002	2003	2004
Crabs	0.9						1.5
Callianassidae	0.2	0.3					
Callianassa spp.						0.1	
Paguridae	0.9						
Hippidae (megalopae)	0.9						
Brachyura (larvae)	1.8	1.1				0.2	
Cancridae	0.4				0.4		
Cancer spp. (megalopae)	4.8	3.6	1.9	3.7		3.0	
Cancer magister (megalopae)	1.6	0.8	2.2	2.2	1.3	0.2	
Pinnotheridae (larvae)	0.6	3.3		0.7			
Fabia zoea		0.3					
Fabia subquadrata		0.3					
Hemigrapsus oregonensis (megalopae)	0.9						
Salpida		0.3					
Osteichthyes	11.3	8.9	21.7	40.0	14.0	8.4	5.4
Fish scales	0.4	0.3				0.1	
Fish bones		0.3			0.4	0.1	
Clupea pallasi	2.6	1.4		9.6	2.6	0.6	1.2
Sardinops sagax	1.0				1.7	0.4	
Engraulis mordax	5.5	0.6		1.5	21.8	9.7	21.8
Oncorhynchus tshawytscha	0.2					0.2	0.5
Osmeridae	0.2	0.6		3.0	0.9	0.5	0.7
Spirinchus starksi	0.2						
Thaleichthys pacificus					0.4	0.7	
Allosmerus elongatus	3.9	1.1		8.1	7.0	1.6	2.7
Microgadus proximus				0.7	1.7	0.5	
Merluccius productus (YOY)	0.9						0.5
Sebastes spp. (YOY)	0.2		2.2			0.2	0.5
Cottidae	0.9						
Agonidae	0.9						
Agonus acipenserinus	0.9						
Cyclopteridae						0.1	
Cymatogaster aggregata	0.2						
Ammodytes hexapterus		1.1			0.4		
Scomber japonicus	0.9						
Pleuronectiformes		0.6					0.2
Citharichthys spp.	0.9	0.8					
Citharichthys sordidus	0.3					0.2	
Citharichthys stigmaeus		0.3					
Pleuronectidae				0.7			
Eopsetta elixis	0.9						
Digested material	15.8	8.3	69.6	26.7	5.2	2.3	0.5

Table 4.2. Percent frequency of occurrence of prey found in jack mackerel, *Trachurus symmetricus*, collected off the Columbia River 1998-2004. N = number of stomachs with prey. YOY indicates young-of-the-year.

Year	1998	1999	2000	2001	2002	2003	2004
Number of stomachs analyzed	129	496	407	428	239	268	115
N	30	283	276	134	80	166	76
Plantae				3.0			
Invertebrates							1.3
Phaeophycophyta						0.6	
Velella velella		0.7				22.3	
Ctenophora		0.4					
Annelida			0.4				
Polychaeta		0.7	0.7				
Mollusca				1.5			
Gastropoda		0.7					
Lacunidae		0.4					
Cerithiopsidae			0.4				
Epitoniidae			0.4				
Eulimidae			0.4				
Corolla spectabilis				0.7			
Cephalopoda			2.2		3.8		2.6
Loligo opalescens		0.4				3.0	
Crustacea	4.8			48.5			
Calanoida		8.1		3.7	1.3		
Thoracica		0.4					
Mysidae		1.8	1.1				
Cumacea		0.4		0.7			
Idoteidae		0.4					
Amphipoda		1.8					
Gammaridea		3.5		0.7			
Hyperiidea		1.4	0.4	0.7			
Hyperia spp.		1.1					
Hyperiella spp.		0.4					
Vibiliidae		2.1					
Vibilia spp.		0.4					
Euphausiidae - unidentified	81.0	80.6	94.2	89.6	71.3	51.2	11.8
Euphausia pacifica	4.8	8.1	10.5	37.3		0.6	
Thysanoessa spinifera	9.5	9.2	14.9	44.0		0.6	
Decapoda				0.7	6.3	0.6	
Caridea				6.0			
Pandalidae		2.8		4.5			
Pandalus jordani				9.0			
Crangonidae			0.4	0.7			
Crangon alaskensis			0.4				
Crabs				0.7	5.0		
Thalassinidea		0.4					

Table 4.2. Continued.

	1998	1999	2000	2001	2002	2003	2004
Paguridae		0.71					
Porcellanidae		7.07					
Hippidae (megalopae)		0.35					
Brachyura (megalopae)		0.35		0.75			
Majidae		1.77					
Oregonia gracilis		1.77					
Cancridae		1.41					
Cancer (megalope)		12.72	12.68	23.13		14.46	1.32
Cancer magister (megalopae)		7.07	3.99	14.93			
Pinnotheridae zoea		6.36					
Fabia spp. zoea		0.71					
Fabia subquadrata		3.18					
Grapsidae		0.35					
Osteichthyes unidentified		3.18	3.62	2.99		0.60	28.95
Sardinops sagax							11.84
Engraulis mordax			0.36			1.20	30.26
Oncorhynchus tshawytscha						0.60	1.32
Osmeridae		1.41	0.72	0.75			
Allosmerus elongatus			5.43	2.24			
Myctophidae		0.35					2.63
Gadidae		0.71					
Microgadus proximus						2.41	
Merluccius productus (YOY)							31.58
Sebastes spp. (YOY)		0.35	3.62				2.63
Hexagrammidae		0.35	0.36				
Cottidae		0.71			2.50		
Cyclopteridae			0.72				
Liparis spp.			0.72				
Ammodytes hexapterus		0.35	0.36		5.00		
Pleuronectiformes		1.06		0.75			
Citharichthys sordidus			0.36				
Errex zachirus			0.36				
Digested material	4.76	34.28	63.04	26.87	7.50	15.06	3.95

Table 4.3. Number of salmon observed in Pacific hake and jack mackerel stomachs collected off the Columbia River, 1998-2004.

Pacific hake

Salmon species (age)	Number eaten	Fork length (mm)	Date	Distance from shore (km)
Oncorhynchus tshawytscha (0.0-age)	1	100	13 Jun 1998	10.0
Oncorhynchus tshawytscha (0.0-age)	1	87	27 Jun 1998	16.3
Oncorhynchus tshawytscha (1.0-age)	1	135	21 May 2003	37.0
Oncorhynchus tshawytscha (0.0-age)	1	96	8 Jul 2004	27.8
Oncorhynchus tshawytscha (0.0-age)	1	109	18 Jul 2004	37.0

Jack mackerel

Salmon species (age)	Number eaten	Fork length (mm)	Date	Distance from shore (km)
Oncorhynchus tshawytscha (0.0-age)	1	100	8 Jul 2003	16.7
Oncorhynchus tshawytscha (0.0-age)	1	85	7 Jul 2004	46.3

Table 4.4. Prey selection, natural log of the odds ratio, for fish prey categories from Pacific hake stomachs versus trawl catches (values in rectangles) by month/year. Percent fish prey and catch were weighted by the number of Pacific hake/trawl. Black rectangles (■) indicate when fish taxa were found in stomachs at higher percentange than in trawl catches (postive selection). Grey rectangles (▒) indicate when fish prey taxa were found in stomachs less than trawl catchs (negative selection). Shaded rectangles with no values indicate prey that were found only in stomachs (black) or trawls (grey). Clear rectangles indicate prey taxa were not found in stomachs or trawls. A * indicates that fish prey were not identifiable to specific taxa. YOY indicates young-of-the-year.

	1998				1999			2000	2001		
	May	Jun	Jul	Aug	May	Jun	Jul	Jul	Jun	Jul	Aug
Number caught	508	7803	3434	2218	1102	500	576	88	33	181	61
Number of stomachs examined	387	920	841	453	116	116	186	46	27	132	31
Number eating fish	50	106	69	28	16	13	20	11	9	57	3
Prey						*					*
Alosa sapidissima			▒	▒			▒	▒		▒	
Clupea pallasii	▒	1.68	-0.77	▒	-1.30		1.96	▒	1.72	-0.78	
Sardinops sagax	▒	-3.22	-0.51				▒	▒	▒	▒	
Engraulis mordax	4.11	1.41	2.31	-1.02	0.35		2.00		3.57	▒	
Oncorhynchus kisutch (1.0-age)				▒					▒		
Oncorhynchus nerka (1.0-age)									▒		
Oncorhynchus tshawytscha (0.0-age)		▒	▒	▒				▒	▒		
Oncorhynchus tshawytscha (1.0-age)		■			▒			▒	▒		
Osmeridae		■							■	■	
Hypomesus pretiosus											
Thaleichthys pacificus					▒		▒				
Allosmerus elongatus		5.64	▒	2.22	-0.96		▒		-0.56	0.53	
Microgadus proximus									▒	■	
Merluccius productus (YOY)		■	▒								
Sebastes spp. (YOY)		■						■			
Cottidae	■										
Agoniidae		■									
Cyclopteridae											
Anoplopoma fimbria											
Cymatogaster aggregata	■		■								
Ammodytes hexapterus					■		■				
Scomber japonicus		■									
Pleuronectiformes							■				
Citharichthys spp.	■		■		■						
Errex zachirus	■		▒								

Table 4.4. Continued.

	2002				2003			2004			
	May	Jun	Jul	Aug	May	Jun	Jul	May	Jun	Jul	Aug
Number caught	11	104	1688	59	1697	909	4657	40	213	2085	116
Number of stomachs examined	11	104	156	35	199	346	452	40	75	148	54
Number eating fish	8	56	29	8	8	91	74	5	23	66	26
Prey											
Alosa sapidissima	▨	▨	▨	▨	▨	▨	▨			▨	▨
Clupea pallasii	0.76	-2.48	3.23	▨	-3.61	-2.75	0.63	▨	0.93	-1.58	1.08
Sardinops sagax	▨	▨	-0.79	-2.56	▨	-2.14	-1.22	▨	▨	▨	▨
Engraulis mordax	-0.37	1.40	1.07	2.71	▨	1.50	0.52	13.12	1.92	-1.16	0.44
Oncorhynchus kisutch (1.0-age)						▨					
Oncorhynchus nerka (1.0-age)											
Oncorhynchus tshawytscha (0.0-age)		2.51		▨	■	▨	▨			5.31	▨
Oncorhynchus tshawytscha (1.0-age)	▨	▨			▨	▨	▨			▨	▨
Osmeridae		■				■	■			■	
Hypomesus pretiosus						▨					
Thaleichthys pacificus	▨	▨	0.82		5.84	-0.45	-1.25			3.59	
Allosmerus elongatus	-0.29	0.01	2.94		-0.65	0.70	1.93			▨	▨
Microgadus proximus		0.08	-2.28	▨			4.94				
Merluccius productus (YOY)											0.07
Sebastes spp. (YOY)						5.07			1.02	■	
Cottidae											
Agoniidae											
Cyclopteridae						■					
Anoplopoma fimbria										▨	▨
Cymatogaster aggregata											
Ammodytes hexapterus											
Scomber japonicus											
Pleuronectiformes									■		
Citharichthys spp.							■				
Errex zachirus											

Table 4.5. Prey selection, natural log of the odds ratio, for fish prey categories in jack mackerel (*Trachurus symmetricus*) stomachs versus trawl catches (values in rectangles). Percent fish prey and catch were weighted by the catch of hake by individual trawl. Black rectangles (■) indicate when fish taxa were found in stomachs at higher percentange than in trawl catches (positive selection). Grey rectangles (▒) indicate when fish prey taxa were found in stomachs less than trawl catchs (negative selection). Shaded rectangles with no values indicate prey that were found only in stomachs (black) or trawls (grey). Clear rectangles indicate prey taxa were not found in stomachs or trawls. A * indicates that fish prey not identifiable to specific taxa. YOY indicates young-of-the-year.

	1999		2000		2001		2002			2003	2004	
	Jun	Jul	Jun	Jul	Jul	Aug	Jun	Jul	Aug	Jul	Jul	Aug
Number caught	871	1033	565	256	1054	364	15	100	270	234	49	63
Number examined	204	272	204	203	381	30	15	100	124	201	47	60
Number eating fish	14	5	28	8	6	3	3	1	2	109	20	42
Prey						*						
Alosa sapidissima	▒	▒	▒	▒	▒					▒		▒
Clupea pallasii	▒	▒	▒	▒	▒				▒	▒	▒	▒
Sardinops sagax	▒	▒	▒	▒	▒					▒	-1.74	-2.82
Engraulis mordax				-1.15					▒	1.23	-1.43	-5.09
Oncorhynchus keta (0.0-age)		▒	▒	▒								
Oncorhynchus kisutch (1.0-age)			▒	▒								
Oncorhynchus tshawytscha (0.0-age)		▒	▒	▒				▒		9.00	■	
Oncorhynchus tshawytscha (1.0-age)			▒	▒				▒				
Osmeridae	■		10.06		■							
Thaleichthys pacificus		▒	▒	▒				▒				
Allosmerus elongatus			-2.19	-1.11	-1.66							
Myctophidae		■									■	■
Gadidae	■											
Microgadus proximus										■	▒	
Merluccius productus (YOY)		▒									■	7.36
Cololabis saira									▒			
Sebastes spp. (YOY)	■		9.98	8.03				▒			■	
Hexagrammidae	■			■								
Cottidae	■								■			
Cyclopteridae			■									
Liparis			■									
Anoplopoma fimbria			■	▒							▒	▒
Cymatogaster aggregata			■									
Ammodytes hexapterus	■		■				0.00	13.95				
Pleuronectiformes	■	■			■							

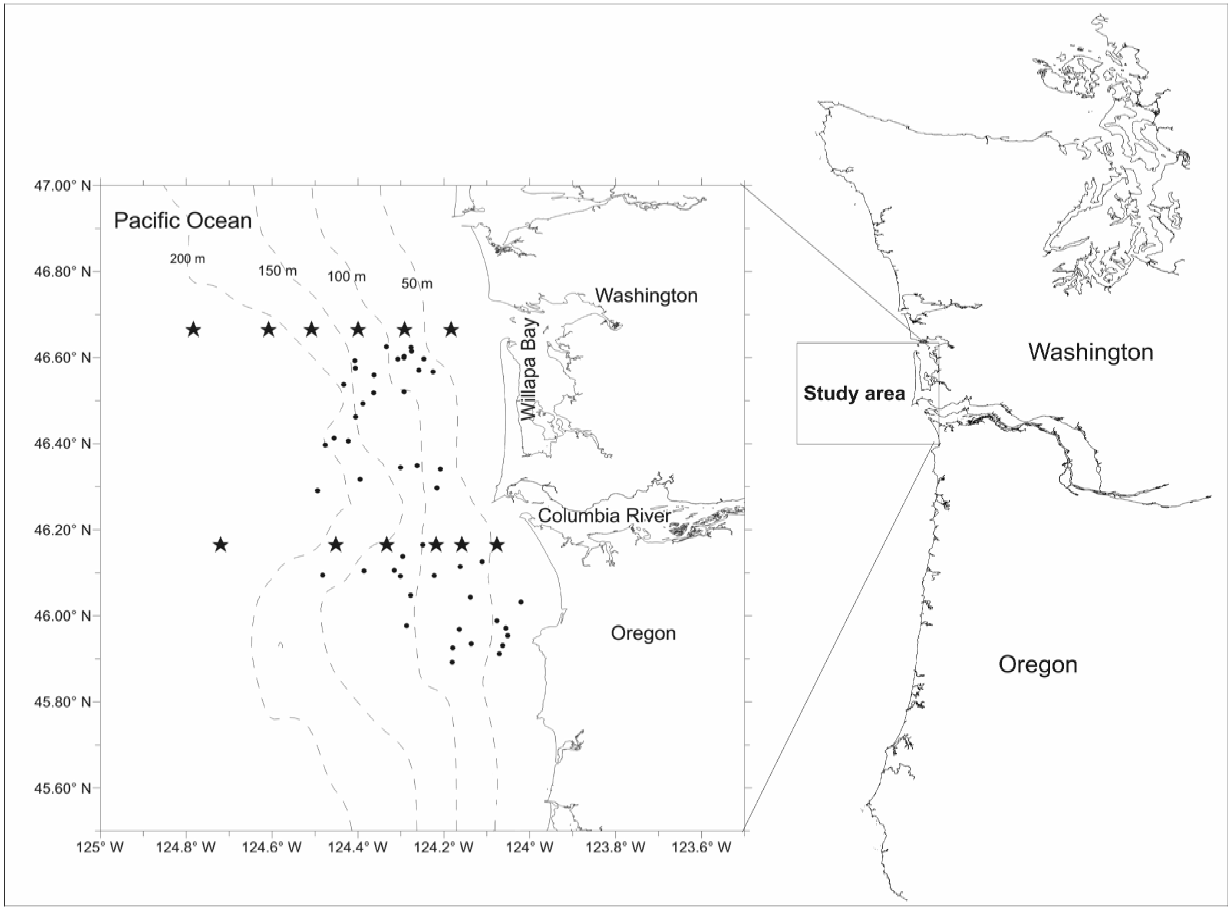
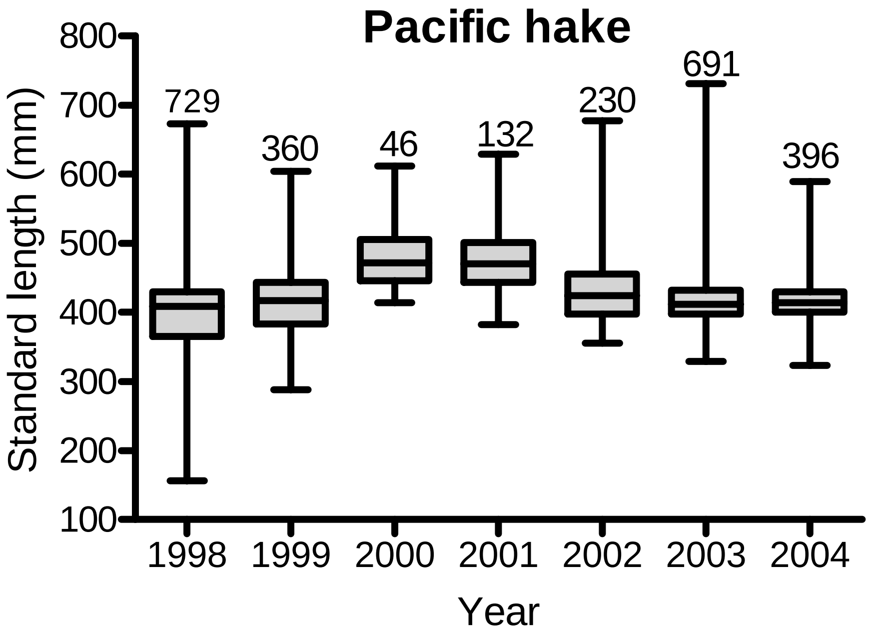


Figure 4. 1. Location of surface trawl stations sampled during spring/early summer 1998 (●) and 1999-2003 (★) off the mouth of the Columbia River.



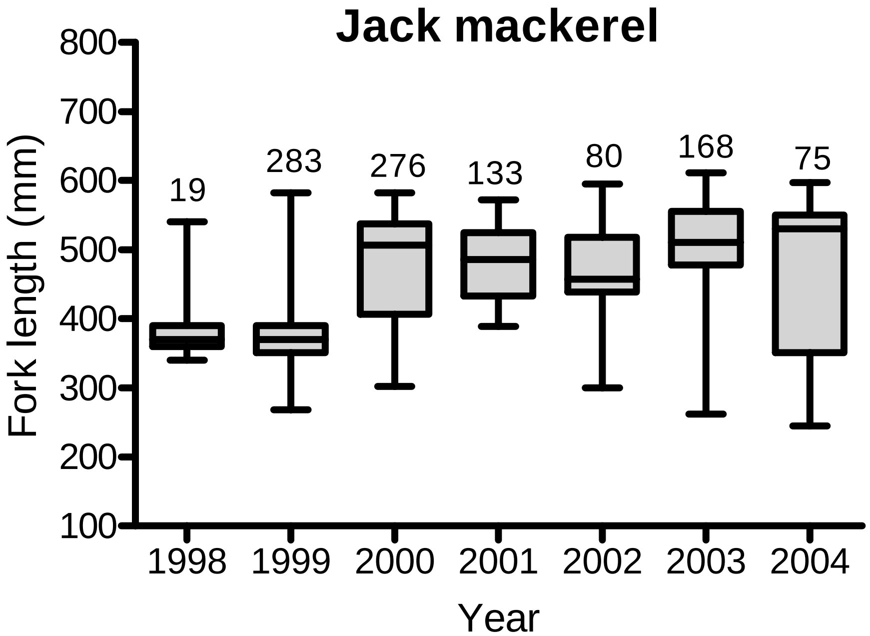
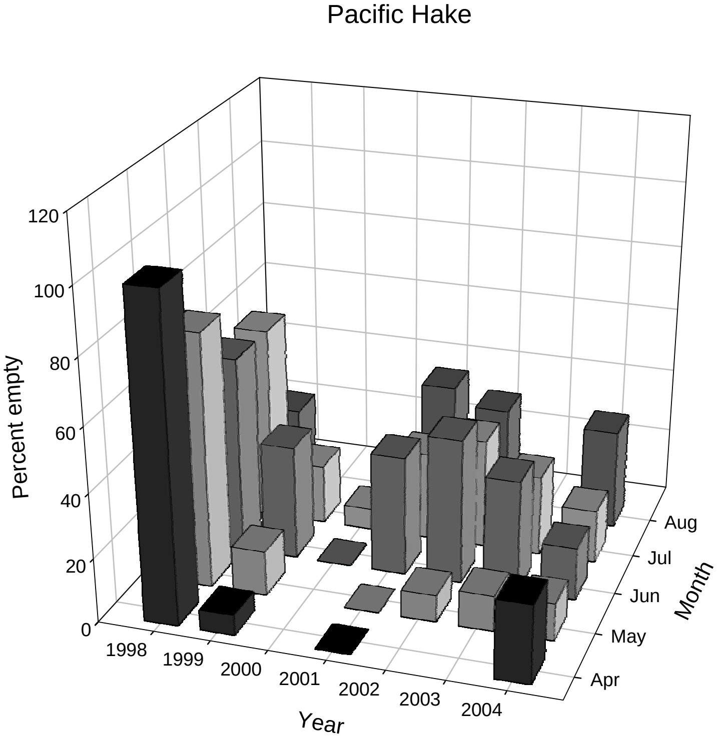
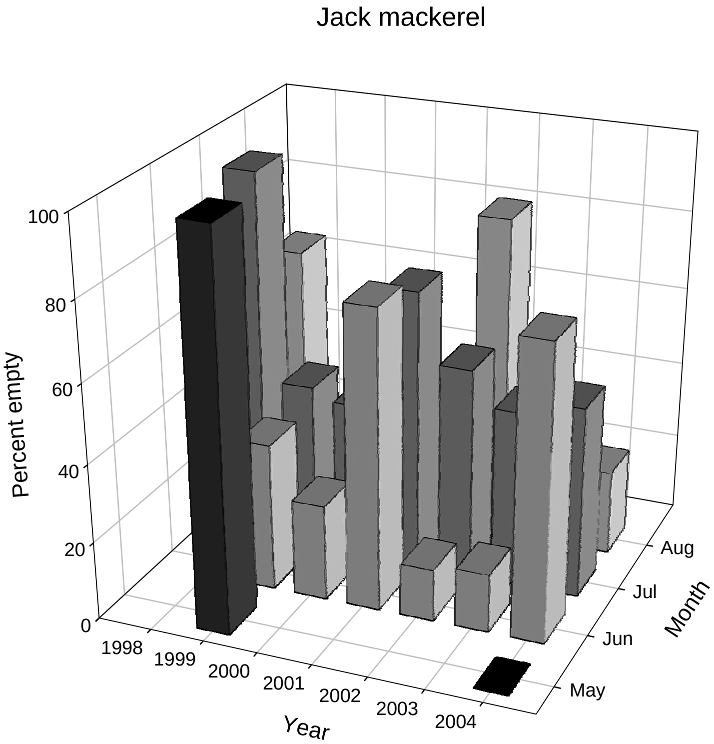


Figure 4.2. Lengths of Pacific hake, *Merluccius productus*, and jack mackerel, *Trachurus symmetricus*, examined for feeding analysis, 1998-2004. Number above each box plot indicates number measured. The top and bottom of each box and whisker plot represent the largest and smallest fish, respectively. The line in the box represent the median length.

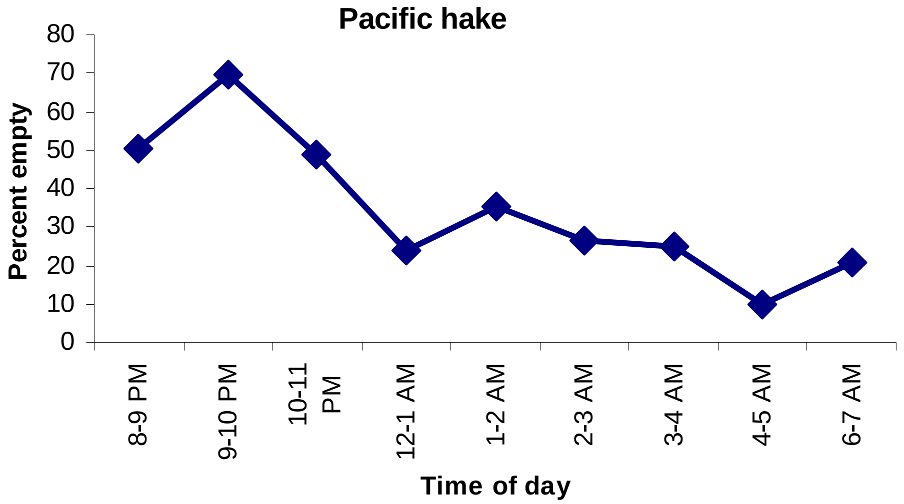


Pacific Hake



Jack mackerel

Figure 4.3. Percent of empty stomach in Pacific hake and jack mackerel collected off the Columbia River, 1998-2004.



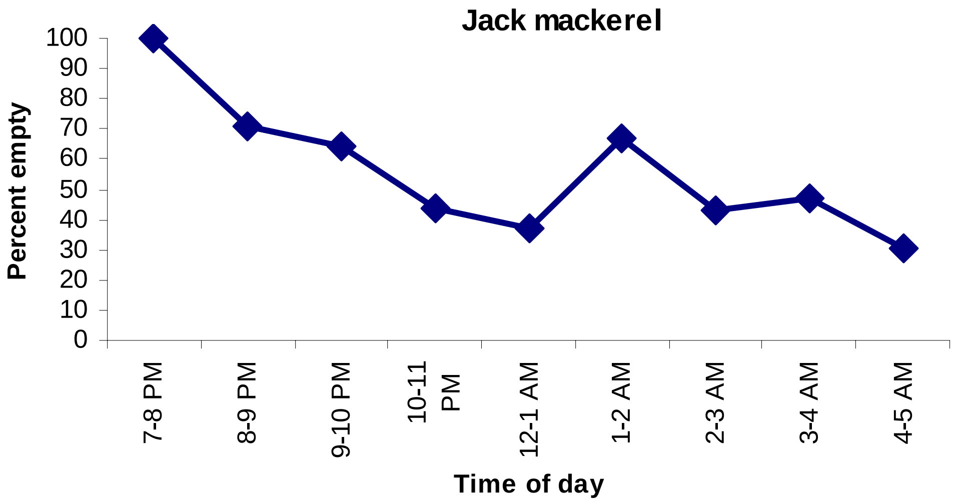


Figure 4.4. The average percent of empty stomachs of Pacific hake and jack mackerel by time of day captured off the mouth of the Columbia River, 1998-2004.

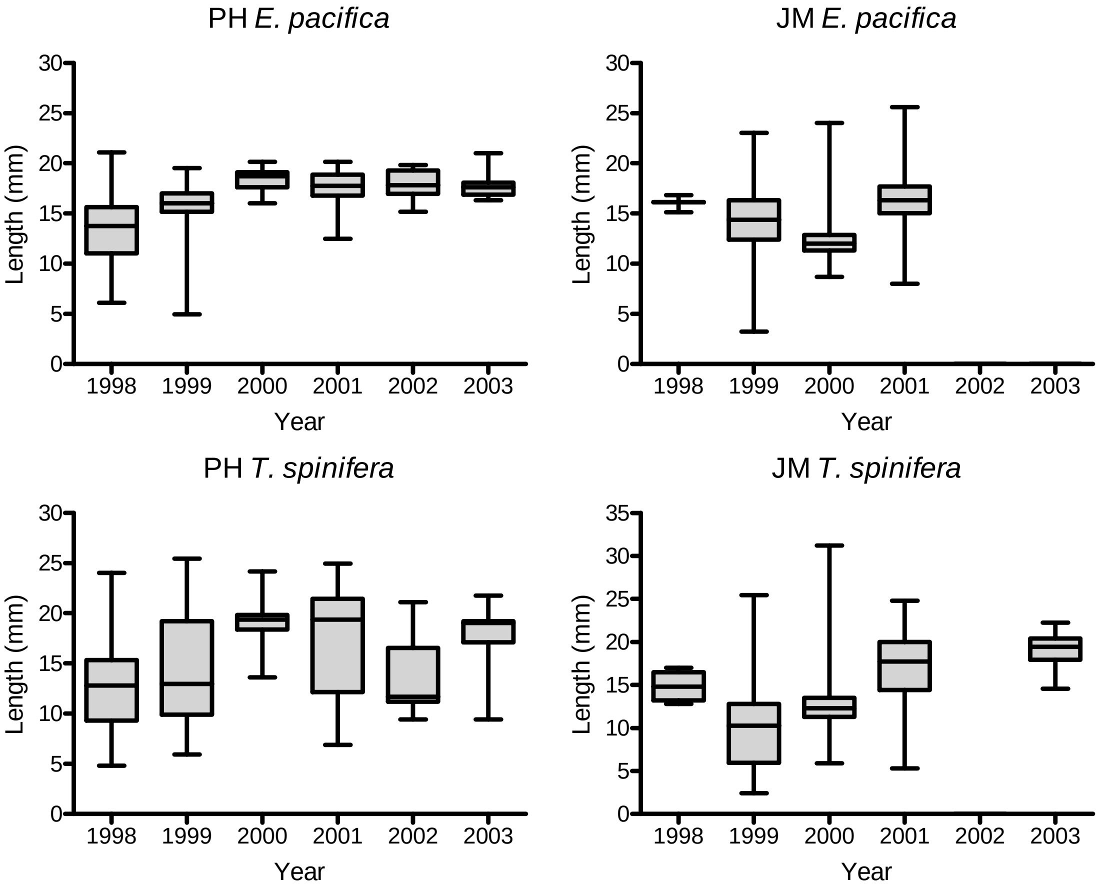


Figure 4.5. Body lengths (from behind the eye to the telson origin) of *Euphausia pacifica* and *Thysanoessa spinifera* found annually in the stomachs of Pacific hake (PH), and jack mackerel (JM), 1998-2003.

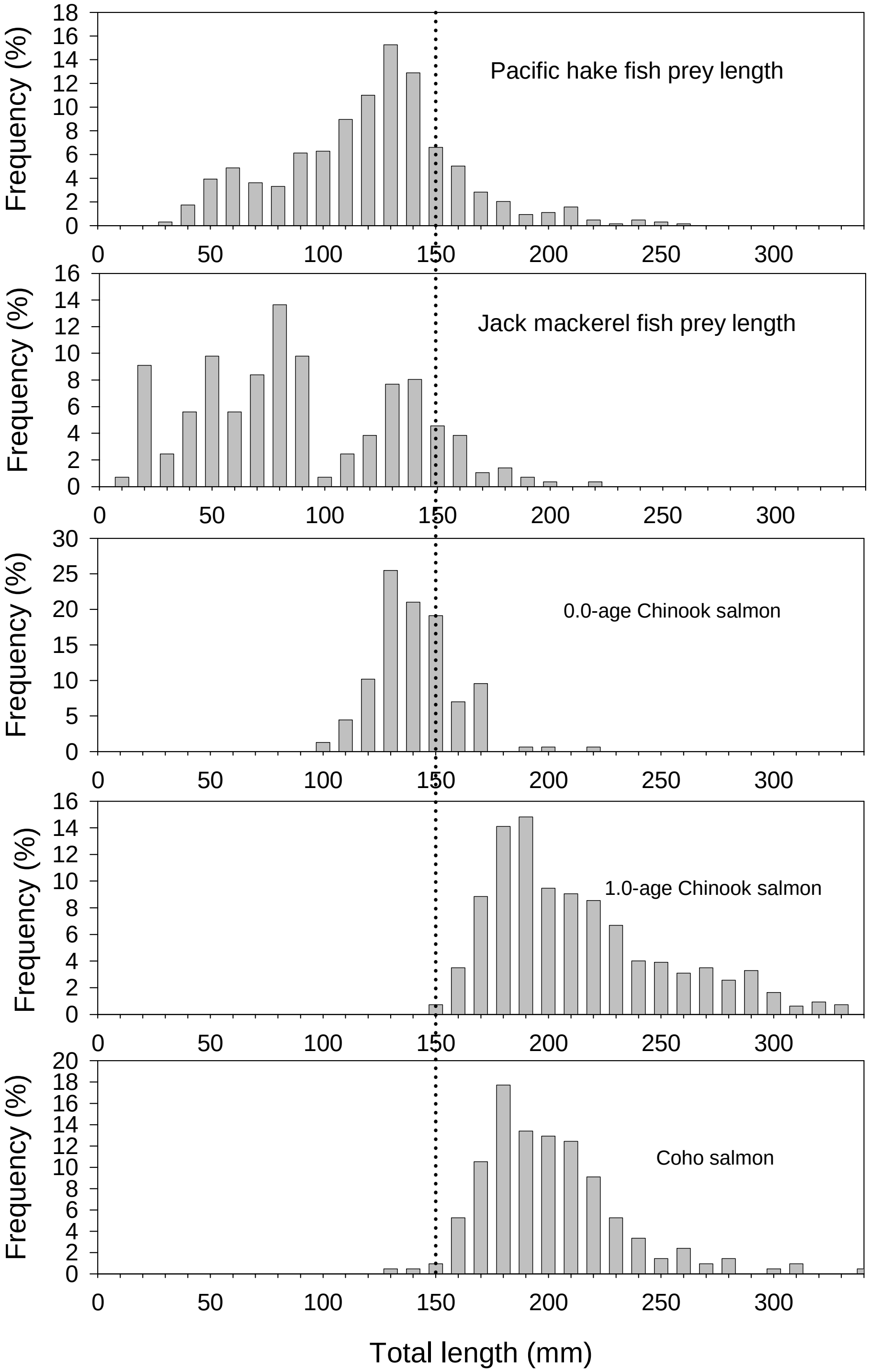
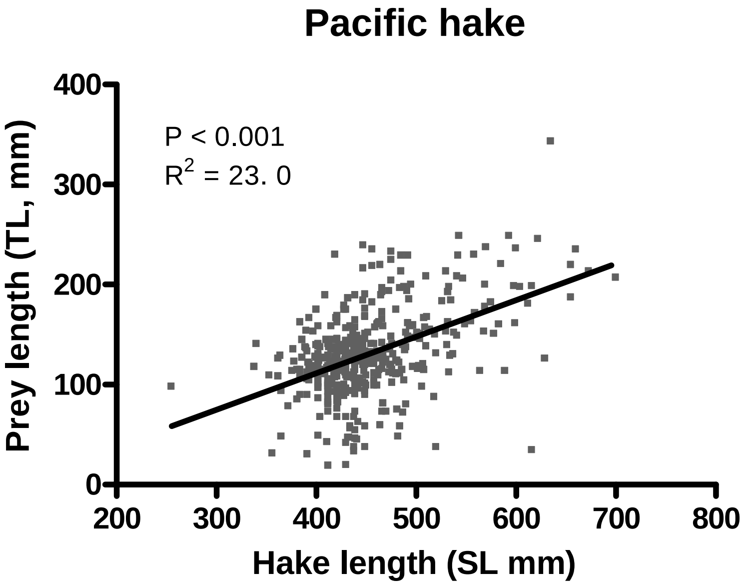


Figure 4.6. Length frequency of fishes measured in Pacific hake and jack mackerel stomachs and juvenile salmonids collected off the Columbia River, 1998-2004.



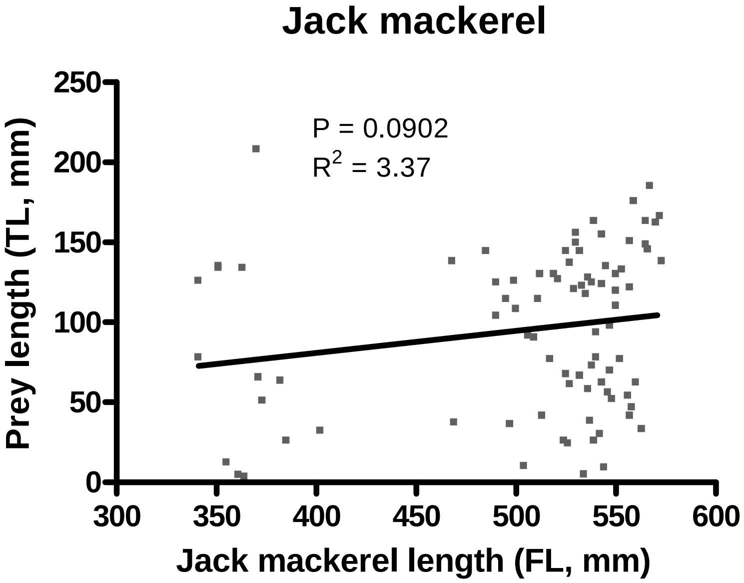


Figure 4.7. Maximum fish prey length consumed by Pacific hake and jack mackerel, 1998-2004.

Chapter 5. The Relationship Between Predatory Fish, Forage Fishes, and Juvenile Salmonid Marine Survival off the Columbia River: A Trophic Model Analysis

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 calculates the number of juvenile salmon that are eaten by Pacific hake off the Columbia River for a given hake and forage fish population. Model results indicate the presence of large numbers of Pacific hake could account for high mortality of juvenile salmonids leaving the Columbia River, and this mortality would be much reduced when forage fish are abundant. Estimates of hake and forage fish abundance, based on field data collected from 1998-2004, were used in the model to derive annual estimates of the number of salmon 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 yearling and subyearling Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon marine survival ($R^2 > 69\%$). Results support the hypothesis that Columbia River salmon 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.

INTRODUCTION

Pacific salmon run sizes are determined by mortality in fresh and marine waters, with both habitats equally important (Bradford 1997; Lawson et al. 2004). While causes of juvenile salmon mortality in fresh water have been extensively studied, what causes mortality in the marine environment remains one of the least resolved questions in Pacific Northwest 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 review) and how fluctuations in physical and biological/physical 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, from off the Columbia River. We have observed that Pacific hake (*Merluccius productus*), a predator on salmonids (Emmett and Krutzikowsky, In review), 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.

Columbia River salmon runs showed large annual fluctuations from 1998-2004, and appeared to reflect changing ocean conditions (Williams et al. 2005). These observations suggest that marine survival of salmon off the Columbia River, and perhaps the Pacific Northwest, may be due to predator/prey 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. 5.1). The 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, 2004) 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 most 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; Beacham 1991; Beamish et al. 1992, 1995; Beamish and Neville 2001; Pearcy 1992; Emmett and Krutzikowsky, In review). For example, from 1998-2004 only 7 juvenile salmonids were identified from 7,402 predator fish stomachs collected off the Columbia River (Emmett and Krutzkowsky, In review). Nevertheless, the negative correlation between marine predator fish abundance and salmon marine survival in the Pacific Northwest provides supporting evidence that fish predation may be important (Emmett and Brodeur 2000; Emmett et al. 2006).

We suspect that one of the reasons that predation on salmon by large fishes has been rarely observed in Northwest marine waters relates to the fact that juvenile salmonids are rare, comprising only a very small portion of the forage fish community in these waters (Emmett and Brodeur 2000; Brodeur et al. 2004; Emmett et al. 2006). For example, while approximately 100 million salmon smolts leave the Columbia River annually (Douglas Marsh, NOAA Fisheries, NWFSC, Seattle, WA, pers. comm.), forage fish populations number in the billions (Emmett et al. 2006). We estimated that at least 5.5×10^9 forage fish [northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasi*), whitebait smelt (*Allosmerus mordax*), and Pacific sardine (*Sardinops sagax*)] resided just off the Columbia River in May 2001. With the forage fish population at this level, overall predation rates on forage fishes (which would include juvenile salmonids) could be high, but observable salmonid predation events (predator fish stomachs containing juvenile salmonids) would be relatively rare.

The Columbia River plume significantly affects physical and biological conditions in our study area, and is usually highly visible in satellite imagery because of its elevated turbidity signature (Thomas and Weatherbee, 2006). Turbidity is known to influence juvenile salmon predatory/prey interactions (Gregory 1998). At moderate levels turbidity can significantly reduce the ability of visual predatory fishes to capture prey fishes, while not affecting planktivorous fishes' ability to feed (DeRobertis et al. 2003). Pelagic fish surveys off the Columbia River also indicate that turbidity is correlated with the offshore distribution of juvenile salmon and predatory and forage fishes (Emmett et al. 2006).

Previous models of salmon marine survival in the PNW have focused primarily on the relationship between growth and mortality (Walters et al. 1978; Gertseva et al., In review). Larger, faster growing, salmonids appear to survive better than smaller, slower growing salmonids (Parker 1971; Holtby et al. 1989; Beamish et al. 2004; Moss et al. 2005). Walters et al. (1978) concluded that abundance of juvenile salmon prey in marine waters could affect juvenile salmon growth and survival rates, but they had inadequate data on zooplankton and the relationship between body size and mortality rates. They also noted that growth rates measured from surviving salmonids may not reflect actual growth rates, since slower growing individuals would have been lost (eaten) and not measured. This agrees with Fisher and Pearcy (1998, 1995) who found only small differences in juvenile salmonid marine growth rates during years where ocean productivity and marine survival varied widely.

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. (In review) found that salmon growth, migration, and mortality were important parameters affecting survival. Using pelagic catches of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon/Washington, they estimated daily marine mortality rates for juvenile coho salmon ranged from 1.5% (2002) to 4% (2001), and that salmon marine survival was determined primarily by top-down mechanisms (predation). They concluded that future investigations needed to identify the abundance, food habits, and feeding rates of salmon predators.

Field (2004) developed an ecosystem-based model of the northern California Current using a mass balance modeling approach (Ecopath/Ecosim) (Christensen and Pauley 1992). He evaluated the effect of changing hake distributions and abundance on hake prey resources by running model simulations, and concluded that hake can affect forage fish resources. However, while his model provided information regarding how much forage fish biomass each group of piscivorous predators (fishes, bird, and mammals) consumed, the model did not have Pacific hake eating juvenile salmonids, nor did it include prey switching by predators when forage populations were low. As such, it did not address the hypothesis we wished to explore with our study.

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 juvenile salmonid off the Columbia River? 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. 5.2) and the April-July 120 period. During this initial ocean entry period, juvenile salmon are similar in size to forage fish and thought to be most vulnerable to predation (Pearcy 1992; Weitkamp 2004; Emmett and Krutzikowsky In review). While the model provides a simplistic view of a complex ecosystem, it presents the major pathways and begins to identify general properties of the pelagic ecosystem off Oregon/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. These data were acquired by conducting regular night-time surface trawling and taking predatory fish stomachs from late April-July, 1998-2004. These efforts provided seasonal density estimates for juvenile salmonids, forage fishes, Pacific hake, and other predatory fishes.

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 (Pearcy 1992; Beamish and Mahnken 2001; Weitkamp 2004). Thus, we located our study site off the Columbia River (Fig 5.2), a river basin in which a large number of salmon spawn. We also conducted our field collections during spring/early summer, the time when most 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 (CCE), and has seasonally variable winds and currents; with northwest winds, southerly currents, and upwelling in the summer, and south winds, northerly currents, and downwelling in winter (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 1999-2004 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. 5.2). 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, WA to Tillamook Head, OR. 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.

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 et al. 2002). The trawl is 100-m long with a fishing mouth area 28-m wide and 12-m deep. The effective mouth area (336 m^2) 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^{-1}) 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.

From each haul, all fish species were identified, enumerated, and 30 of each species randomly measured. However, when haul catches were large (~>200), a random sample of 30 individual fish from each species was measured, and subsamples of each species (approximately 5-30 kg, depending on fish size) were 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 were 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 volume water each haul fished. 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 log normal 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 2 or 3 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} m^3) was calculated by multiplying the study area (1.3×10^{10}m^2) (Fig. 5.2) by an assumed surface trawl sampling depth of 12 m.

Forage fish generally migrate into the study area in early May and peak in late May (Emmett et al. 2006). The model incorporates these fluctuations by gradually increasing forage fish numbers until the end of May (Fig. 5.3), after which forage fish immigration is discontinued. Recruitment, the addition of zero-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 hatchery 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, WA to J. Lecky, NMFS, Portland, OR, 25 Aug. 2005). This provides a total estimate of 200 million smolts enter the Columbia River annually. However, approximately half of all smolts die before they reach the ocean (Douglas Marsh, NOAA Fisheries, Seattle, WA, pers. comm.), so we estimated that about 100 million smolts entered the ocean from the Columbia River in 2004, and we assume that smolt numbers were similar in other years.

The annual smolt (juvenile salmon) migration through the Columbia River estuary is well documented. Yearling [coho and spring Chinook salmon (*O. tshawytscha*)] 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 in to the ocean each day (Fig. 5.3) 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 3 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 (Pearcy and Fisher 1988; Fisher and Pearcy 1995) after spending time in the Columbia River plume, or moving 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. 5.2) 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 estimate may be high. Decreasing the migration rate would increase predation rates on juvenile salmon in the study area.

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 during one meal. Cartes et al. (2004) reported that European hake (*Merluccius merluccius*) ate 1.01 to 5.51% of their body weight/day. As such, we estimated that our average Pacific hake, which averaged 447 g, had a maximum daily consumption rate of approximately 25 g/day, similar to the value in Field (2004). Since the average northern anchovy, a primary prey of Pacific hake (Emmett and Krutzikowsky, In review) was approximately 25 g (unpublished data), we estimated that Pacific hake had a maximum consumption rate of 1 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 (Pearcy 1992). The model has one major predator (*Hake*) and two prey groups, *Salmon* and Forage Fish (*FF*) (Fig. 5.4). Pseudo-code for the STELLA mathematical model is presented in Appendix 1.

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 was derived by multiplying the number of fish eaten (*FFSalmon_Eaten*) by the proportion of *FFSalmon* comprised by juvenile salmon:

(1) $$\text{Salmon\_Eaten} = \text{FFSalmon\_Eaten} * (\text{Salmon}/\text{FFsalmon}).$$

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*) times feeding rate (*FR*):

(2) $$\text{FFSalmon\_Eaten} = \text{Hake} * \text{FR}$$

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

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

Since the maximum feeding rate (*MaxFF*) was estimated to be equal to 1 forage fish/day, it can be ignored in the equation. The half-saturation feeding constant, *Ks*, was estimated by minus the intercept from a linear regression of the observed annual average percent 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 (*FFsalmon*) over the hake fish feeding rate (Eppley and Thomas 1969) (Fig. 5.5). At very high forage fish/juvenile salmon densities, *FR* approaches 1. At low prey densities, *FR* approaches 0 and the number of forage fish/juvenile salmon consumed also approaches 0.

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

$$\text{Salmon}(t) = \text{Salmon}(t-1)+\text{Salmon\_Entering}(t)-\text{Salmon\_Eaten}(t)-\text{Salmon\_Migrating}(t) \tag{4}$$

for t = 1 to 120.

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

$$\text{FF}(t) = \text{FF}(t-1) + \text{Forage\_Fish\_arriving}(t) - \text{Forage\_Fish\_eaten}(t) \tag{5}$$

A list of parameter and constant values is provided in Table 5.1.

Model evaluation

Calibration/Confirmation

This model serves as an initial “framework” to evaluate whether if 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 the 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 three observed measures of salmon marine survival: the Oregon Production Index Area (OPI) hatchery coho salmon (*Oncorhynchus kisutch*) marine survival (PFMC 2005), and spring 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 Fisheries, Seattle, WA, pers. comm.), jack counts, which 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 predicted number of salmon eaten by hake was log transformed to normalize the data.

Using multiple regression models with Chinook salmon jack returns and coho salmon marine survival as dependent variables, we also investigated if the annual numbers of salmon eaten, as predicted by the trophic model, and Columbia River flow (average May/June flows) could account for much of the observed variation in Chinook salmon jack returns or coho salmon marine survival. We suspected that spring river flow would have an effect on marine survival because the study area is strongly affected by peak flows of the Columbia River that occur during spring, which is when most of Columbia River smolts enter the marine environment.

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. 5.6). The model also predicts that juvenile salmon mortality is inversely related to forage fish abundance in a curvilinear fashion (Fig 5.6).

Under “good” ocean conditions – when hake numbers are less than $1.0x10^6$ and forage fish are abundant, hake eat relatively few salmonids (Fig. 5.7). However, when the hake are abundant and forage fish are not, the number of salmon hake eaten by hake rises sharply (Fig. 5.7). When forage fish are very abundant (greater than $1.0x10^9$), they serve as a strong alternative prey and over a wide range of values for hake abundance few salmonids are eaten (Fig. 5.7).

Model estimates of salmon mortality of salmon mortality versus salmon marine survival indexes

Seven sets of observed average annual May/June abundance estimates for hake and forage fish in the study area were used in the model to generat model predictions of the numbers of salmon eaten. These resulting model estimates of salmon mortality were then compared with three annual measures of salmon survival (Table 5.2). The regression analysis found that Oregon OPI hatchery coho salmon survival was negatively correlated with the predicted number of salmon eaten (regression, $P = 0.03$, $R^2 = 56.8$). However, fall Chinook salmon jack counts at Bonneville dam were weakly related to the predicted numbers of salmon eaten ($P = 0.16$, $R^2 = 22.1$), and spring Chinook salmon jack counts at Bonneville Dam were poorly related to the model predictions ($P = 0.77$, $R^2=-17.8$).

The results of these simple regressions indicate that the simulation model does not accurately mimic variability in salmon marine survival that has been observed. However, if average spring (May/June) Columbia River flows are included with the predicted number of salmon eaten in a multiple regression model, significant predictive relationships are obtained. The multiple regression with Columbia River flows and predicted salmon predation as independent variables accounted for 89.6% (R^2) of the OPI coho salmon smolt to adult returns (P = 0.005). Similarly, this regression model accounted for 69.0% (R^2) of the variation in Columbia River spring Chinook jack counts (P = 0.04), and 75.1% (R^2) of the variation in fall Chinook jack counts (P = 0.03).

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 plays 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 very poor salmon survival when hake populations in the study area were abundant and forage fish populations were low. 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).

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 of consumption of forage fish by hake 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.

Large piscivorous predatory fishes feeding rates are strongly affected by turbidity, while small fishes (juvenile salmon and forage fish) feeding is 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 (Emmett et al. 2006), suggesting these fishes may be using turbid marine waters to evade predators and 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 seams a sensible extension and it would be useful if future oceanographic surveys 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.

The 120-day period in the model, April-July, covers the peak of migration for most juvenile salmonids leaving the Columbia River. Captures of coded wire tagged (CWT) juvenile salmonids on the northern Washington coast indicate that juvenile salmonids generally leave our study area relatively quickly (Pearcy and Fisher 1988; Fisher and Pearcy 1995). However, recent ocean catch data indicate that some juvenile salmon may reside in our study area for months (J. Fisher, Oregon State Univ., Corvallis, OR, pers. comm.). If smolts have an extended residence time in the study area, mortality rates would rise accordingly. Furthermore, the distribution of hake and other predators also extends northward, with hake sometimes distributed to waters off southeast Alaska during warm years (McFarlane et al. 2000). Juvenile salmonids probably do not escape fish predation pressure until they grow large enough that most fish predators can not catch and eat them (Walters et al. 1978). As such, health (disease and parasites), size, feeding, and growth of juvenile smolts also likely influence their susceptibility to predation.

We used abundance estimates of Pacific hake and forage fish in our study area to parameterize the model. However, these fish abundance estimates must be considered minimum values. As stated earlier, our research trawl only fished the top 12 m, and the net capture efficiency was probably less than 100%. As such, our abundance estimates for hake and forage fishes could be low by an order of magnitude or more. Furthermore, predators and forage fishes have very patchy distributions in the study area. These patches strongly influence catch rates and predator/prey interactions. We suspect that predator/prey patches probably have significant effects on juvenile salmonid marine survival, but acoustic profiles or other data to quantify these patches, are presently unavailable, and a simulation model that incorporated patch dynamics would be very complicated.

The predictions from the simulation model correlated well with the marine survival of coho and fall and spring Chinook salmon, but only after Columbia River flows were included in a multiple regression model. At high Columbia River flows, salmon marine survival is higher for given abundance levels of predator and forage fishes off the Columbia River. 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 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 flow is high and Pacific hake and other predators' ability to see and capture near-surface prey (salmonids) would be reduced during turbid high flow conditions (Gregory 1993; Gregory and Levings 1998; DeRobertis et al. 2003).

In the current model configuration the user selects hake and forage fish population levels that remain constant throughout the 120 day simulation. In reality, highest levels of these two variables generally vary during any year, with highest levels often occurring in May or June, or sometimes later. However, for simplicity, we did not incorporate this feature into the model. Our primary purpose in developing this model was to evaluate whether annual differences in salmonid marine survival could be accounted for by differences in predator/forage fish abundances if forage fish were acting as alternative prey.

The results of our model and our observational data (Emmett et al. 2006) indicate that forage fish, when abundant, provide a predation buffer for salmonids. This agrees with the findings of Collis et al. (2004) who found that avian predation on juvenile salmonids decreased as forage fish abundance increased in the Columbia River estuary, and Svenning et al. (2004) who found that predatory fishes ate primarily the abundant sandeels (*Ammodytes marinus*) instead of salmonids in a Norwegian estuary. However, we propose that different forage mechanisms operate in estuarine versus ocean environments. While forage fishes in the Columbia River estuary are often near the surface and actively feeding during the day, (when most bird and mammals feed) depending on the tide (Zamon 2001; Emmett pers. observ.), in the ocean, most forage fishes reside at depth during the day, coming to the surface primarily during crepuscular periods and night (Blaxter and Holliday 1963; Neilson and Perry 1990). This can leave juvenile salmonids residing in the ocean environment with relatively few forage fish (i.e., alternative predator prey) actually near them during daylight and crepuscular periods. The importance of diel migrational behaviors of forage fishes and salmonids needs further investigation. A series of 24-hour studies, comparing night- versus day-time feeding habits of predators, including fishes, birds, and mammals, would be very informative.

We believe 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, and juvenile salmon 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, 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 study indicates that Pacific hake and forage fish populations, along with Columbia River flows, have a very strong influence on salmon survival in our study area. Columbia River flows affect coastal turbidity and forage and predatory fish abundance, distributions, and predator/prey interactions. The Columbia River plume is presently smaller and probably less turbid than it was historically (Sherwood et al. 1990), it would be valuable to model trophic interactions using estimated historical conditions.

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 can determine Columbia River salmon marine survival. Output from our trophic model along with average May/June Columbia River flows in a multiple regression analysis indicate that juvenile salmon marine mortality and thus adult salmon run sizes are related to the number of Pacific hake, the abundance of forage fish, and Columbia River flows. River flows and associated turbidity and other physical factors probably play an important role in predator/prey interactions, and are influenced by Columbia River hydropower operations. Future research should further quantify existing variables and explore whether adding other variables to this model can produce evern more accurate predictions of salmon marine survival. Further, this type of model could 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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Table 5.1. Constants and parameters for model simulations.

Parameter or constant	Description	Value
Ks	Half-saturation feeding constant	$2.3x10^9$
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

Table 5.2. Average spring (May/June) estimates of Pacific hake (*Merluccius productus*) and forage fishes off the mouth of the Columbia River from surface trawls 1998-2004. 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 and fall Chinook salmon (*O. tshawytscha*) jack counts (corrected for year of ocean entry).

	Observed		Model prediction	Observed			
Year	Pacific hake	Forage fish	Salmon eaten	Coho salmon OPI % SAR	Spring Chinook salmon	Fall Chinook salmon	Average Columbia River May/June flows (m^3/sec)
1998	47,655,442	8,867,411	43,572,056	1.3	11,081	23,582	10,082
1999	3,266,796	7,508,749	4,841,367	2.5	28,472	55,538	10,497
2000	81,414	1,378,052,066	31,283	4.6	22,000	74,496	7,695
2001	144,068	4,280,770,092	26,110	2.8	11,308	40,215	4,621
2002	505,760	1,202,111,144	212,987	4.0	22,245	47,722	8,913
2003	7,882,295	2,984,177,499	1,909,801	2.7	16,928	38,557	7,991
2004	3,065,483	513,088,377	2,223,774	2.0	7,016	21,214	7,293

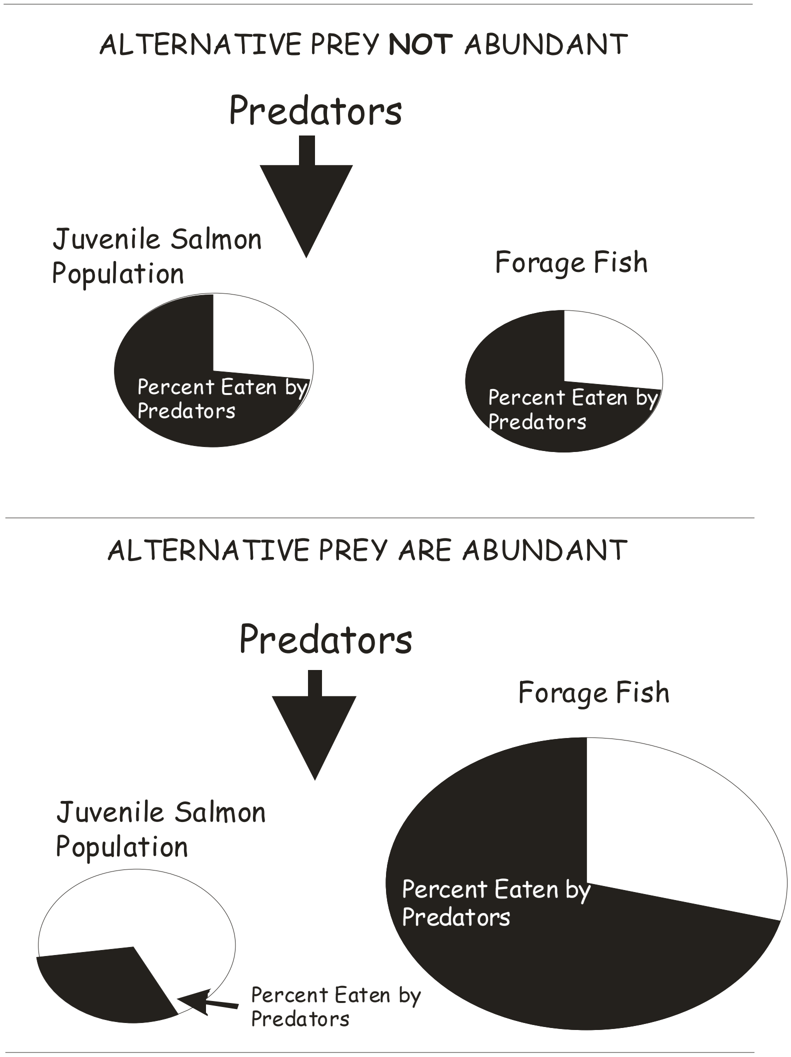

Figure 5.1. Diagram of the hypothesized role that alternative prey (forage fishes) play in reducing predation on juvenile salmonids in the marine environment.

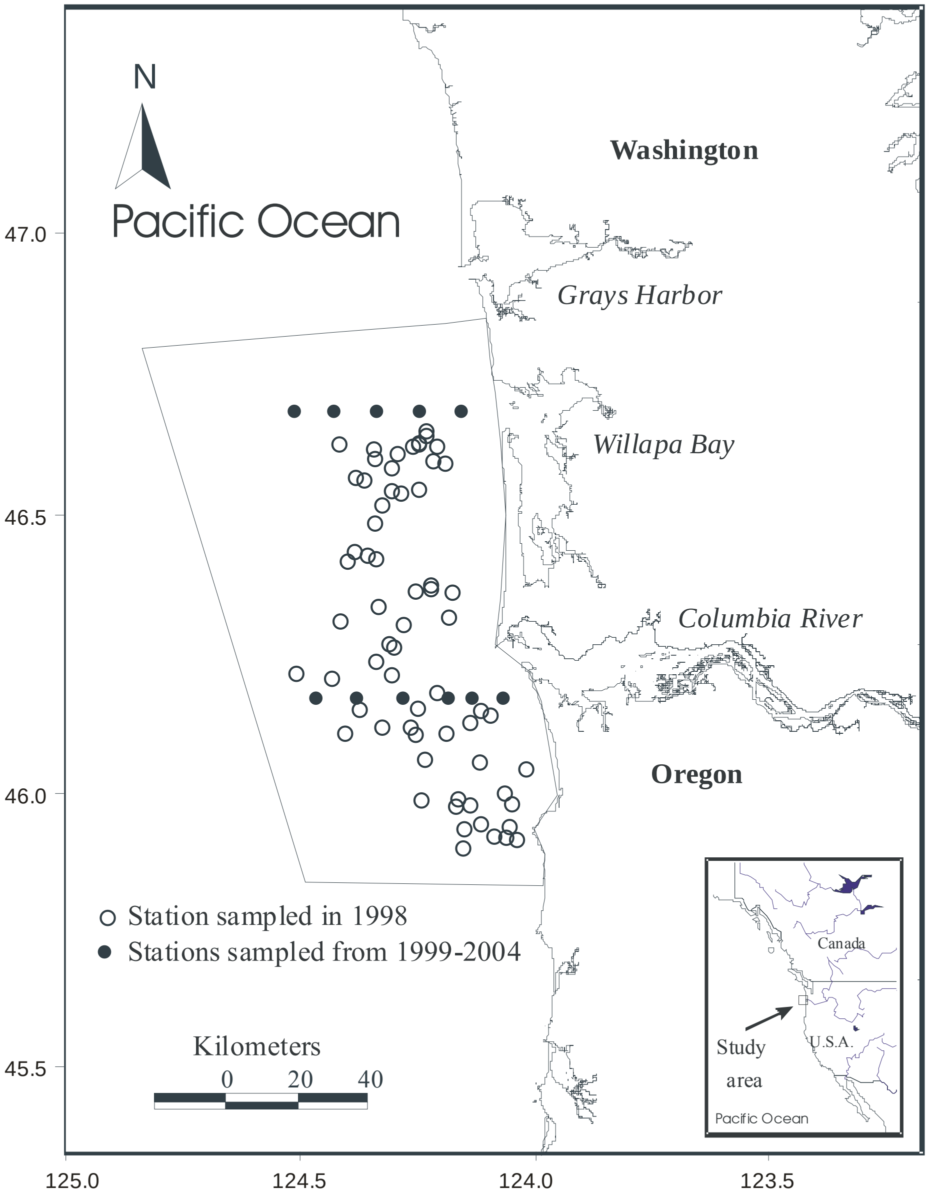

Figure 5.2. Location of stations off the Columbia River region sampled by surface trawl at night during spring/summer 1998-2004. Also shown is the estimated total coastal area representatived by the trawl data.

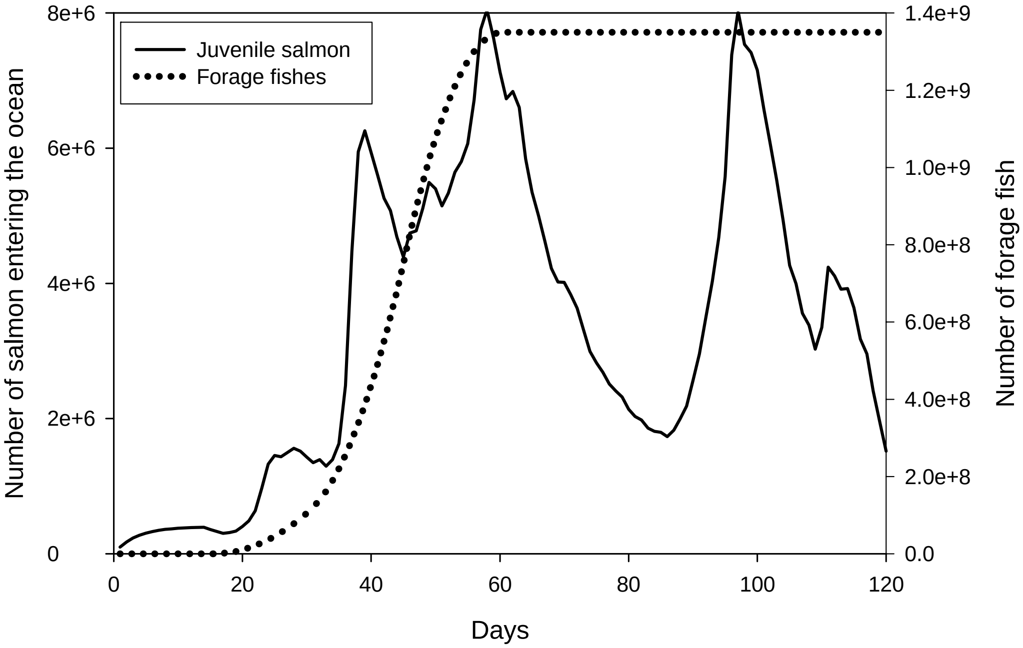

Figure 5.3. Graphic representation of how the trophic model populated the study area off the Columbia River with number of juvenile salmon entering per day and number of forage fish off the Columbia River.

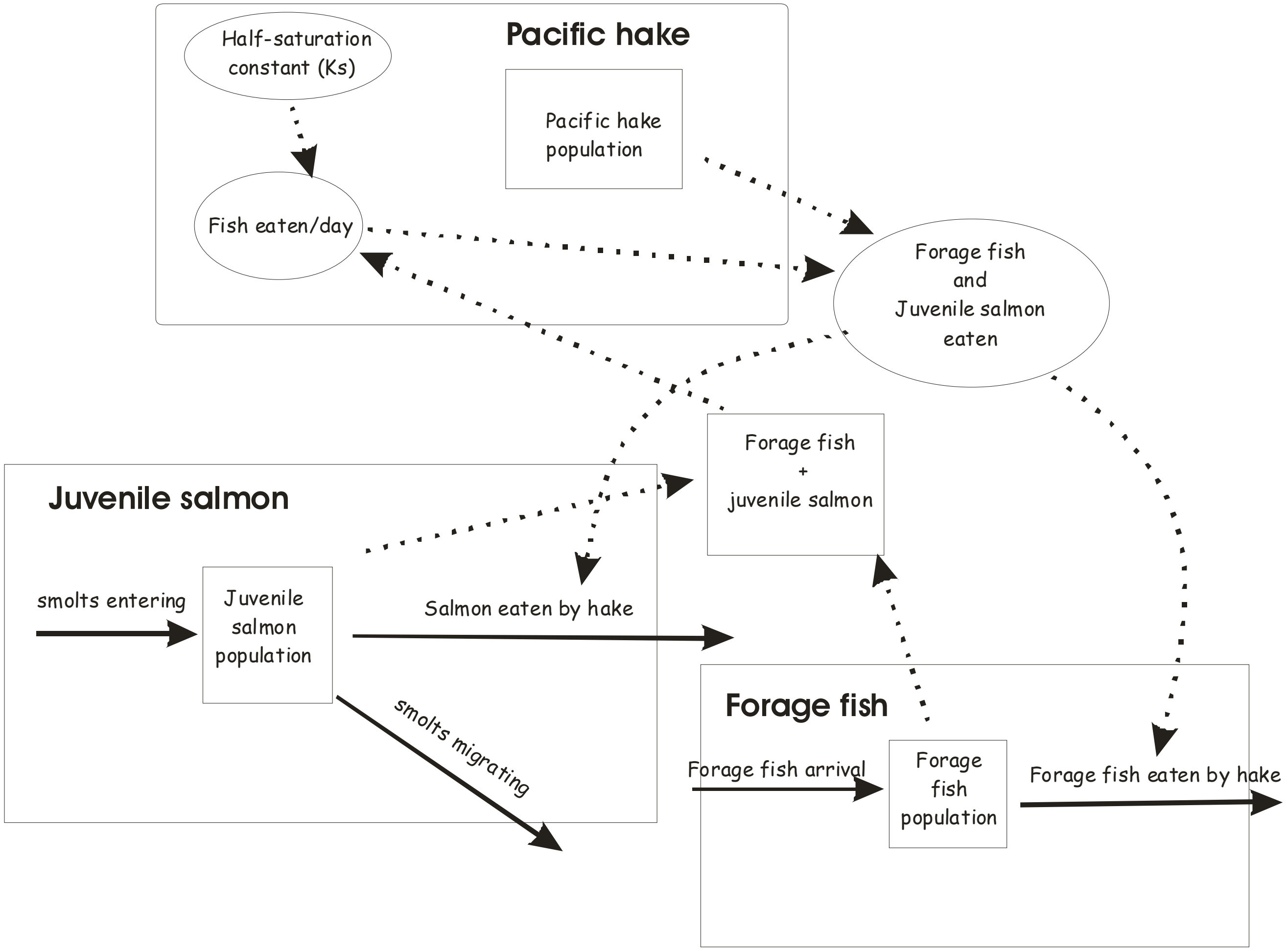

Figure 5.4. Graphical representation of the trophic model developed to evaluate the influence of Pacific hake (*Merluccius productus*) predation on forage fish and juvenile salmon off the mouth of the Columbia River.

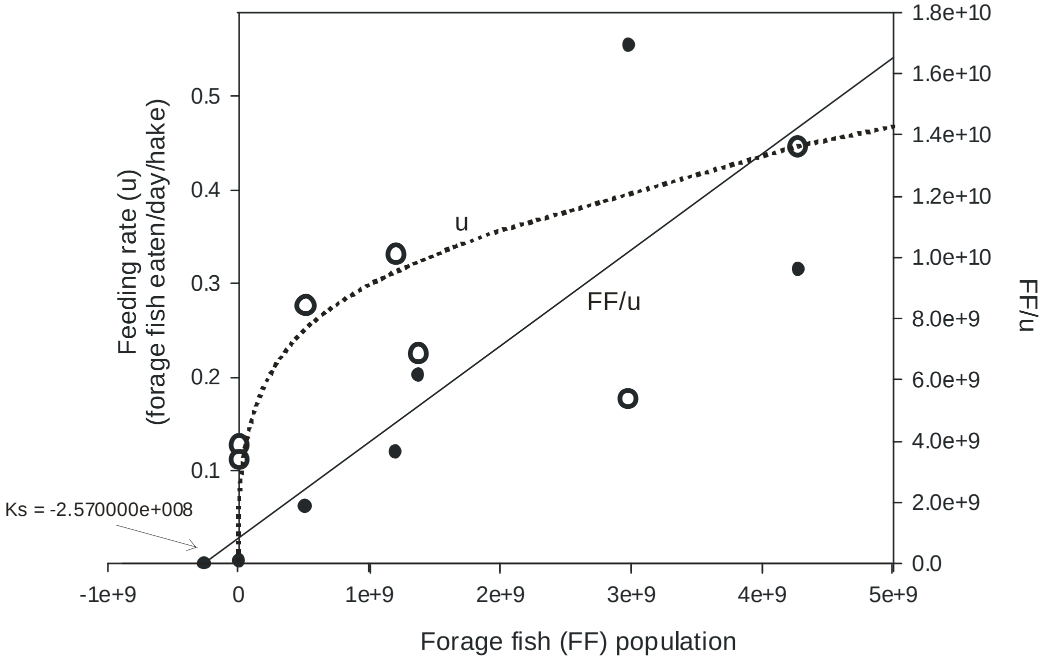

Figure 5.5. The relationship between the percent Pacific hake (*Merluccius productus*) feeding on fishes (○) (estimated hake fish feeding rate) and forage fish population abundance. The straight line is the regression of the forage fish population/hake fish feeding rate ratio versus forage fish population abundance (●) from which the Michaelis-Menton Ks (half-saturation feeding constant) was estimated.

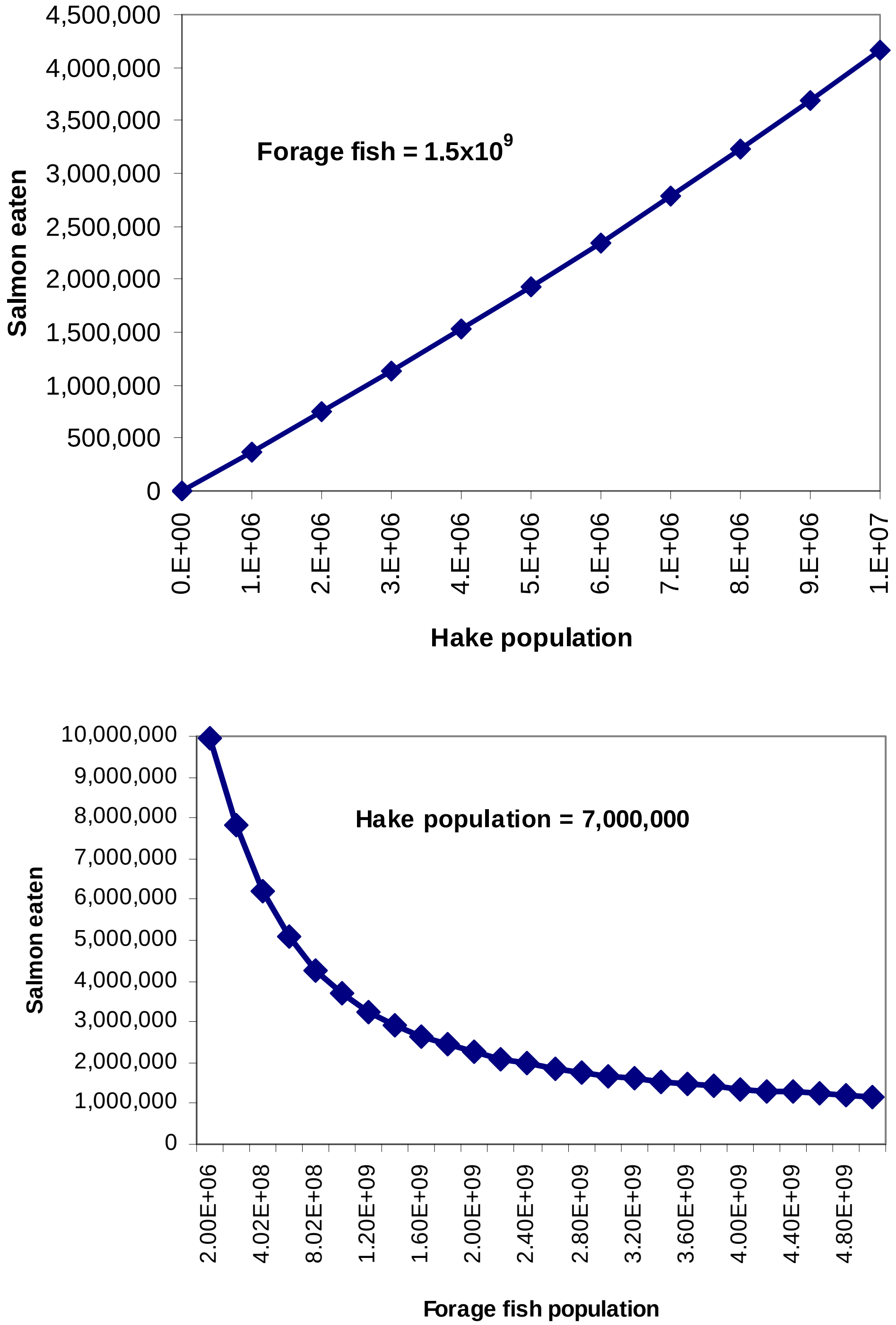

Figure 5.6. Model output showing the estimated number of salmon eaten at: various Pacific hake (*Merluccius productus*) population sizes (top) and when the forage fish population is 1.5x10^9, and at various forage fish population sizes (bottom) when Pacific hake are constant.

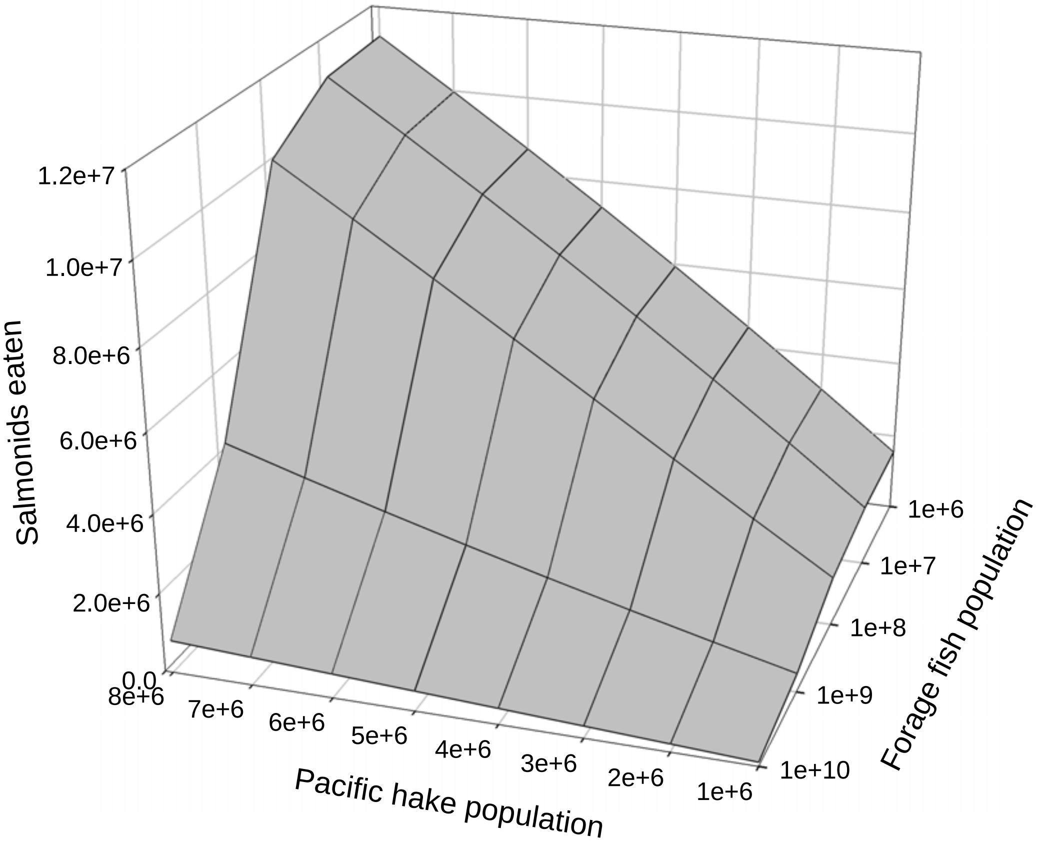

Figure 5.7. Output from the trophic model of Pacific hake, forage fish, and juvenile salmon. Shown is the estimated number of salmon eaten under various population sizes of Pacific hake (*Merluccius productus*) and forage fishes

Appendix 5.1. Mathematical model written in STELLA describing the feeding of Pacific hake (*Merluccius producus*) on juvenile salmonids and forage fish off the Columbia River. Comments are italicized.

Forage Fish Sector
(*FF = number of forage fish off the Columbia River*)
(*FF = forage fish arriving – forage fish eaten*)

FF(t) = FF(t - dt) + (FFarrival - FF_eaten) * dt
INIT FF = 0

INFLOWS:
FFarrival = FF_Begin*arrival_day
OUTFLOWS:
Forage_Fish_mortality = FF_eaten_Hake
Total_FF_eaten(t) = Total_FF_eaten(t - dt) + (FF_eaten) * dt
INIT Total_FF_eaten = FF_eaten

INFLOWS:
FF_Begin= 1500000000 (*value can be set by user*)
arrival_day = GRAPH(Day)
(0.00, 0.00), (15.0, 0.00), (30.0, 0.01), (45.0, 0.05), (60.0, 0.00), (75.0, 0.00), (90.0, 0.00), (105, 0.00), (120, 0.00)

Hake off the Columbia River Sector
(*Hake = number of hake off the Columbia River*)

Hake(t) = Hake(t - dt)
INIT Hake = 10000000 (*value can be set by user*)

(*Salmon_eaten = smolts_dying_from_hake_predation*)

OUTFLOW FROM: Salmon (IN SECTOR: **Juvenile Salmonids**)
(*MaxFF=Max forage fish eaten per day*)
MaxFF = 1
Feeding_Rate = MaxFF * (FFSalmon)/(Ks+FFSalmon)
FFSalmon_eaten = Hake* Feeding_Rate
FF_eaten = FFSalmon_eaten*(FF/FFSalmon)
Salmon_eaten = FFSalmon_eaten* Salmon/FFSalmon
Hake_Max_FF_per_day = 1
Ks = 2.5e+8

Appendix 5.1. Continued.

Juvenile Salmonids Sector
Day(t) = Day(t - dt) + (seasonal_progression) * dt
INIT Day = seasonal_progression

INFLOWS:
(*Salmon = juvenile salmon population off the Columbia River*)
Salmon(t) = Salmon (t - dt) + (smolts_entering - Salmon_eaten - Migrating) * dt
INIT Salmon = smolts_entering
seasonal_progression = 1

INFLOWS:
smolts_entering = Total_smolts*Percent_smolts_entering

OUTFLOWS:
Salmon_eaten (IN SECTOR: **Hake off the Columbia River**)
Migrating = Number_migrating
total_Salmon_eaten(t) = total_Salmon_eaten(t - dt) + (Salmon_eaten) * dt
INIT total_Salmon_eaten = Salmon_eaten

INFLOWS:
Number_migrating = Salmon *Percent_Migrating
Percent_Migrating = 0.25 (*percent migrating per day out of the study area*)
Total_smolts = 1.E8 (*number of Columbia River smolts*)

(GRAPH(Day) *allows smolts to migrate in normally*)
Percent_smolts_entering = GRAPH(Day)
(0.00, 0.001), (1.01, 0.001), (2.02, 0.001), (3.03, 0.001), (4.03, 0.001), (5.04, 0.001), (6.05, 0.001), (7.06, 0.001), (8.07, 0.001), (9.08, 0.001), (10.1, 0.001), (11.1, 0.001), (12.1, 0.001), (13.1, 0.001), (14.1, 0.000572), (15.1, 0.000623), (16.1, 0.000553), (17.1, 0.000932), (18.2, 0.00101), (19.2, 0.00162), (20.2, 0.00186), (21.2, 0.00287), (22.2, 0.00541), (23.2, 0.00614), (24.2, 0.00419), (25.2, 0.00325), (26.2, 0.0045), (27.2, 0.00433), (28.2, 0.00319), (29.2, 0.00282), (30.3, 0.00274), (31.3, 0.0042), (32.3, 0.00189), (33.3, 0.00507), (34.3, 0.00618), (35.3, 0.0153), (36.3, 0.0306), (37.3, 0.0238), (38.3, 0.0152), (39.3, 0.0111), (40.3, 0.0116), (41.3, 0.0101), (42.4, 0.012), (43.4, 0.00703), (44.4, 0.00974), (45.4, 0.0174), (46.4, 0.00893), (47.4, 0.0193), (48.4, 0.0148), (49.4, 0.0114), (50.4, 0.0107), (51.4, 0.0178), (52.4, 0.0154), (53.4, 0.0159), (54.5, 0.0182), (55.5, 0.0246), (56.5, 0.0295), (57.5, 0.0159), (58.5, 0.016), (59.5, 0.0121), (60.5, 0.0156), (61.5, 0.0202), (62.5, 0.0089), (63.5, 0.00886), (64.5, 0.0107), (65.5, 0.00881), (66.6, 0.00854), (67.6, 0.0064), (68.6, 0.0113), (69.6, 0.00821), (70.6, 0.00825), (71.6, 0.00659), (72.6, 0.00477), (73.6, 0.00564), (74.6,

Appendix 5.1. Continued

0.00601), (75.6, 0.00505), (76.6, 0.00493), (77.6, 0.00574), (78.7, 0.00401), (79.7, 0.0039), (80.7, 0.00503), (81.7, 0.00361), (82.7, 0.00395), (83.7, 0.00476), (84.7, 0.00345), (85.7, 0.00489), (86.7, 0.00625), (87.7, 0.00607), (88.7, 0.00918), (89.7, 0.00949), (90.8, 0.0128), (91.8, 0.0133), (92.8, 0.0163), (93.8, 0.0173), (94.8, 0.0331), (95.8, 0.0277), (96.8, 0.0144), (97.8, 0.0179), (98.8, 0.0167), (99.8, 0.0123), (101, 0.0115), (102, 0.0101), (103, 0.00832), (104, 0.00523), (105, 0.00834), (106, 0.00533), (107, 0.0075), (108, 0.00433), (109, 0.01), (110, 0.018), (111, 0.00938), (112, 0.00818), (113, 0.0101), (114, 0.00706), (115, 0.00444), (116, 0.00586), (117, 0.00193), (118, 0.00148), (119, 0.00052), (120, 0.00148)

Not in a sector
FFSalmon = FF+Salmon

GENERAL DISCUSSION

This research was initiated to explore the working hypothesis that predatory and forage fish abundance influence Columbia River juvenile salmon marine survival. I investigated if forage fish could act as alternative prey for juvenile salmonids, and thus increase juvenile salmon marine survival when forage fish were abundant. The distribution and abundance of predator fishes relative to oceanographic conditions and the distribution and abundance of forage fishes and juvenile salmonids was examined to identify possible species interactions. I also analyzed stomachs from Pacific hake and jack mackerel for juvenile salmonids. All these analyses incorporated some physical oceanographic conditions, to evaluate how trophic relationships were altered as oceanographic conditions changed. I also created a trophic model incorporating hake and forage fish populations, and hake food habits, and analyzed all the variables simultaneously to predict the number of juvenile salmon eaten by hake under various environmental conditions. A statistical model which included the number of salmon eaten by hake along with Columbia River spring flows was highly correlated with indices of Columbia River juvenile salmon marine survival. This indicated that Columbia River juvenile salmon marine survival is probably determined by predation events that occur when they enter the ocean, and perhaps still in the Columbia River plume

The following paragraphs summarize the analysis and results from each chapter, highlight the findings, and comment on whether the result supports the working hypothesis.

CHAPTER 1

In this chapter I reviewed fish data from a variety of sources, to see if there were trends in predatory and forage fish populations that were similar to trends in juvenile salmon marine survival. The NMFS triennial bottom trawl survey data showed that when hake became more abundant in the 1990s in the Columbia River region, juvenile salmon marine survival, as measured by coho salmon OPI survival, decreased. These data also showed that forage fish abundance fluctuated widely from 1977-1998. I also created a hake predation index, defined as the ln(hake biomass)-ln(northern anchovy biomass). Anchovy are known to be an important hake prey in this region (Livingston 1983). Percent coho salmon marine survival was strongly related to the hake predation index. These results indicated that the number of predators alone does not appear to effect juvenile salmon marine survival.

I also reviewed the coastal purse seine catch data collected by Oregon State University from 1981-1985 to look for trends in predatory and forage fish populations off Oregon/Washington. Similar to the triennial trawl survey data, the number of predator fishes was highest in 1983, a year when juvenile salmon survival was very poor. Forage fish numbers were also low that year, perhaps because of hake predation or ocean conditions.

Surface trawl data from 1998-1999 from the NMFS Predator and Plume Studies were also analyzed. These data also indicated large differences in predatory and forage fish populations between these years.

Warm ocean conditions have been correlated with poor salmon marine survival (Cole 2000; Hobday and Boehlert 2001; Logerwell et al. 2003) but biological mechanisms relating warmer temperatures with reduced salmon marine survival have not been identified. I found a direct relationship between higher April-May sea surface temperatures at Neah Bay, WA and the abundance of Pacific hake off Oregon/Washington. These data support the argument that predators, in particular Pacific hake, which become more abundant during warm ocean conditions, produce significant mortality of juvenile salmon off Oregon/Washington.

All of the data sets I analyzed for this chapter supported the working hypothesis. In all cases, when predators became more abundant and forage fish less abundant, juvenile salmon marine survival declined. The number of predatory fishes increased during years of warm ocean conditions. These findings support the argument that predation by marine fishes, particularly Pacific hake, is one of the primary mechanisms controlling juvenile salmon marine survival.

CHAPTER 2

This chapter focused on the relationship between forage fish abundance, changing ocean conditions and salmon marine survival from 1998-2004. While juvenile salmon marine survival and forage fish both increased during the study, I did not find any statistical relationship between forage fish abundance and juvenile salmon marine survival. These data do not support the working hypothesis. However, these results support the argument that salmon marine survival is not determined by one single environmental variable, but rather by several variables in concert. Other environmental variables that are most likely important include the abundance of predatory fishes, turbidity, and Columbia River flows.

These data do support the argument that forage fish can act as “alternative” prey for juvenile salmonids. Forage fish were found to be of similar size and in the same nearshore habitat as juvenile salmonids. I also found that forage fish were generally most abundant in May, which is also the peak of the yearling salmon migration. I hypothesize that the timing of the juvenile salmon migration to the ocean in spring, may be a life history strategy that is linked to the arrival of forage fish in the spring. The survival of smolts that migrate early, in April for example, is consistently less than those that migrate in May (unpublished data).

One of the most interesting findings was the strong statistical relationship between the abundance of cold-water copepods and the number of forage fish the following year. This relationship makes biological sense. Abundant, large, lipid-rich copepods would be an ideal prey for forage fish larvae, allowing them to grow and survive at a much higher rate than when warm-water or lipid-poor copepods are abundant. It would be valuable to study the feeding and growth rates of forage fish larvae and juveniles under different cold- versus warm-water copepod conditions. The strong relationship between cold-water copepods and forage fish abundance is supporting evidence of a trophic link between the abundance of cold-water copepods and salmon marine survival (Peterson and Schwing 2003).

CHAPTER 3

This chapter focused primarily on the distribution and abundance of predatory fishes. It also highlighted the inshore/offshore distributions of predatory and forage fishes. One of the most interesting findings was that the abundance of Pacific hake was strongly related to the date of the spring transition and warm ocean temperatures. Logerwell et al (2003) found these two physical oceanographic variables to be strongly related to juvenile coho salmon marine survival, but they provided no biological mechanism to account for the relationships. That hake abundance in the study area is related to these two oceanographic variables suggest that predation by hake on juvenile salmon could be a significant factor determining salmon marine survival.

This chapter also highlighted that juvenile salmon comprise only a very small proportion of the forage fish community. As such, finding juvenile salmon in predator stomachs would be a very rare occurrence. However, because some predators such as

Pacific hake are very abundant, they could still account for the loss of many juvenile salmon. These data do support the working hypothesis.

CHAPTER 4

This chapter reported on the feeding habits of hake and jack mackerel off the Columbia River. From 1998-2004, only 7 juvenile salmonids were identified in predatory fish stomachs, which suggests that hake and jack mackerel are not important predators of juvenile salmonids, an unsurprising result given that juvenile salmon comprise a very small percentage of forage fish population. However, if salmon predation events are episodic, significant predation could occur, but they would be difficult to observe. Furthermore, if the estimates of predator populations are biased low, the actual number of juvenile salmonids eaten could be much larger. This chapter revealed the difficulty in obtaining direct evidence of fish predator feeding on juvenile salmon. However, the chapter highlights that Pacific hake may provide top-down control over forage fish species, such as anchovy and whitebait smelt, when they are abundant. While the results of this chapter do not support the working hypothesis of fish predators influencing juvenile salmon marine survival, it did highlight that hake predation can affect forage fish population abundance. As such, hake predation probably also affects juvenile salmonid survival. It is just difficult to observe directly.

CHAPTER 5

In this chapter I developed a relatively simple trophic ecosystem model for the pelagic environment off the Columbia River. The model included Pacific hake, forage fish, and juvenile salmon as input variables and it predicted the number of juvenile salmon eaten by Pacific hake during the 120 day period of the simulation, April through July. The total number of salmon eaten by hake was affected by both the number of hake and the number of forage fishes. When forage fishes were abundant hake ate few juvenile salmon. However, when forage fishes were not abundant hake ate many salmon. Using observed values for the abundance of hake and forage fishes in the model produced estimates for the number of juvenile salmon eaten by hake during each study year. Regression of these estimates versus estimates of salmon marine survival indicated a negative relation between the predicted number of salmon eaten and coho salmon marine survival only. However, a multiple regression analysis using Columbia River spring flows and the trophic model's estimates of the number of salmon eaten as independent variables to predict juvenile salmon marine survival revealed that these variables could account for > 65% (R^2) of the variation in Columbia River salmon marine survival.

These results suggest that juvenile salmon marine mortality off the Columbia River is a consequence of at least three variables: the number of Pacific hake, the number of forage fish, and Columbia River spring flows. This conclusion is supported by past research finding that ocean temperatures, date of the spring transition (Logerwell et al. 2003), and cold-water copepods (Peterson and Schwing 2003) were related to salmon marine survival. Pacific hake and forage fish abundance off the Columbia River are autocorrelated with those variables. These data indicate that Columbia River salmon marine survival will be low when Columbia River spring flows are low. Plume turbidities, which may effect predation, are also low during low flow conditions. The interaction between Columbia River flows and ocean productivity probably controls coastal turbidity, which has been found to strongly influence predator fish feeding (De Robertis et al. 2003). Future research should investigate how turbidity affects Pacific hake feeding.

CONCLUSION

The results from this dissertation support the argument that predation/trophic interactions when juvenile salmon first enter the ocean strongly influences Columbia River juvenile salmon marine survival. However, while these predation/trophic interactions are complex, they are not complicated. The trophic interactions are complex because they change as predator/forage populations and physical conditions change, but these trophic interactions can be easily modeled. Predatory fish populations, forage fish populations, and juvenile salmonid survival off the Columbia River change significantly with changes in ocean conditions: ocean currents, spring transition, cold-water copepods, Columbia River flows and probably turbidity. However, a major conclusion of this dissertation, that fish predation, strongly influenced by biological/physical oceanographic conditions, strongly influences salmon marine survival, agrees with what is presently known about juvenile salmon marine survival.

Some authors have suggested that the marine ecosystem off the Pacific Northwest is primarily a bottom-up ecosystem, whereby upper trophic levels respond to effects at the primary production or phytoplankton level (Fig. 6.1). Ware and Thomson (2005), for example, showed that resident fish catches in the Northeast Pacific Ocean are strongly correlated with primary production. However, this is counter to findings by Hannah (1995) who showed that Pacific hake feeding influenced the abundance of pink shrimp (*Pandalus jordani*), and Ware and McFarlane (1995) who found that predation by Pacific hake influenced the abundance of Pacific herring off British Columbia, Canada. Field et al. (2006) also found evidence that Pacific hake can exercise top-down control in the California Current ecosystem. In a top-down controlled ecosystem, lower trophic levels respond to changes which are initiated at the top of the food web (Fig. 6.2).

In other upwelling regions research has indicated that marine populations may operate under wasp-waist ecosystem control (Fig. 6.3) (Rice 1995; Cury et al. 2000; Cury and Shin 2002; Bakun 2006; Hunt and McKinnell 2006). In this type of ecosystem control, environmental conditions affect the populations of a few dominant forage fish species, which in turn influences the abundance of top predators and lower trophic levels (Fig. 6.3).

None of these ecosystem models (top-down, bottom-up, or wasp-waist) however, appear to adequately represent the forage fish and predatory fish population changes I observed off the Oregon/Washington. Instead, I propose that the pelagic ecosystem off the Pacific Northwest is a “forage fish squeeze” ecosystem (Fig. 6.4). In this system, both bottom-up and top-down processes operate simultaneously, but are strongly influenced by climatic conditions. During cool climate conditions, bottom-up processes (e.g., upwelling, cold-ocean periods) stimulate abundant primary production and enhance appropriate zooplankton species (cold-water copepods), which enhances resident forage fish populations (anchovy, herring, and smelt). This is similar to bottom up ecosystem control. However, the forage fish-squeeze differs from bottom-up control because predator abundance is not controlled by forage fish abundance. In this system, fish predators, which are primarily migrants from the south, have their abundance controlled by climate/oceanographic factors outside of the Pacific Northwest. In the forage fish squeeze ecosystem model, top-down effects on forage fish, which include juvenile salmon, are strongly affected by the abundance of large migratory fishes (hake and mackerel). Since these predatory fishes are migratory and spawn outside the Pacific Northwest, direct feedback loops, that would exert some control on the number of these predatory fishes, are severely reduced.

Under forage fish-squeeze control, when ocean climate conditions are cool, primary production is high and cold-water copepods are abundant. Coincidentally, under cool ocean climate conditions, migratory predators, which have southern or warm water affinities, are not abundant. As a result, forage fishes, such as anchovy and smelt, quickly increase in abundance, and juvenile salmon marine survival is high. On the other hand, during warm years, primary production is low and cold-water copepods are not abundant, but migratory predatory fishes are abundant. Under these ocean climate conditions, forage fish recruitment is low and their numbers decline quickly because recruitment can not stay ahead of losses to predation. These are also years when juvenile salmon marine survival is low.

Evidence indicates that the marine ecosystem off the Pacific Northwest can shift quickly between warm and cold ocean climate conditions (Mantua et al. 1997; Peterson and Schwing 2003). During my study period I saw a gradual warming trend during 2003 and 2004, not an abrupt ocean climate shift. However, once the point is reached where forage fish recruitment is less than losses to mortality, the ecosystem will change abruptly

The dissertation results are based on only seven years of field work and covers a limited range on environmental conditions. If we are going to maintain and rebuild Pacific Northwest salmon runs, it is vital that we know what influences and controls salmon marine survival. Salmon spend most of their lives in the marine environment. We can only appropriately manage these salmon populations if we understand their complete life history. I suspect that, similar to terrestrial populations, there will be years when other biological factors, besides predation, such as disease and food, could be more important than predation in determining salmon marine survival. As such, we must continue to sample juvenile salmonids in the ocean and the marine environment if we are going to appropriately manage salmon resources in the future.

This research revealed that juvenile salmon marine survival is directly linked to the trophic interactions in the fish community and ecosystem that they live in. Ironically, while the purpose of this dissertation was to identify what controls juvenile salmon marine survival, relatively few juvenile salmonids were captured. Instead, this work centered on the fish trophic interactions and the marine ecosystem where juvenile salmon live. I believe this dissertation clearly shows that ecosystem-based fishery management (Botsford et al. 1997; Pikitch et al. 2004) will be necessary if we are to influence juvenile salmon marine survival. However, ecosystem-based fishery management requires adequate knowledge of the populations and important trophic interactions (Livingston and Jurado-Molina 2000). Off the Columbia River, additional information on the abundance and feeding habits of marine birds and mammals would be very helpful.

Finally, during the seven years of this study it became clear to me that there is no such thing as a “normal” ocean year. Each year had a unique set of physical and biological conditions. It is also clear that the oceans are warming (Levitus et al. 2000). As noted earlier, this will alter Pacific hake, and other species’ migrational behaviors. As warm ocean conditions become more common off the Pacific Northwest, I suspect that large numbers of Pacific hake will reside off the Columbia River during spring and summer. If, at the same time, forage fish populations are unable to successfully recruit (i.e., limited by the lack of cold-water copepods), and are unable to maintain high populations, the predation rates on Columbia River juvenile salmon will be very high. Juvenile salmon marine survival will also be affected if Columbia River spring flows are reduced by climate change. Only when we are able to take actions that will ensure adequate juvenile salmon marine survival will we will be able to enhance and maintain viable salmon runs in the Pacific Northwest.

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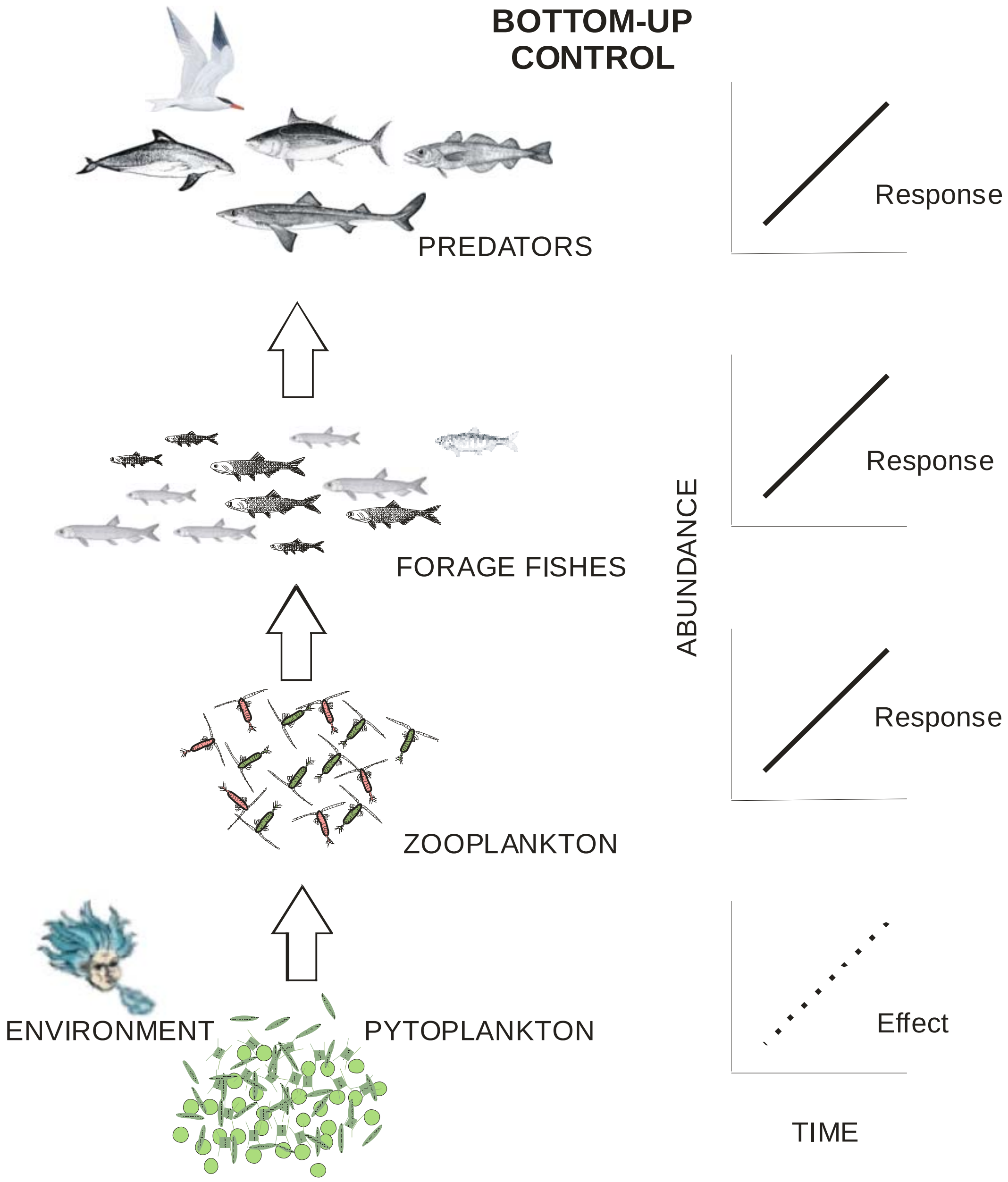

Figure 6.1. A diagram of a bottom-up food web and responses of various trophic levels to environmental change at the phytoplankton level. Redrawn from Cury et al. (2002).

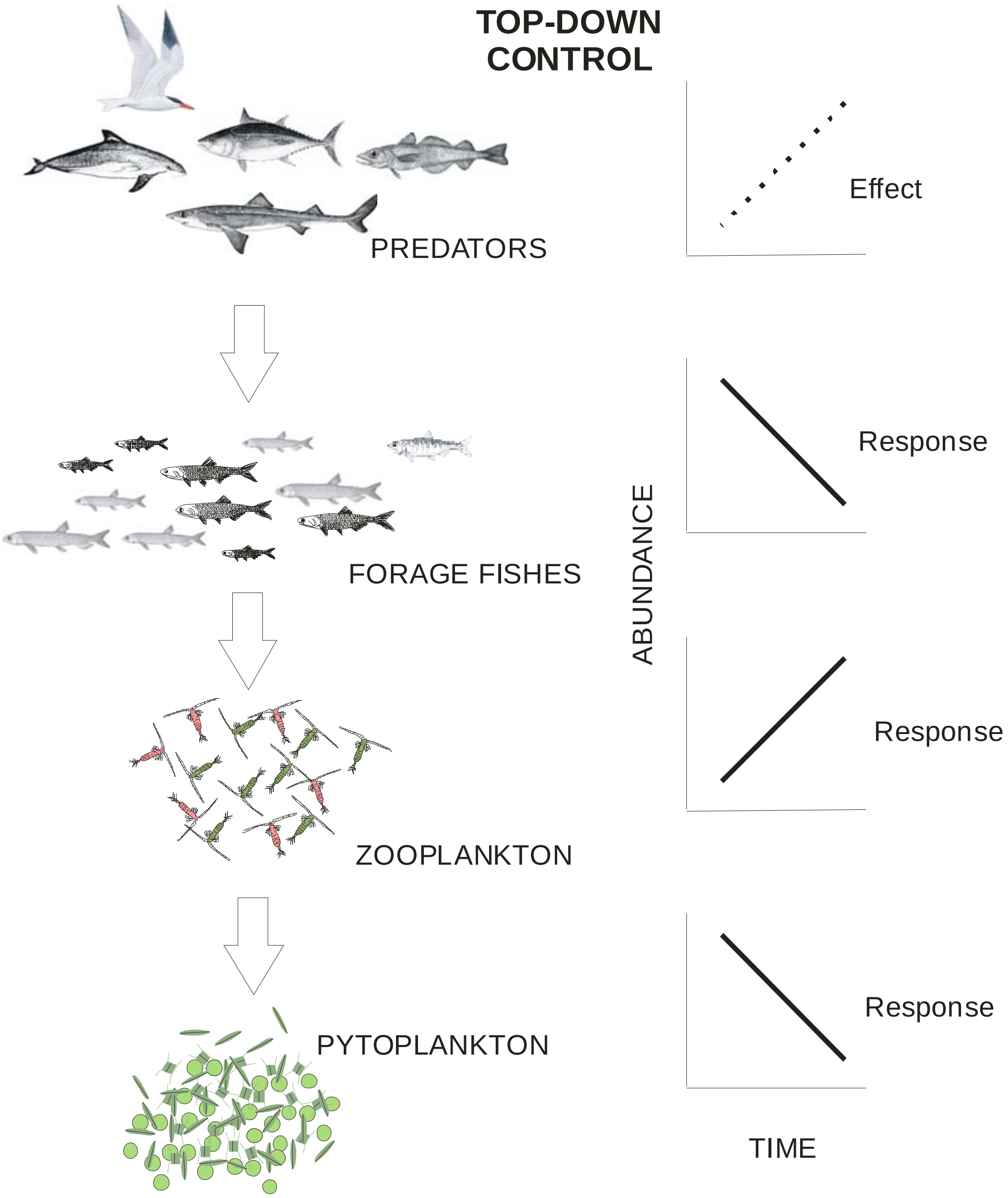

Figure 6.2. A diagram of a top-down food web and the responses of various trophic levels to increased predation pressure. Redrawn from Cury et al. (2002).

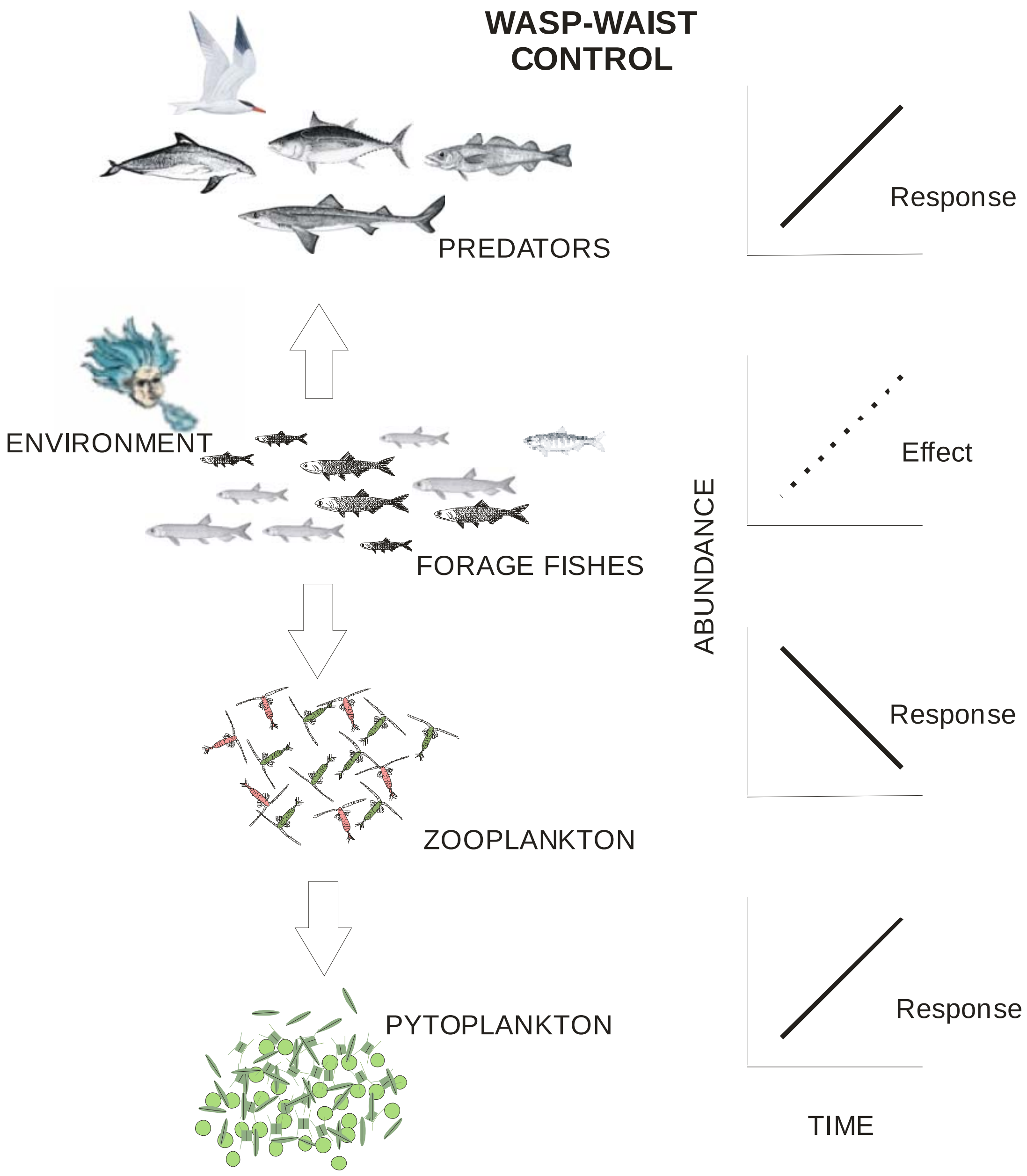

Figure 6.3. A diagram of a wasp-waist controlled food web and the responses of various trophic levels to fluctuations in forage fish abundance. Redrawn from Cury et al. (2002).

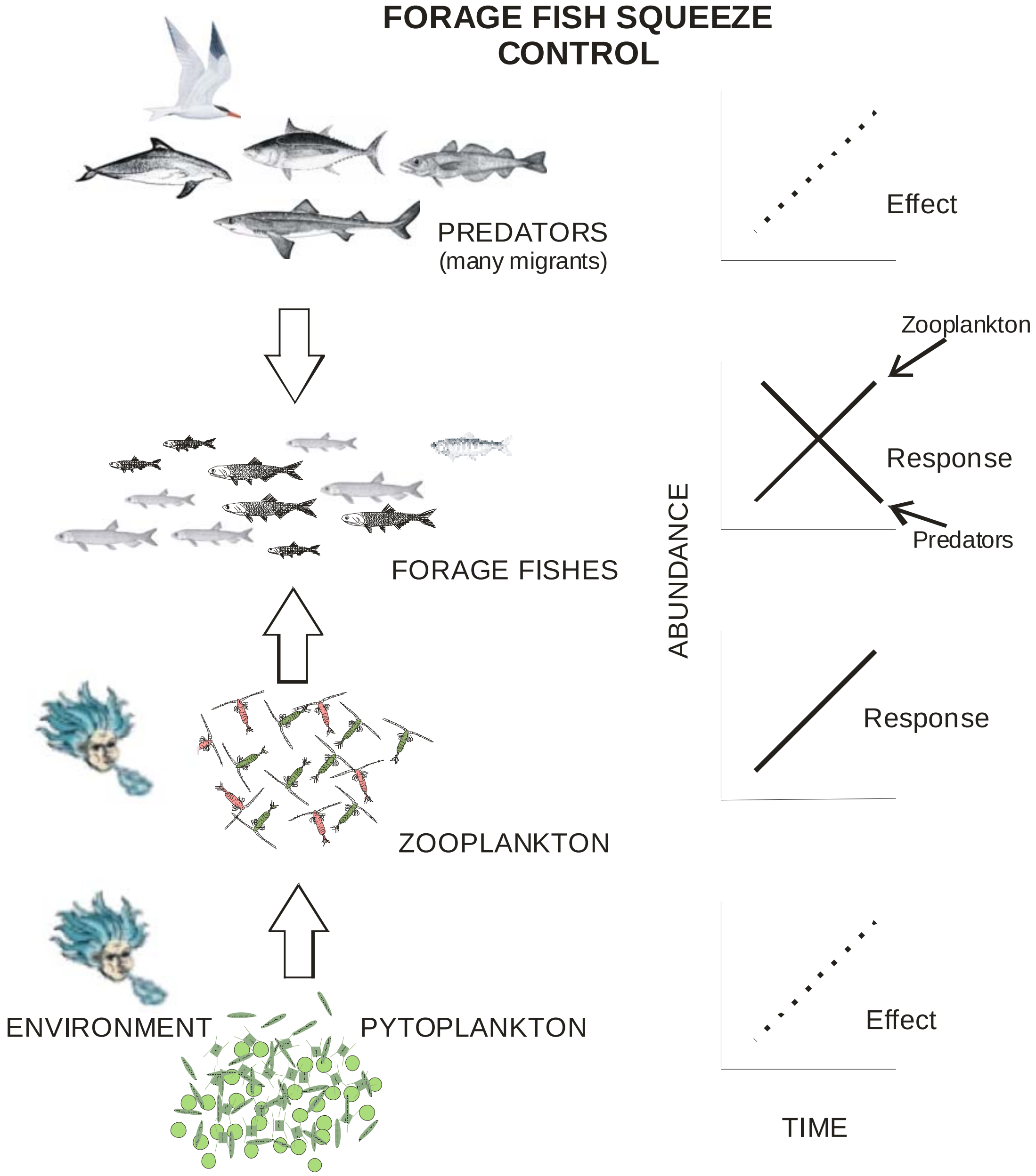

Figure 6.4. A diagram of a proposed “forage fish squeeze” food web for the Oregon/Washington coast. The forage fish population is affected by environmental changes at lower levels and the abundance of predators, which migrate into the region from the south.

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