Research Conducted by the United States on the Early Ocean Life History of Pacific Salmon

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Abstract: Research on juvenile Pacific salmon in coastal U.S. waters began almost 50 years ago in Southeast Alaska, and has continued somewhat sporadically since then. The National Marine Fisheries Service (NMFS), through its various laboratories in Alaska and along the West Coast of the United States, has done much of the research on the early life history of many Pacific salmon stocks in all habitats of U.S. waters, including their period of residence in coastal and oceanic waters. In addition, several of the leading universities in this region (University of Washington, Oregon State University, University of Alaska) have contributed greatly to our knowledge of salmon in their early ocean residency. Much of the early research was done using fine-mesh purse seines, but recently surface fine-mesh trawl nets and gill nets have been used more widely. A large number of programs are actively sampling in coastal waters at the present time, and the geographic and temporal coverage is the most complete it has ever been. In this paper, we provide a brief overview of many of the studies that have been done, synthesize their major findings, and discuss some of the areas where we believe future efforts should be concentrated.

INTRODUCTION

There has been considerable recent interest by a large number of investigators in the early marine life history of salmonids (*Oncorhynchus* spp.) in the North Pacific Ocean. Some of this interest is derived from the recognition that relatively high rates of mortality occur in salmon in the first few months at sea, a period termed by Hartt (1980) as the "first critical summer". Indeed, it has been shown that cohort mortality at sea is often equivalent to that in freshwater (Bradford 1995). Much of the current research on salmonids in the ocean has focussed on understanding processes related to this early ocean mortality (Pearcy 1984a, 1992; Emmett and Schiewe 1997; Brodeur et al. 2000). Such an understanding may lead to better predictability of salmon returns and other management benefits (Bisbal and McConnaha 1998; Beamish et al. 2000).

The purpose of this paper is to review studies on juvenile salmon conducted in coastal waters of the United States. We define juvenile salmon as those that are in their first year in the marine environment prior to the time that the first marine annulus forms on their scales. Pacific salmon inhabit coastal waters in the Eastern Pacific from southern California all the way to the Beaufort Sea. However, they occur in substantial numbers only from northern California to the Bering Sea, and the geographic coverage of our review encompasses the U.S. continental shelf across this range. Naturally, salmon are highly migratory and do not recognize international boundaries. A substantial amount of research has been done on juvenile salmon in Canadian coastal waters and is reviewed by Beamish et al. in this volume. We will not include studies of immature salmon after their first ocean year or maturing salmon, which were reviewed by Burgner (1992) and Myers et al. (2000). We instead focus on exposed coastal and oceanic regions and semi-enclosed areas such as Puget Sound, the inside waters of Southeast Alaska, and Prince William Sound. The voluminous U.S. studies that have specifically examined juvenile salmon utilization of smaller estuaries are beyond the scope of this review.

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Our aim is to highlight studies that have examined abundance and distribution patterns of juvenile salmonids during their early ocean existence. In addition to sampling salmon, most studies collected ancillary data on the biotic and abiotic conditions in which they were caught. Secondary information on the salmon themselves, such as growth, condition, diseases, food habits and stock origin, was also gathered generally at a later period in the laboratory. We cannot cover all these studies in detail; however, we discuss many of them briefly, especially in terms of their contribution to the understanding of salmon survival.

HISTORICAL OVERVIEW OF THE IMPORTANCE OF SALMON TO THE UNITED STATES

Seven anadromous species of the genus *Oncorhynchus* are native to the U.S. waters: sockeye or "red" salmon (*O. nerka*), chum or "dog" salmon (*O. keta*), pink or "humpback" salmon (*O. gorbuscha*), coho or "silver" salmon (*O. kisutch*), chinook or "king" salmon (*O. tshawytscha*), steelhead trout (*O. mykiss*), and coastal cutthroat trout (*O. clarki clarki*). Spawning stocks of sockeye salmon are distributed in U.S. waters from the Columbia River to Kotzebue Sound, Alaska, and the world's largest spawning population of sockeye salmon is in Bristol Bay, Alaska. Significant spawning populations of chum salmon range from Tillamook Bay, Oregon, to Kotzebue Sound, Alaska. Spawning stocks of pink salmon are distributed primarily from Washington to Norton Sound, and the largest populations are in central Alaska (Prince William Sound and Kodiak Island) and southeastern Alaska. Coho salmon spawning stocks are distributed in numerous streams from Monterey Bay, California, to Norton Sound, Alaska. Commercially important spawning stocks of chinook salmon occur primarily in large rivers from the Sacramento River, California, to the Yukon River, Alaska. The historical distribution of steelhead trout spawning stocks extended from the eastern Bering Sea (north side of the Alaska Peninsula and Unimak Island in the Aleutians) to the California-Mexico border, and the center of abundance is the Columbia River basin and adjacent rivers to the north and south (Burgner et al. 1992). Coastal cutthroat trout are distributed from northern California to Prince William Sound, Alaska.

Pacific salmon have been important to the native peoples of North America as a food for subsistence, a commodity for trade, and a cultural icon for many thousands of years. Sediment core data from salmon nursery lakes in Alaska, spanning the past two millennia, indicate that from AD 1200 to 1900 salmon abundance was relatively high and coincided with human population growth and high use of salmon fishing gear (Finney et al. 2002). At the time of arrival of the first European explorers, Native American fishermen were using a wide variety of methods to catch salmon, including bare hands, clubs, spears, gillnets, dip nets, traps, and weirs (e.g., Netboy 1974; Roppel 1986; Lichatowich 1999). Annual subsistence harvest in Alaska was probably more than 12 million salmon (Wertheimer 1997). Russian fur traders, established their first permanent settlement in Alaska on Kodiak Island in 1784, and supplied dried and salted salmon to Native American hunters, but their later attempts in the 1850s–1860s to market salted salmon were not successful (Roppel 1986).

The first U.S. salmon cannery began operating on the Sacramento River in California in 1864 and the first salmon hatchery was built on the McCloud River (a tributary of the Sacramento River) in 1872 (Lichatowich 1999). The U.S. salmon canning industry expanded rapidly northward to the Columbia River in 1866, southeastern Alaska in 1878, Cook Inlet and Kodiak in 1882, and Bristol Bay in 1884 (Browning 1974), and followed a boom and bust cycle as natural salmon runs were exploited and depleted. In Alaska, the number of salmon canneries peaked at 159 in 1929, and the salmon pack peaked at 8,454,348 cases canned in 1936 (Freeburn 1976). Commercial fisheries, first established to supply salmon to the canneries, used a wide variety of gear (e.g., beach seines, purse seines, drag seines, gillnets, traps, fish wheels, ocean trolling), and there were often conflicts over catch allocation among fishermen using different gear and between fishermen and processors over salmon prices. As the years passed, improvements in cold storage techniques and transportation systems opened new national and international markets for fresh and frozen U.S. salmon. After World War II, Alaska salmon runs declined, likely due to overfishing during a period of low ocean productivity, but prior to the expansion of the walleye pollock fishery in the 1970s, Alaska's salmon industry was regarded as the single most valuable U.S. commercial fishery in the North Pacific Ocean (Browning 1974). Sport or recreational salmon fisheries developed concurrently with commercial salmon fisheries.

Historically, ocean salmon fisheries were largely unregulated, and freshwater commercial and sport salmon fisheries were managed by the states. Alaskan fisheries were managed by the federal government from the purchase of Alaska in 1867 through 1959. Since the establishment of the U.S. 200-mile fishery Conservation Zone in 1976, the federal government has managed ocean salmon fishing from 3 miles offshore. The recognition of Native American fishing rights by the federal courts has led to a resurgence of tribal ceremonial and subsistence salmon fisheries since the late 1960s. Treaty tribes in western Washington and major tribes in the Columbia

River Basin are apportioned an equal share of the annual commercial salmon harvest and function as co-managers with the State. Since the 1990s, subsistence fisheries have taken precedence over all other fisheries in federally reserved waters in Alaska, and the federal government now manages these fisheries.

Over the past 200 years, the cumulative effects of overfishing, unfavorable climate, poor hatchery practices, human development, and environmental degradation have resulted in the decline or extirpation of many natural salmon populations. Since 1991, 27 anadromous salmon and steelhead trout stocks in the U.S. Pacific Northwest have been listed as threatened or endangered under the federal Endangered Species Act (ESA). Even in areas with pristine habitats and healthy salmon runs, commercial salmon fisheries are experiencing difficulties because of the loss of foreign markets, overcapitalization of fisheries, competition with farmed salmon, increasing management restrictions, and reduced harvests forced by the ESA. The estimated landed value of the Alaska commercial salmon catch has declined from $489 million in 1994 to $141 million in 2002 (Alaska Department of Fish and Game (ADFG), Commercial Fisheries, Juneau, USA, personal communication). Public awareness and understanding of the ecological and economic problems facing the salmon industry are now at an all-time high. New sectors of the industry involving marketing, research, management, conservation, restoration, education, information, and ecotourism are developing. Perhaps more than ever before, Pacific salmonids seem to be important to the United States as a natural, economic, and cultural resource.

TRENDS IN COMMERCIAL SALMON LANDINGS

In the U.S. Pacific Northwest region (Washington, Oregon, Idaho, and California), commercial landings in metric tonnes of most salmon species peaked prior to 1920, and from then until the late 1980s and early 1990s, there was a decline in chinook, coho, and pink salmon landings, no clear trend in sockeye salmon landings, and chum salmon landings declined until the late 1950s and then increased (Kope and Wainwright 1998; Fig. 1). Over the same period, commercial fisheries shifted from predominantly freshwater (terminal) to ocean (mixed-stock) fisheries, and much of the natural production in this region was replaced by hatchery production. In the 1990s, the predominant species by weight in the commercial landings in Washington, Oregon, and California (total of 149,007 mt from 1990 through 1999) were chinook (29%) and chum (27%) salmon, followed by sockeye (20%), pink (12%), and coho (12%) salmon (National Marine Fisheries Service (NMFS), Fisheries Statistics and Economics Division, Silver Spring, MD, USA, personal communication). There are no commercial salmon harvests in Idaho.

In Alaska, commercial salmon fisheries began in the 1880s and landings increased to a peak of 290,000 mt in 1936, then declined steadily through the 1950s to a level below 100,000 mt (Fig. 2). Conservation measures in the 1960s and favorable climate conditions in the late 1970s led to a sharp increasing trend that continued to the mid-1990s (Wertheimer 1997), with a peak in 1995 at 412,000 mt (ADFG, Commercial Fisheries, Juneau, USA, personal communication). In the 1990s, the predominant species by weight in the commercial landings in the Alaska region (total of 3,318,693 mt from 1990 through 1999) were pink (41%) and sockeye (38%) salmon, followed by chum (14%), coho (6%), and chinook (1%) salmon (NMFS, Fisheries Statistics and Economics Division, Silver Spring, MD, USA, personal communication).

Fig. 1. Time series of commercial catches in metric tonnes from the U.S. West Coast (Washington, Oregon, and California) for the period 1900–2001. The dotted line indicates the long-term mean. The 1900–1980 data are from Shepard et al. (1985) and the 1981–2001 data are from the Pacific States Marine Fisheries Commission PacFIN database.

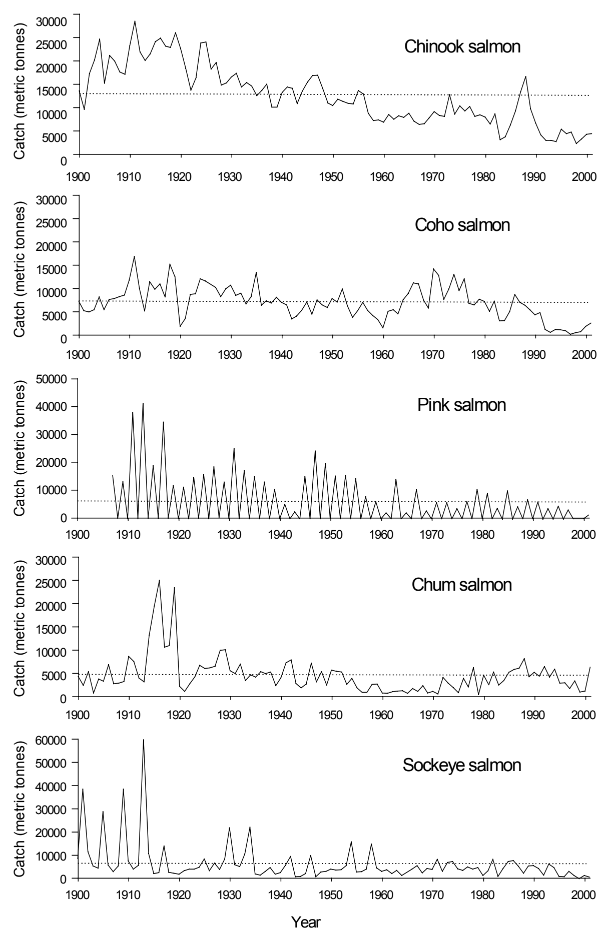
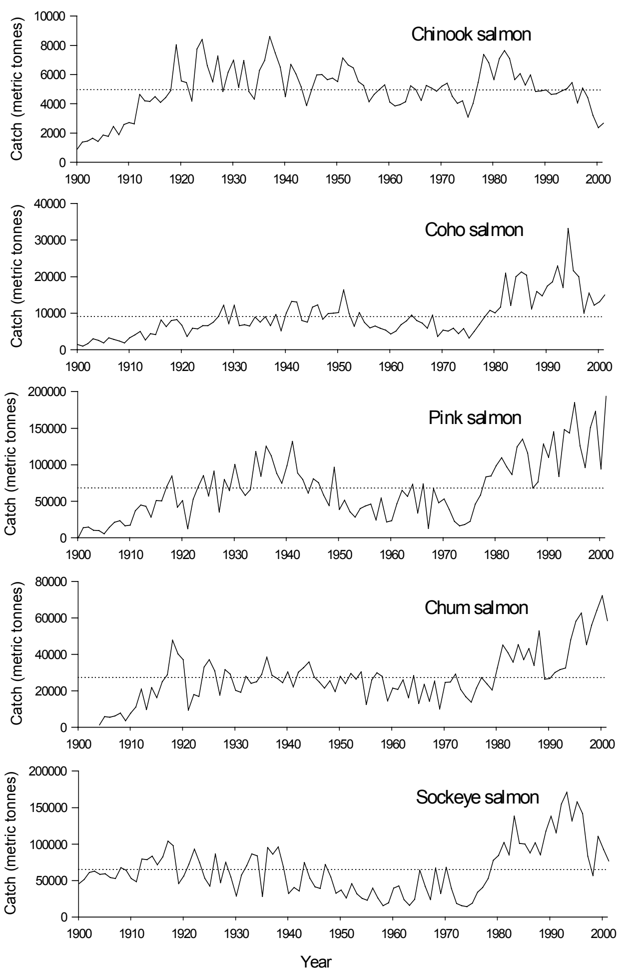


Fig. 2. Time series of Alaska commercial salmon catches in metric tonnes for the period 1900–2001. The dotted line indicates the long-term mean. Data sources: 1900–1949 (INPFC 1979; annual catches in numbers of fish were converted to rough estimates of catches in metric tonnes by using a constant annual average weight of individual fish of each species, calculated from data in Table 93, as follows: sockeye – 2.78 kg, chum – 3.4625 kg, pink (odd years) – 1.6975 kg, pink (even years) – 1.62375 kg, coho – 3.36875 kg, and chinook – 8.3175 kg); 1950–2000 (National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD); 2001 (preliminary data, Alaska Department of Fish and Game, Juneau, AK).



In both the Alaska and U.S. Pacific Northwest regions, precipitous early declines in commercial landings were largely due to overfishing and the lack of adequate (science-based) fishery management before the 1950s (Royce 1988). The two regions also seem to have inverse salmon production regimes linked to climate, and, in particular, to wind stress at the ocean's surface (e.g., Francis and Sibley 1991; Mantua et al. 1997; Hare et al. 1999).

STATUS OF NATURALLY SPAWNING STOCKS

California

Mills et al. (1997) reviewed the status of naturally reproducing California salmon and steelhead populations. Virtually all stocks had declined to record or near-record low levels from 1980 to 1995. Klamath and Sacramento basin fall-run chinook salmon were consistently below escapement goals. The Sacramento winter-run chinook salmon was listed under the ESA as threatened in 1990 and endangered in 1994. Spring run chinook salmon were extinct in the San Joaquin River basin, and there were few spawners in the Klamath, Smith, and Sacramento river basins. Many steelhead trout stocks in California were also close to extinction. Coastal cutthroat trout were depleted. Coho salmon spawners (historically near 1 million fish) had decreased to approximately 5,000 natural spawners per year. A few chum salmon, never a significant native species in California, still remain in the Sacramento River basin and Trinity River. Historically small runs of pink salmon in the Sacramento and Russian rivers are probably extinct.

Oregon and Washington

Kostow (1997) reviewed the status of salmon and steelhead trout in Oregon in the early 1990s. Sockeye and chum salmon populations were depressed or nearly extinct throughout their range in Oregon. The status of chinook and coho salmon populations varied by geographic region. Along the mid- to north coast chinook salmon populations were considered to be in good condition, while they were depressed on the south coast, and in the Columbia and Snake rivers. Many coastal populations of coho salmon were small and declining, and Columbia River Basin coho salmon populations were depressed to extinct. Most coastal and inland steelhead trout populations were stable or slightly declining. The run sizes of most species of salmon and steelhead trout in Washington State increased through the 1970s and 1980s, and then declined in the 1990s (Johnson, T.H., et al. 1997).

Idaho

Hassemer et al. (1997) reviewed the status of Idaho salmon and steelhead trout. All naturally reproducing anadromous sockeye salmon, chinook salmon (spring, summer, and fall), and steelhead trout populations in the Snake River, except Clearwater River drainage chinook salmon and Snake River steelhead trout, have been listed as endangered under the ESA.

Alaska

Wertheimer (1997) reviewed the status of Alaska salmon and steelhead trout. In the 1990s, there were predominantly no trends or increasing trends in spawning escapements for all species evaluated. The high productivity of stocks was attributed to pristine rearing and spawning habitats, effective salmon management policies within the state, the elimination of high seas driftnet fisheries, increased hatchery production, and favorable climate conditions.

TRENDS IN CLIMATE, ABUNDANCE, AND BODY SIZE

A growing body of scientific evidence supports hypotheses about the direct and indirect effects of climate change on the ocean production of salmon (e.g., see reviews by Pearcy 1997; Kruse 1998; Myers et al. 2000; Hare and Mantua 2001; Hollowed et al. 2001). Most U.S. research has focused on two natural climate phenomena that affect the abundance and growth of salmon, the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). ENSO is a short-term climate change event (lasting about 8–15 months) that occurs at irregular intervals (every 3–7 years) and alternates between two phases, the El Niño (warm) phase and the La Niña (cool) phase. Pearcy (1992) reviewed the effects of the 1957–58 and 1982–83 El Niño events on Oregon coho salmon, which included northward shifts in ocean distribution of juveniles, reductions in ocean growth and survival of juveniles, jacks (precociously mature), and adults, and low fecundity. Although the long-term effects of the 1997/1998 ENSO are not yet understood completely, there were no apparent effects on body size of returning adult coho salmon to the Columbia River as there was in 1983 (Pearcy 2002).

The PDO is a multi-decadal (20–30 year) ENSO-like pattern of North Pacific climate change (Mantua et al. 1997; Zhang et al. 1997; Hare and Mantua 2001). The PDO seems to drive an inverse relation between salmon abundance in the Alaska and U.S. West Coast regions, e.g., during a positive PDO phase, the abundance of Alaska salmon is high, and the abundance of U.S. West Coast salmon is low (Francis and Sibley 1991; Hare et al. 1999; Hollowed et al. 2001). An abrupt change between positive and negative PDO phases is called a *regime shift*. Conceptual models suggest that an enhanced Aleutian Low (atmospheric) pressure system may be the physical forcing mechanism that links the positive PDO phase to enhanced production of Alaska salmon (Hare 1996; Francis et al. 1998).

A dramatic increasing trend in the abundance of Alaska salmon that began in the late 1970s has been correlated with many factors. Among these are a change in Alaska salmon management policies, the elimination of Asian high-seas driftnet fisheries, enhancement by Alaska hatcheries, increase in Alaska salmon fishing effort, warm seawater temperatures in the North Pacific, increase in productivity (zooplankton biomass) in the eastern subarctic Pacific, and a regime shift to a positive PDO phase in 1976–77 (e.g., Rogers 1984; Rogers and Ruggerone 1993; Brodeur and Ware 1995; Farley and Murphy 1997; Mantua et al. 1997; Wertheimer 1997; Downton and Miller 1998; Eggers 1998). Hare and Mantua (2001) hypothesized that a sharp negative shift in the PDO climate index in fall of 1998 may signify a climate change event that will reverse salmon production trends established by the winter 1976–77 regime shift. Since the late 1990s Western Alaska has experienced extremely low chinook and chum salmon returns, but annual returns of salmon to south-central and southeast Alaska have sometimes reached historical highs (e.g., McNair and Geiger 2001; Eggers 2002). In general, salmon returns to many U.S. Pacific Northwest streams have improved since the late 1990s.

A multi-decadal decrease in body size and increase in age at return of many stocks of U.S. salmon is well established (Helle and Hoffman 1995; Bigler et al. 1996; Helle and Hoffman 1998). Several retrospective studies of scale patterns indicate that growth reductions in Alaska salmon occur during their second or third summers in the ocean, and are negatively correlated with high salmon abundance (Isakov et al. 2000; Sands et al. 2001; Ruggerone et al. 2003). Pearcy (1992) reviewed evidence of ocean carrying capacity (density-dependent mortality or growth) effects in salmon. Density-dependent effects on salmon growth in summer may be linked to increased ocean mortality during winter, particularly in years when winter seawater temperatures are warmer than average (Beamish and Manhken 2001; Ruggerone et al. 2003).

The variability in ocean life history patterns of salmon that we see today reflects their evolutionary response to changing climatic conditions (Pearcy 1992). Run reconstructions from salmon-derived nutrients in nursery lake sediment cores showed multi-centennial regimes of anomalously low or high salmon abundance in Alaska, which correspond to major paleoclimatic changes (Finney et al. 2002).

TRENDS IN HATCHERY PRODUCTION

Mahnken et al. (1998) reviewed annual production rates from the U.S. Pacific Northwest (Washington, Oregon, Idaho, and California) and Alaska hatcheries from 1950–1992. Since the early 1970s, production of pink, chum, and sockeye salmon has increased, and since 1985, the production of coho salmon, chinook salmon, and steelhead trout has decreased. In 1992, an estimated 1.8 billion juvenile

Pacific salmon were released into the North Pacific Ocean by U.S. hatcheries, enhancement and ocean ranching programs (Heard 1998).

Since 1993, the North Pacific Anadromous Fish Commission (NPAFC) has compiled and published statistics on the annual releases of juvenile hatchery salmon by country and area (North Pacific Anadromous Fish Commission 1997–2002, Table 1). Among U.S. states, Alaska is the major producer of hatchery salmon, accounting for an average of 77% of the annual (1993–1998) releases into the North Pacific Ocean. Alaskan hatcheries are the major producers of sockeye, pink, and chum salmon, and Washington hatcheries are the major producers of coho and chinook salmon. Hatchery production of sockeye and pink salmon is highest in the central Alaska region, and hatchery production of chum salmon is highest in the southeast Alaska region. There is no hatchery salmon production in the Arctic-Yukon-Kuskokwim region of Alaska. Hatchery production of steelhead trout is highest in Washington and Idaho.

OVERVIEW OF MAJOR FIELD RESEARCH PROGRAMS

Table 2 summarizes some of the major sampling programs conducted in coastal waters of the U.S. by geographic region and includes type of sampling undertaken for each program. The majority of field research has been conducted by National Marine Fisheries Service (NMFS) laboratories on the West Coast and Alaska, or by universities funded in part by NMFS. However, new sources of funding have recently become available through other programs such as GLOBEC (Global Ocean Ecosystem Dynamics) that have juvenile salmon as one of their primary target species (U.S. GLOBEC 1996). Our coverage of these studies has been grouped by geographic region (Fig. 3), progressing from south to north, for ease of presentation.

Table 1. Hatchery releases of juvenile salmon (millions of fish) by species in Alaska, Washington, Oregon, Idaho, and California in 1993–1998.

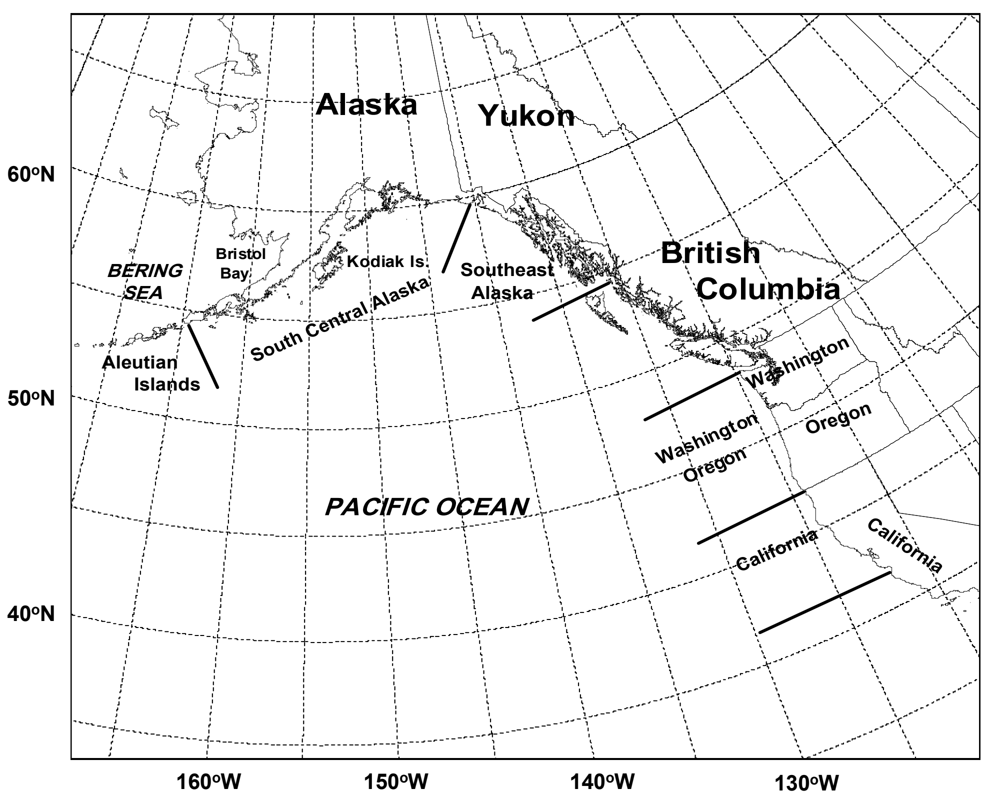
Region	Year	Sockeye	Pink	Chum	Coho	Chinook	Steelhead	All Species	Source*
Alaska	1993	54.8	819.2	468.7	14.6	11.4	0.1	1368.8	NPAFC 1997
	1994	69.7	790.3	407.2	17.8	9.8	-	1294.8	NPAFC 1998
	1995	81.4	920.5	473.2	17.4	6.7	<0.05	1499.3	NPAFC 1999
	1996	75.3	999.1	535.4	21.0	7.0	<0.05	1637.8	NPAFC 2000
	1997	76.5	773.3	478.1	23.2	7.6	0.0	1358.7	NPAFC 2001
	1998	70.6	872.5	479.2	21.6	8.7	<0.05	1452.6	NPAFC 2002
Washington	1993	3.5	-	59.8	63.2	139.1	11.0	276.6	NPAFC 1997
	1994	8.6	3.5	60.0	56.4	141.7	9.8	280.0	NPAFC 1998
	1995	16.3	0.1	59.1	57.0	159.3	10.6	302.4	NPAFC 1999
	1996	13.2	4.6	58.9	59.6	151.4	10.6	298.3	NPAFC 2000
	1997	27.4	-	46.8	52.6	151.1	11.3	289.2	NPAFC 2001
	1998	21.1	5.1	45.0	54.1	143.9	12.2	281.3	NPAFC 2002
Oregon	1993	-	-	-	4.5	17.3	2.4	24.2	NPAFC 1997
	1994	-	-	-	14.9	48.8	6.6	70.3	NPAFC 1998
	1995	-	-	-	13.1	60.6	6.8	80.5	NPAFC 1999
	1996	<0.05	-	-	13.5	56.2	6.5	76.2	NPAFC 2000
	1997	-	-	-	10.3	37.0	6.4	53.7	NPAFC 2001
	1998	0.1	-	-	8.2	27.0	6.1	41.3	NPAFC 2002
California	1993	-	-	-	0.8	49.0	5.6	55.4	NPAFC 1997
	1994	-	-	-	0.7	60.4	6.4	67.5	NPAFC 1998
	1995	-	-	-	0.9	60.2	5.8	66.9	NPAFC 1999
	1996	-	-	-	0.2	59.0	5.3	64.5	NPAFC 2000
	1997	-	-	-	0.8	50.3	3.7	54.8	NPAFC 2001
	1998	-	-	-	0.9	59.7	3.5	64.0	NPAFC 2002
Idaho	1993	-	-	-	-	4.9	7.8	12.7	NPAFC 1997
	1994	<0.05	-	-	-	7.8	8.1	15.9	NPAFC 1998
	1995	-	-	-	0.6	7.7	8.7	17.1	NPAFC 1999
	1996	-	-	-	-	1.8	8.9	10.7	NPAFC 2000
	1997	-	-	-	-	1.5	8.5	10.0	NPAFC 2001
	1998	<0.05	-	-	-	3.3	7.8	11.1	NPAFC 2002

*NPAFC: North Pacific Anadromous Fish Commission

Table 2. Studies on juvenile salmon conducted in U.S. coastal waters and types of sampling done in each study.

Geographic Region	Principal Investigators	Dates	Gear	Physical	Plankton	Food	Growth	Migration	Predators
California	McFarlane, Grimes, Norton	1996–2002	Surface trawl	x	x	x	x	x	
Washington/	Miller, Williams, Sims	1980	Purse seine	x		x			
Oregon	Pearcy, Fisher, Brodeur	1979–1985	Purse seine	x	x	x	x	x	x
	Dawley, Ledgerwood, Jensen	1979–1980	Purse seine						
	Casillas, Brodeur, Emmett, Peterson	1998–2002	Surface trawl	x	x	x	x	x	x
	Emmett, Bentley, Krutzikowsky	1998–2002	Midwater trawl	x					x
	Brodeur, Emmett	2000–2002	Surface trawl	x	x	x	x	x	x
	Pearcy, Fisher	1985	Gill net	x				x	
SE Alaska	Hartt, Dell	1964–1968	Purse seine			x	x	x	
	Jaenicke, Celewycz	1983–1984	Purse seine	x	x	x	x	x	
	Jaenicke, Brodeur	1982	Gill net	x		x		x	
	Orsi, Wertheimer, Heard	1997–2002	Surface trawl	x	x	x	x	x	x
	Helle, Carlson, Welch	1995–2002	Surface trawl	x	x	x	x	x	
N. Gulf of Alaska/	Hartt, Dell	1964–1968	Purse seine			x	x	x	
Aleutians	Helle, Carlson, Welch	1995–2002	Surface trawl						
	Haldorson, Boldt	1998–2001	Gill net	x	x	x	x		x
	Helle, Haldorson, Beauchamp, Myers	2001	Surface trawl	x	x	x	x	x	
Bering Sea	Hartt, Dell	1964–1968	Purse seine			x	x	x	
	Straty, Jaenicke	1966–1969	Purse seine	x	x	x	x	x	x
	Farley, Helle, Guthrie	1999–2002	Surface trawl	x	x	x	x	x	

Fig. 3. Locations of geographic areas covered in this review.



Central California

The Tiburon/Santa Cruz Laboratory of NMFS has conducted limited sampling for juvenile salmon in the Gulf of the Farallones, off San Francisco Bay, since 1997. Primary objectives of these studies are to monitor growth, physiological condition, and contaminant levels of juvenile chinook salmon and compare these factors to those measured on fish collected earlier in the year in San Francisco Bay (MacFarlane and Norton 2002). Near-surface pelagic trawls were used to collect the juvenile salmon, and concurrent depth-stratified and surface (neuston) plankton tows were taken to compare food availability with the juvenile salmon diets. Environmental data (water column temperature and salinity, transmissivity, fluorescence, and currents) are collected concurrently with the salmon, the associated fish community, and the plankton samples. Preliminary results from 1997 suggest that salmon grow rapidly in coastal waters at the expense of depleting energy reserves (MacFarlane and Norton 2002). This work is continuing, and the ultimate goal is to assess how interannual variations in ocean conditions, including such major perturbations as El Niño/Southern Oscillation (ENSO) events, affect the distribution and survival of juvenile chinook salmon.

Washington and Oregon

Substantial effort has been expended on studies of the marine distribution and ecology of juvenile salmonids, particularly coho and chinook salmon, in coastal waters off Washington and Oregon. One of the earliest and most extensive of these studies was conducted by Oregon State University (OSU) under the direction of W.G. Pearcy and colleagues and was funded by NMFS and OSU Sea Grant. Pilot cruises were conducted in June of 1979 and 1980 followed by multiple cruises run from May through September 1981 to 1985, for a total of 17 cruises. Fine-mesh purse seines were set at predetermined station locations to capture juvenile salmonids and associated biota. Sampling generally ranged from northern Washington (48°N) to Cape Blanco (43°N) in southern Oregon, although in July 1984 the sampling was extended to northern California and off Vancouver Island, British Columbia. In addition to purse seining, some environmental (temperature, salinity, and ambient light) and biological (chlorophyll and zooplankton) sampling was done at each station. Details of sampling, environmental conditions, and catch of juvenile salmon and other nekton can be found in Brodeur and Pearcy (1986) and Pearcy and Fisher (1990).

Scientific studies resulting from this sampling were numerous and details are available in Pearcy (1992). Analyses were done on salmonid growth based on scale analysis (Fisher and Pearcy 1988; Pearcy et al. 1990; Fisher and Pearcy 1995), and migration based on recoveries of coded-wire tags (CWT) and external tags (Pearcy and Fisher 1988; Fisher and Pearcy 1995). Feeding ecology (Peterson et al. 1982; Brodeur 1989; Brodeur and Pearcy 1990; Pearcy et al. 1990; Brodeur 1991) and food consumption (Brodeur and Pearcy 1987; Brodeur et al. 1992) were also studied. The diets of adult salmon and non-salmonid fishes were examined for potential predation on juvenile salmon (Brodeur et al. 1987). A strength of this research was that sampling occurred under highly contrasting oceanographic conditions from strong upwelling to anomalous ENSO conditions, and the effects of this variability on salmon survival and the ecosystem in general were examined (Pearcy et al. 1985; Brodeur and Pearcy 1992; Pearcy 1992).

Personnel at the NMFS Point Adams Field Station conducted similar fine-mesh purse seining studies in coastal waters during three cruises from May until early September 1980. Sampling was done on transects mainly in the vicinity of the Columbia River plume. Although all five species of salmon and both species of trout were captured, the majority of the catch was juvenile coho and chinook salmon (Miller et al. 1983). In addition to information on abundance and distribution, some studies were done on the size, direction of migration, and food habits of juvenile salmon, as well as the environmental conditions in which the salmon were caught (Miller et al. 1983; Emmett et al. 1986; Loch and Miller 1988).

A much smaller and shallower purse seine was used to sample juvenile salmon in the very nearshore regions in the mouth of the Columbia River and adjacent littoral areas north and south of the river mouth in 1979 and 1980. Sampling was conducted intermittently at several sites from May through September. Subyearling chinook salmon was the dominant juvenile salmonid caught, although many other forage fishes such as smelts (Osmeridae) and anchovy (*Engraulis mordax*), were also caught (Dawley et al. 1985a; Miller 1992).

An additional type of diel sampling was done by a pelagic small-mesh gillnet at one station off the central Oregon Coast in 1985 from the Hokkaido University training ship, *Oshoro maru*. Nets were set simultaneously at two depth levels over four different time periods. The salmonid catch consisted primarily of juvenile coho salmon (Pearcy and Fisher 1988) that were found to be residing in the upper two meters of the water column. Additional data were collected on physical conditions, zooplankton biomass, and size, growth, and feeding habits of the juvenile salmon.

Beginning in 1998, researchers from NMFS and OSU have been sampling the coastal waters from northern Washington to central Oregon using large surface trawls. Multiple cruises have been conducted each year, generally during May, June, and September. The purpose of these studies, funded by Bonneville Power Administration (BPA), is to assess the importance of the Columbia River Plume to juvenile salmon survival. Trawling is done from both chartered fishing boats and fishery research vessels, and is accompanied by extensive surface and depth-integrated plankton sampling, water column physics, and chlorophyll measurements, and some ancillary measurements including currents, light transmission, and acoustics.

One of the goals of this research is to compare how the pelagic community has changed since the previous intense sampling period in the early 1980s (Emmett and Brodeur 2000). Salmon catches during the 1990s were dominated by juvenile chinook salmon, as opposed to the earlier sampling when coho salmon were predominant. The non-salmonid community has also changed somewhat, with large increases in sardine (*Sardinops sagax*) and a corresponding drop in northern anchovy and squid (Emmett and Brodeur 2000). Process studies have examined the diel vertical distribution and catch rates (Emmett et al. unpublished manuscript) and feeding chronology and selectivity (Schabetsberger et al. 2003) of juvenile salmon in the Columbia River plume. Studies presently underway include analysis of juvenile salmon growth, bioenergetics, health, condition, genetic composition, habitat associations, and feeding habits relative to available prey.

A parallel study has been underway to sample potential predators along two transects near the mouth of the Columbia River (Emmett et al. 2001). Nighttime sampling, again using surface trawls, was conducted biweekly from April through August during 1998–2001. Substantial seasonal and interannual variation in the abundance of potential predators and juvenile salmon was observed reflecting major changes in oceanographic conditions during the study period (Emmett and Brodeur 2000; Emmett et al. 2001).

Sampling for juvenile salmon and associated biota off the U.S. West Coast has been a component of the GLOBEC Northeast Pacific Program. The main goal of this program is to assess how the physical environment affects the ecosystem, including juvenile salmon and their prey. A number of retrospective, monitoring, modeling, and field process studies have been funded to attain this goal. The study site chosen for this research extends from central Oregon to northern California and bridges a major oceanographic and zoogeographic break at Cape Blanco in southern Oregon. The first field sampling took place in June and August of 2000 and involved the coordinated activities of three vessels. Continuous underway sampling of physical, biological, and acoustical properties of the water column was carried out on one research vessel, while biological sampling (depth-stratified plankton tows, shipboard laboratory studies, bird and marine mammal observations) was done on a second research vessel. The salmon sampling was done by surface trawl using the gear previously described for BPA work on the third vessel, a chartered fishing boat, in close proximity to the other sampling. Both mesoscale grid and fine-scale opportunistic trawling were conducted. Catches of juvenile salmon were relatively low in 2000 compared to BPA collections further north at about the same time, despite the presence of strong upwelling and high zooplankton biomass. Analyses of salmon and other nekton distributions in relation to biophysical parameters are presently being conducted, along with analyses of juvenile salmon growth, condition, genetic stock composition, diseases, and trophic interactions with predators and prey (Brodeur et al. 2003). A second major field season was completed during the summer of 2002.

Puget Sound

There has never been a comprehensive NMFS field research program on juvenile salmonids in the marine waters of Puget Sound and the Strait of Juan de Fuca. Investigations from the early 1960s to present by the University of Washington, School of Aquatic and Fishery Sciences (SAFS; formerly the School of Fisheries, the College of Fisheries, and its research branch, the Fisheries Research Institute) form the only comprehensive major field research program in this region. The results, reports, and publications from these studies are summarized in the SAFS annual or biennial report series, *Research in Fisheries* (Fisheries Research Institute 1960–1996). An online database of reports and publications at the SAFS Publications internet website can be used to access information on historical and ongoing studies of juvenile salmon in Puget Sound and adjoining estuaries (http://www.fish.washington.edu/Publications/).

Many field investigations by federal, state, county, city, and tribal agencies, private consulting firms, non-profit organizations, and other universities, particularly with respect to the effects of human activities on juvenile salmonids and their habitats, have also contributed to our knowledge of the early marine life history and ecology of juvenile salmonids in Puget Sound. The results of SAFS and other studies were synthesized and reviewed by Iwamoto and Salo (1977), Simenstad et al. (1982), and Weitkamp (2001). These reviews include some previously unpublished data with respect to early marine survival, timing and size at entry, species residence times, habitat utilization, food habits, growth, and predation. Status reviews of U.S. West Coast salmon, steelhead and cutthroat trout by NMFS also provide a useful synthesis of information from Puget Sound field investigations, particularly on migratory timing and size at entry of fry and smolts (Weitkamp et al. 1995; Busby et al. 1996; Hard et al. 1996; Gustafson et al. 1997; Johnson, O.W., et al. 1997, Myers et al. 1998; Johnson et al. 1999).

The combined results of field investigations conducted since the 1950s show that Puget Sound is a very important early marine habitat for anadromous juvenile salmonids. The investigations were conducted with a variety of gear, including beach seines, trap nets, tow nets, purse seines, and trawls, and also included some tagging and marking studies to determine movement and migration patterns. Five species of Pacific salmon occur naturally in Puget Sound and the Strait of Juan de Fuca, although coho, chinook, and chum salmon are more prevalent than pink and sockeye salmon. Juvenile chinook and chum salmon apparently make more extensive use of estuarine and nearshore habitats in Puget Sound than juveniles of other salmon species. Steelhead and cutthroat trout also occur naturally in Puget Sound. Some salmon and trout populations rear to adults in Puget Sound, never migrating to the Pacific Ocean. Salmon and steelhead trout populations in Puget Sound have been continuously enhanced with artificially propagated fish since the early 1900s; however, we are not aware of comprehensive investigations of hatchery and wild juvenile salmonid interactions in Puget Sound. Historically, Puget Sound salmon have had higher marine survival rates than coastal salmon populations. Water pollution and shoreline development, among other factors, have contributed to the decline of Puget Sound salmonid populations, some of which are listed as threatened or endangered under the U.S. ESA or are candidates for listing. Recent field investigations in Puget Sound have primarily involved assessment of the effects of pollution and shoreline development or habitat restoration on juvenile salmonids.

Coastal Waters off Southeast Alaska

Small mesh experimental gillnetting similar to that described earlier for research off Oregon, was conducted off Southeast Alaska by the research vessel *Oshoro maru* in July 1982 as part of a cooperative U.S./Japan survey (Jaenicke et al. 1984). Information was gathered on the species composition, size, depth and direction of travel, and food habits of all (mostly coho) juvenile salmon caught.

During the summers of 1983 and 1984, juvenile salmon were the primary focus of a study to examine the nearshore ecosystem off Southeast Alaska and northern British Columbia (1984 only) using fine-mesh purse seines. Sampling was done with a seine, mainly during the daytime. About half of the sampling was done in protected bays and passages in inside waters of Southeast Alaska (Jaenicke and Celewycz 1994). Purse-seine sampling in outside waters was augmented by temperature measurements and surface (neuston) and oblique plankton tows down to 50 m. Catch rates and size of salmonids are presented in Jaenicke and Celewycz (1994), and their feeding habits relative to plankton availability were examined by Landingham et al. (1998).

During October 1995, scientists from the newly formed Ocean Carrying Capacity (OCC) program at the NMFS Auke Bay Laboratory worked jointly with biologists from the Canadian Department of Fisheries and Oceans Biological Station in Nanaimo, British Columbia on a survey along the coastal waters of Southeast Alaska. The objective of the survey was to compare the effectiveness of two gear types (Bernard-Sigmund Beam trawls and mid-water rope trawl) at catching juvenile salmon at sea. Paired trawling between two vessels along the coastal waters of Southeast Alaska indicated that the mid-water rope trawl was more efficient at catching juvenile salmon in the ocean. Incidental catch of juvenile salmon in coastal waters of Southeast Alaska by the mid-water rope trawl indicated large numbers of juvenile pink, chum, and coho salmon still present in this region during October. Sampling for juvenile salmon by the OCC group continued off Southeast Alaska in 1996 (Carlson et al. 1996) and 1998 (Carlson et al. 1998).

The early marine life history of juvenile Pacific salmon has been studied since 1997 as part of the Southeast Alaska Coastal Monitoring (SECM) project of the NMFS Auke Bay Laboratory. Although the majority of this sampling took place in inshore waters (Orsi et al. 2000), stations were sampled along a transect off Icy Point, just north of Cross Sound, and off Cape Edward just to the south. Cruises are conducted on a monthly basis from May to October of each year. The sampling platform was the NOAA ship *John N. Cobb,* and hauls were made using a Nordic 264 trawl. Also collected were physical data (continuous thermosalinograph and CTD at each station) and zooplankton (vertical 0–20 m NORPAC, oblique bongo). Catch rates for salmon (mainly pink and chum salmon) were highest inshore and most juveniles were caught within 25 km of shore (Murphy et al. 1999). Sablefish, herring, and capelin were the dominant non-salmonid species caught. Additional work is underway to examine seasonal habitat use by salmonids during migration using CWT and thermal marks, diet and lipid analysis, and determination of potential predators (Orsi et al. 2001a).

Inside Waters of Southeast Alaska

A comprehensive synthesis of research on marine ecology of juvenile salmon in southeast Alaska was presented by Heard et al. (2001). An ongoing program to monitor habitat use by juvenile salmon in southeast Alaska was described by Orsi et al. (2001a). The reader is referred to these detailed reviews for a historical summary as well as a description of the ongoing research on juvenile salmon in southeast Alaska.

Southeast Alaska has many large islands along the coast that provide a maze of bays and channels between the islands and the mainland (Fig. 3). Many rivers and streams flow from the islands and mainland into the bays and provide ideal spawning and rearing areas for all species of Pacific salmon and other anadromous species (e.g. cutthroat trout and Dolly Varden char (*Salvelinus malma*)). Research on the early marine life history of juvenile salmon concentrated on developing methods to capture these small fish in the marine waters.

Studies on juvenile salmon were started in the mid-1950s in southeast Alaska by the U.S. Fish and Wildlife Service (USFWS), Bureau of Commercial Fisheries (BCF; predecessor of NMFS), and the Fisheries Research Institute (FRI) of the University of Washington, and were primarily focussed on methods for capturing juvenile salmonids. Large pile-driven and floating traps, both with leads to shore, were the primary method used to capture adult salmon in the 1950s in southeast Alaska (Dumont and Sundstrom 1961; Scudder 1970). These traps also caught juvenile salmon, and starting in the mid-1950s, investigators attempted to relate numbers of juvenile pink salmon in traps to adult returns one year later (Mattson and Sears 1963). These studies were terminated after 1958, as traps would no longer be used as a commercial sampling gear after the state of Alaska assumed control of salmon management in 1960 from the federal government.

A small floating trap was developed in 1957 for capturing juvenile salmon by J.W. Martin of FRI (Martin 1958). Also in 1957, beach seines, gill nets, paired towed hoop nets, a floating trap, and an Isaacs-Kidd midwater trawl were tested and evaluated, but these methods generally had only minor success in capturing juvenile salmon (Mattson and Sears 1963). In 1958 a Lampara seine was tested in bays and open water channels by BCF and this proved to be the most successful method to date for capturing juvenile salmon (Sears 1958).

In 1962–65, Martin, then with BCF, successfully captured large numbers of juvenile pink and chum salmon using a round haul seine in bays and channels throughout Southeast Alaska and in large numbers in lower Chatham Strait as late as 10 September during 1963 (Martin 1964; 1966). The pink salmon ranged in size from 135–200 mm and the chum salmon from 135–165 mm (Martin 1964). Martin also tried to capture juvenile salmon using baited floating longlines but was not successful. Bailey et al. (1975) used dip nets from boats and floating traps anchored nearshore to capture pink and chum salmon juveniles for a study on food habits in the mid-1960s.

Beach seines were later used to capture juvenile salmon in northern Southeast Alaska by Orsi and Landingham (1985) and Celewycz et al. (1994). Beach seines and dip nets were used by Mortensen and Wertheimer (1988) to capture juvenile salmon in Auke Bay. Juvenile salmon were captured nearshore with beach seines and offshore with a small surface trawl in Auke Bay in 1986–89 (Mortensen et al. 2000). Jaenicke et al. (1985) used paired beach seines opened in opposite directions to study the migrations of juvenile salmon in Southeast Alaska channels in the early 1980s. In 1983 and 1984, Jaenicke and Celewycz (1994) used both drum and table purse seines to capture juvenile salmon and associated species throughout the passages of Southeast Alaska as described previously for the outside waters. Orsi et al. (1987) and Orsi (1987) evaluated trolling with small lures and herring bait for capturing juvenile chinook and coho salmon in 1985. Finally, in the most recent sampling, a Nordic trawl fished at the surface has become the gear of choice for sampling juvenile salmon in the channels as part of the SECM project described previously (Orsi et al. 1997; Murphy et al. 1999).

Pink and chum salmon fry and sockeye, coho, and chinook salmon smolts migrate out of the rivers and streams into the marine waters as early as late February and generally are gone from freshwater by early June. Pink and chum salmon migrate along the shores and feed in the littoral areas. Sockeye, coho, and chinook salmon smolts move away from the shore into open water sooner than smaller pink and chum salmon fry. In June and July all species of salmon are moving away from shore into the channels and in August and September most juvenile salmon have entered the Gulf of Alaska (GOA) where they move northward and westward along the continental shelf. Some Alaska and more southerly stocks of juvenile chinook salmon may stay in the inside waters of Southeast Alaska through December (Orsi and Jaenicke 1996).

Coastal North Pacific Ocean to Aleutian Islands

Some of the earliest directed sampling for juvenile salmon was undertaken by the Fisheries Research Institute (FRI) of the University of Washington, under contract to NMFS. The sampling began in 1964 and continued until 1968 using fine-mesh purse seines towed as a semicircle for a half hour and then pursed as in normal operations (Hartt 1980; Hartt and Dell 1986). Sampling mainly occurred from July through October from the coastal waters off Southeast Alaska to Attu Island in the Aleutian Islands. Juvenile salmon were found along the coastal waters from southern Southeast Alaska to as far west as Unimak Pass. The dominant species of juvenile salmon caught within this region consisted of sockeye, chum, and pink salmon. During the summer (July–August), these juvenile salmon were generally found along the continental shelf from nearshore to the 200-m contour. Coho and chinook salmon were also caught but were farther offshore (beyond the 200-m contour) by late summer.

One of the objectives of the FRI study was to determine the migration routes and speed of juvenile salmon during their early ocean migration. An extensive tagging operation was undertaken and with the exception of steelhead trout that migrated directly to the open ocean, most juvenile salmon migrated northward in a counter-clockwise direction around the coastal waters of the Gulf of Alaska after entering the ocean (Hartt and Dell 1986). Other information gathered during the surveys included growth (derived from change in length) and food habits data (Andrews 1970; Hartt and Dell 1986).

During 1993, the North Pacific Anadromous Fish Commission (NPAFC) and the North Pacific Marine Science Organization (PICES) agreed to jointly examine the effects of changes in productivity in the North Pacific Ocean on salmon populations. Primary issues of concern were (1) identifying factors that affect current changes in ocean productivity and how these changes affect salmonid carrying capacity, and (2) identifying factors that affect changes in growth, age and size at maturity, marine distribution, and survival of Pacific salmon. In response to this call for marine research on Pacific salmon the NMFS Auke Bay Laboratory in Juneau, Alaska, initiated the OCC research program. Since its inception, the OCC program has conducted three broad-scale field studies (1996, 1997, and 1998) of the coastal waters of the North Pacific Ocean (Carlson et al. 1996, 1997, 1998). The surveys occurred during July and August and generally sampled between southern Southeast Alaska and Attu Island using a mid-water rope trawl rigged to fish in near surface waters. In addition to trawl sampling, some environmental (CTD) and biological (zooplankton) sampling was done at selected stations and genetic samples of salmon were taken for stock identification analysis.

Examination of juvenile salmon catch data indicated that species dominance, distribution, and migration characteristics were similar to those found for juvenile salmon in the earlier studies by FRI. Analyses of salmon otoliths for hatchery thermal marks indicated a large proportion (roughly 20–30%) of the juvenile pink and chum salmon captured during the OCC surveys were from hatcheries located in Southeast Alaska and Prince William Sound (Farley and Munk 1997; Carlson et al. 2000). Further analyses of the growth and condition factor of hatchery juvenile pink and chum salmon were presented in Farley and Carlson (2000), and Auburn and Ignell (2000) examined their feeding habits with respect to habitat.

Fine mesh gill nets and surface trawls were the main sampling gear used to collect juvenile salmon as part of a multidisciplinary GLOBEC effort by University of Alaska scientists under the direction of Dr. L. Haldorson. The sampling has taken place several times a year (summer and fall) since 1998 along the Seward hydrographic line extending from Seward Alaska across the shelf out into the Gulf of Alaska. An extended suite of physical, biological, and acoustical measurements was taken concurrently with the salmon from a different vessel. Juvenile pink and chum salmon were the main fishes caught inshore, whereas coho salmon and other non-salmonids (saury, rockfishes, capelin) were common offshore (Boldt 2001). Dietary and caloric analyses have been conducted on the pink salmon (Boldt and Haldorson in press) and bioenergetic consumption estimates were estimated (Boldt and Haldorson 2002).

The large-scale field studies conducted by the OCC program and FRI have provided a basis for future planned juvenile salmon studies in the coastal waters of the Gulf of Alaska. These surveys have shown that juvenile salmon have a strong preference for coastal waters (continental shelf near the Alaska Coastal Current) along the Gulf of Alaska over offshore waters (near the Alaska Stream). The strong preference by juvenile salmon for the coastal waters is not fully understood but may be related to survival. In order to further understand this relationship, the OCC program conducted cruises in July and August of 2001 in the coastal Gulf of Alaska from Yakutat to the western end of Kodiak Island as part of the Gulf of Alaska GLOBEC program. The main objective of the program is to quantify the relationships between biological and physical oceanographic processes that affect the distribution of juvenile salmon in the coastal Gulf of Alaska. The OCC program conducted a pilot survey of the area west of Prince William Sound within the project survey area during August 2000 and in July 2001 and 2002. Details of sampling and catch of juvenile salmon and other associated nekton for the first year can be found in Farley et al. (2000a).

Prince William Sound

Sampling for juvenile salmon started in Prince William Sound by the Bureau of Commercial Fisheries in July and August 1957 (Kirkwood 1962). These studies lasted only one year, and various types of gear were evaluated such as beach seines, gill-nets, a small shrimp trawl towed at the surface, and a cone-shaped net towed between two skiffs. Juvenile pink and chum salmon were caught with all gear types except for gill-nets, which were generally fouled with adult salmon. Pink salmon close to shore were around 100 mm while those captured 0.15 km or more offshore were greater than 130 mm. The largest pink salmon caught were around 155 mm, which Kirkwood (1962) concluded is the size at which they leave the sound. Researchers caught chum salmon in southwestern Prince William Sound in September and late October 1961 using a midwater trawl. These fish, which were deposited in a museum collection, were later measured and the circuli on their scales counted to determine growth (Helle 1979). The fish ranged from 140–200 mm and were noteworthy considering they were captured in Prince William Sound so late in the year.

Much of the earlier research focused on pink salmon, the dominant salmon in terms of production in Prince William Sound, and its utilization of nearshore habitats in the first few weeks after entering marine waters (Cooney et al. 1981). A major oil spill in the region in 1989 led to substantial research on the biological effects of the oil on juvenile salmon and other biota in the sound (Sturdevant et al. 1996; Wertheimer and Celewycz 1996; Willette 1996; Paul and Willette 1997). A subsequent program entitled Sound Ecosystem Assessment (SEA) examined the role of juvenile pink salmon and other forage fishes in Prince William Sound (Willette et al. 1999; Cooney et al. 2001; Willette et al. 2001). Results from the SEA program have been summarized in a special journal volume dedicated to this program (Cooney et al. 2001).

Eastern Bering Sea

Similar to that reported above, the Fisheries Research Institute conducted substantial sampling inside Bristol Bay and along the north side of the Alaska Peninsula using purse seines (Hartt and Dell 1986). Most of the catch was sockeye salmon collected between 18 and 54 km offshore. Dell (1963) reported that juvenile sockeye (age .0) ate euphausiids and fish in Bristol Bay.

The Auke Bay Laboratory initiated research on the distribution and migration of juvenile sockeye salmon in Bristol Bay during 1966–67 and 1969–72 (Straty 1974; Carlson 1976; Straty and Jaenicke 1980; Straty 1981). The surveys were conducted using purse seines and occurred within inner Bristol Bay east of Port Heiden and along the coastal waters of the Alaska Peninsula west of Port Heiden (outer Bristol Bay). In addition to purse seining, some environmental (sea temperature and salinity) and biological (zooplankton) sampling took place at selected stations throughout the survey area. A summary of this research on the horizontal and vertical distribution, migration routes and rates, food habits, and predators of juvenile sockeye in Bristol Bay is given by Straty (1974).

These studies found that juvenile sockeye salmon from all river systems entering Bristol Bay follow the same southwesterly seaward migration route along the coastal waters of the eastern Bering Sea. The migration rate of juvenile sockeye salmon through inner Bristol Bay is rapid, whereas their migration rate slows once they enter outer Bristol Bay, presumably due to increased food resources encountered in this region. The seasonal timing of this migration can be influenced by annual differences in environmental conditions, such as time of ice breakup on lakes and anomalously cold sea temperatures. For example, during 1971, a year characterized by anomalously cold sea temperatures from spring through fall, juvenile sockeye salmon were virtually absent in outer Bristol Bay in early July; whereas, they were abundant in this area during 1967, a year with warm spring through fall sea temperatures.

The Auke Bay Laboratory's OCC program renewed research on juvenile salmon in Bristol Bay and the eastern Bering Sea during 1999–2002. The primary goal of the annual assessment is to establish and verify the linkages between adult sockeye salmon survival and annual variations in biological characteristics of juvenile sockeye salmon. The surveys have generally occurred within the coastal and middle domains of the eastern Bering Sea between 166°W and 158°W during July, August, and September. The primary sampling gear was a mid-water rope trawl rigged to fish in near surface waters. Biological (zooplankton) and physical (CTD) oceanographic data were also collected at every trawl station. Initial results of the surveys have indicated that environmental conditions found during early marine residence of juvenile sockeye salmon affect their distribution, migration, and growth. Further details of sampling, catch of juvenile salmon and other associated nekton, as well as environmental conditions can be found in Farley et al. (1999, 2000a, 2001a, c).

In September/October 2002, Auke Bay Laboratory's OCC program initiated juvenile salmon surveys with a chartered fishing vessel *Sea Storm* in the eastern Bering Sea north from Bristol Bay off the Kuskokwim and Yukon rivers and into Norton Sound. These surveys extended north and west of St. Lawrence Island to the Russian boundary. Another chartered OCC vessel, *Northwest Explorer*, and the Japanese research vessel *Kaiyo maru* fished stations throughout the Bering Sea west to the Russian boundary and south to the Aleutian Islands. A Russian research vessel *TINRO* fished stations throughout the Russian portion of the Bering Sea. These three vessels met in the area north of Attu Island in the Aleutian Islands and did side-by-side tows to calibrate their trawl gears. All of these surveys were coordinated within a multiyear NPAFC sponsored research plan: Bering-Aleutian Salmon International Survey (BASIS).

MOVEMENTS IN COASTAL WATERS

Overview

A large body of U.S. research has focused on the timing of movements, distribution, migration routes, and migration rates of juvenile salmonids in coastal marine waters. Much of the field work has emphasized coastal surveys of juvenile salmon distribution, recoveries of tagged and marked fish to determine stock-specific migration routes and migration rates, and investigations of the relations between juvenile salmon movements and various biotic (species, stock, age, size, growth, physiology, and behavior) and abiotic factors (natal stream locations, shoreline and basin bathymetry, current patterns, and oceanographic conditions).

In warm U.S. regions (California), juvenile salmon tend to move quickly through river estuaries in late winter, spring, and early summer to cool, upwelling coastal waters (e.g., MacFarlane and Norton 2002). In cold U.S. regions (Alaska) timing of movements to coastal waters tends to correspond to spring ice breakup in rivers and maximal water temperatures along migration corridors (e.g., Straty 1974; Orsi et al. 2000). In general, juvenile sockeye, pink, and chum salmon from U.S. West Coast populations (Oregon and Washington) move to coastal waters earlier in the spring or summer and at a larger size than those from Alaskan populations (e.g., Hartt and Dell 1986; see reviews by Heard 1991; Salo 1991; Burgner 1992). In contrast, coho salmon do not show a clear geographic pattern for timing of outmigration, which generally peaks in May when smolts measure 90–115 mm fork length (Weitkamp et al. 1995). Some juvenile pink, chum, coho, and chinook salmon entering inside marine waters (e.g., Puget Sound, Washington, and Southeast Alaska) in the spring or summer do not move to coastal waters until late fall, winter, or the following spring, and *resident* fish may remain in inside waters or river estuaries for most or all of their marine life (e.g., Jensen 1956a, b; Haw et al. 1967; Wright 1968; Williams et al. 1975; Myers 1980; Hartt and Dell 1986; Orsi et al. 1987).

Timing of movements of juvenile chinook salmon to U.S. coastal waters varies by life history type. *Ocean-type* chinook salmon migrate to coastal waters in their first year, some immediately after hatching in the spring (30–45 mm), but most as fry (60–150 days post hatching) or fingerlings, which migrate in late summer and fall (Myers et al. 1998). Small, slow growing ocean-type chinook salmon may rear for extended periods in estuarine, inside, or coastal waters near their natal streams before moving to more distant coastal waters (Reimers 1973; Myers 1980; Kjelson et al. 1982; Nicholas and Hankin 1988; Fisher and Pearcy 1990; but see MacFarlane and Norton 2002). In contrast, large *stream-type* chinook salmon smolts typically move quickly from freshwater to coastal areas in the winter, spring, or early summer of their second year; however, juveniles from some Southeast Alaska stocks reside in the inside waters of Southeast Alaska (Orsi and Jaenicke 1996). Some stream-type chinook salmon from Southeast Alaska (Stikine, King Salmon, and Chilkat rivers) may remain in the coastal waters of Southeast Alaska throughout their lives (ADFG 1997). Most *spring* chinook salmon stocks (adults return to rivers in the spring) have a stream-type life history as juveniles, and most *fall* chinook salmon stocks have an ocean-type life history as juveniles.

Steelhead and cutthroat trout juveniles exhibit diverse life histories with respect to timing of movements to U.S. coastal waters. Timing of juvenile steelhead trout movement to coastal waters, however, appears to be size-specific (at approximately 160 mm; see review by Burgner et al. 1992). Juvenile *half-pounder* steelhead trout of the Rogue, Klamath, Mad, and Eel rivers of southern Oregon and northern California return to fresh water after only 2–4 months in the ocean, overwinter in fresh water, and then move to coastal waters again in the following spring (e.g., Snyder 1925; Kesner and Barnhart 1972; Everest 1973). Coastal cutthroat trout, which range from northern California to Southeast Alaska, typically migrate as juveniles to marine waters in late winter or spring, feed in marine waters in summer, and then overwinter in freshwater (Loch and Miller 1988; Pearcy et al. 1990; Johnson et al. 1999). Some precociously maturing steelhead and cutthroat trout, and male chinook salmon spawn in freshwater before their first ocean migration (Shapovalov and Taft 1954).

At first entry to U.S. coastal marine waters, small juvenile salmon typically are distributed in shallow, littoral habitats (beach areas between low and high tide). As summer progresses and fish grow, juvenile salmon move to neritic habitats (shallow, pelagic areas near shore or over a continental shelf, from low-tide mark down to a depth of about 200 m). The extent of distribution of juvenile salmon over and beyond the continental shelf varies regionally, annually, seasonally, and by species and stock (e.g., Straty and Jaenicke 1980; Straty 1981; Miller et al. 1983; Hartt and Dell 1986; Pearcy and Fisher 1990; Jaenicke and Celewycz 1994; Carlson et al. 2000). Vertical distribution of juvenile salmon in neritic habitats is influenced by biotic (species, age, size, forage location) and abiotic (water temperature, salinity, season, light, turbidity, currents, tides, and bottom topography) factors (e.g., Orsi and Wertheimer 1995). Seasonal habitat use is linked to species, stock, water temperature, and zooplankton distribution (e.g., Orsi et al. 2000).

Broad-scale field investigations and tagging experiments along the North American coastline from

Cape Flattery, Washington, to Attu Island at the end of the Aleutian Island chain have established that in summer (July–August) juvenile salmon are concentrated in neritic waters throughout the Gulf of Alaska westward to Unimak Pass (Hartt and Dell 1986; Carlson et al. 1996, 1997, 1998, 2000). Concentrations of juvenile salmon over the continental shelf, the net direction of their movements, and their rapid migration rates are associated with the relatively narrow, intense, counter-clockwise Alaska Coastal Current (e.g., Hartt and Dell 1986). The extent of offshore distribution of juvenile salmon varies regionally, and roughly corresponds to the width of the continental shelf. For example, one major distribution ranges from nearshore to 93 km offshore off southern Southeast Alaska (shelf width approximately 75 km) and another from nearshore to as far as 185 km offshore in the region west of Prince William Sound (shelf width nearly 200 km) (Carlson et al. 2000). Similar broad-scale juvenile salmon surveys were initiated throughout U.S. waters in the Bering Sea in 2002 by the OCC program.

Tagging and transplanting studies have shown that the direction of movement and migratory routes of salmon in coastal waters are inherited or specific to regional stock groups (e.g., Brannon and Hershberger 1984; Hartt and Dell 1986; Brannon and Setter 1987; Nicholas and Hankin 1988; Myers et al. 1996). Genetic and regional diversity in migration timing, distribution, migration routes, and migration rates of juvenile salmon in coastal waters are keys to their short-term and evolutionary success. In the following sections, we review some of the major results of U.S. field research (arranged by geographical location) on the timing of movements, distribution, migration routes, and migration rates of juvenile salmon in coastal waters.

California

Chinook salmon is the most abundant species in the California region, and is considered to have an ocean-type life history throughout this region. Even though some juveniles migrate as yearlings, the majority of California chinook salmon migrate to coastal waters as sub-yearling fry in winter and spring, a tendency linked to poor river conditions in summer (low flows and high temperatures; Myers et al. 1998). Juvenile chinook salmon leaving California's Central Valley spend about 40 days transiting the San Francisco Estuary (mean migration rate of 1.7 km•day^{-1}), primarily in May and June, and enter the ocean in the Gulf of the Farallones (MacFarlane and Norton 2002). Migration rates, calculated from coded-wire tagged juveniles caught in the estuary, were 1.7–13.5 km•day^{-1} (5–38 days estuarine residence times) (Table 3). An earlier study showed that juvenile chinook salmon fry migrated through the upstream delta at 10–18 km•day^{-1}, and tended to remain in the estuary for almost 2 months (Kjelson et al. 1982).

Less is known about coastal movements of other species of juvenile salmon in the California region. Tag recovery data show that at least some California coho salmon juveniles move northward along the coast and are distributed from the outer coast of Vancouver Island, B.C., to Yakutat, Alaska, in July and August (e.g., Hartt 1980; Hartt and Dell 1986; Myers et al. 1996).

Pearcy et al. (1990) hypothesized that California steelhead trout populations may reside for their entire marine life in the strong upwelling coastal zone off northern California and southern Oregon. However, coastal recoveries of California steelhead trout tagged as immatures and adults in offshore waters of the northeastern Pacific (between 45–54°N latitude, west to approximately 160°W longitude) show that at least some California steelhead trout move well offshore during juvenile or subsequent life history stages (Myers et al. 1996).

Oregon, Washington, and Columbia River

The two most abundant juvenile salmon species in research catches along the Oregon and Washington coasts are coho (highest catches inshore of 37.2 km) and chinook (usually inshore of 27.9 km) salmon (Pearcy and Fisher 1990; Brodeur et al. 2003). All Puget Sound and coastal Oregon and Washington chinook salmon populations are considered to be ocean-type fish, and the Columbia River has both ocean- and stream-type chinook salmon. Juvenile chum, pink, and sockeye salmon, as well as steelhead and cutthroat trout also occur in this region.

In Oregon, coho salmon smolts move rapidly through river estuaries to coastal waters in May (e.g., Myers 1980). Upon ocean entry, juvenile Oregon and Washington coho salmon tend to be advected southward of their natal streams by coastal surface currents in May and June, and by August and September most have reversed their direction and are caught northward of their natal streams (Pearcy and Fisher 1988). The maximum migration rates against southward-flowing surface currents for marked juvenile hatchery coho salmon caught within 10 days after release were over 18.8 km•day^{-1}, equivalent to 1.7 body lengths (BL) per second (s), which is within the range of optimal cruising speeds (1–3 BL•s^{-1}) for small (< 20 cm) pelagic fishes (Pearcy and Fisher 1988). Many Oregon and Washington coho salmon may reside in the coastal waters off Oregon, Washington, and northern California during their first summer, and many remain there perhaps during their entire ocean life (Miller et al. 1983; Pearcy and Fisher 1987, 1988). More recent genetic and CWT

Table. 3. Summary of information on migration rates of juvenile salmon in U.S. waters.

Region	Species	Location	Migration Rates (km•day^{-1})	Source
California	chinook	estuary	1.7–13.5	MacFarlane and Norton (2002)
	chinook	river delta	10.0–18.0	Kjelson et al. (1982)
Oregon-Washington	chinook	outer coast	4.1	Fisher and Pearcy (1995)
	coho	outer coast	18.8	Pearcy and Fisher (1988)
	chum	Puget Sound	4.0–14.0	Bax (1982, 1983a)
Southeast Alaska	chinook	inside waters	0.3	Orsi and Jaenicke (1996)
	chinook	inside waters	1.3	Orsi et al. (2000)
	chinook	outer coast	6.9	Orsi and Jaenicke (1996)
	chinook	outer coast	19.1	Orsi et al. (1987)
	coho	inside waters	3.2	Orsi et al. (2000)
	coho	outer coast	28.6	Orsi et al. (2000)
	pink	inside waters	5.5–22.2	Martin (1966)
	pink	outer coast	10.0–45.0	Sakagawa (1972)
	chum	inside waters	1.6–2.4	Orsi et al. (2000)
	sockeye	outer coast	6.5–26.7	Hartt and Dell (1986)
	all species	outer coast	18.5	Royce et al. (1968)
Bering Sea-Aleutian Islands	sockeye	outer coast	3.9–6.7	Hartt and Dell (1986)

recovery data suggest that some Puget Sound and southern British Columbia coho salmon also reside along the Oregon and Washington coasts during their first summer at sea (Teel et al. in press). In years of unfavorable ocean conditions (e.g., El Niño years), however, Oregon and Washington juvenile coho salmon may make more extensive northward movements. Recovery of juvenile coho salmon show that at least some Washington, Columbia River, and Oregon coho salmon juveniles migrate far to the north and west, and are distributed from Southeast Alaska to waters well offshore of Kodiak Island, Alaska (e.g., Hartt 1980; Hartt and Dell 1986; Myers et al. 1996, 2001a). In Southeast Alaska, coded-wire tagged U.S. West Coast (Columbia River Basin and Washington) coho salmon juveniles have been recovered only in outer coast waters, to which they migrate at much faster rates (28.6 km•day^{-1}) than Southeast Alaska stocks distributed in inside waters (Orsi et al. 2000).

The direction of coastal migrations of juvenile chinook salmon from the Washington-Oregon regions is stock-specific (Nicholas and Hankin 1988). Northward-migrating stocks move to waters off Washington, British Columbia, or Alaska. These include Oregon coastal stocks from streams north of Cape Blanco, Puget Sound stocks, Columbia River Basin stocks from the Willamette and Klickitat rivers (spring runs), lower Yakima River (fall runs), and summer- and fall-runs from the mainstem Columbia River and its tributaries. Southward-migrating stocks include Oregon coastal stocks from natal streams located south of Cape Blanco and Columbia River Basin fall-run chinook salmon from the Snake and Deschutes rivers. These stocks apparently remain in waters off Oregon and California. Migration rates of stream-type juvenile chinook salmon off the coast of Oregon and Washington (primarily Columbia River stocks) average 4.1 km•day^{-1} (Fisher and Pearcy 1995). Chinook salmon juveniles from Oregon and Washington have been caught in both inside and outside waters off Southeast Alaska (Orsi and Jaenicke 1996).

The median date of ocean entry of stream-type chinook salmon from the Columbia River is generally prior to May 15 (Miller et al. 1983; Dawley et al. 1985b). Their abundance off Oregon and Washington is much higher in May–June than in August–September, indicating rapid northward movement (Fisher and Pearcy 1995). Columbia River Basin stream-type stocks have been caught off Southeast Alaska only in outside waters, and they migrate at much faster rates (19.1 km•day^{-1}) than the stream-type stocks of Southeast Alaska, which are distributed almost exclusively in inside waters (Orsi et al. 1987). Early (June) recoveries off Southeast Alaska of stream-type chinook salmon juveniles from the Columbia River Basin, indicate a critical, early marine-entry period for these stocks (Orsi et al. 2000). By August, tag recoveries show that the coastal distribution of juveniles from these stocks extends to the northern Gulf of Alaska (Hartt and Dell 1986).

Subyearling (ocean-type) chinook salmon juveniles from the Columbia River Basin are more abundant in Oregon and Washington neritic habitats in late summer than in spring and early summer (Fisher and Pearcy 1995; Brodeur et al. 2003). In spring and early summer, ocean-type chinook salmon juveniles are distributed primarily in littoral habitats in estuarine or coastal waters, and offshore movement appears to be strongly size dependent at a minimum size of approximately 130 mm FL (Miller et al 1983; Fisher and Pearcy 1995).

There is comparatively little information on migration patterns of sockeye, chum, and pink salmon juveniles in this region. Much of the U.S. marine research on Oregon and Washington chum salmon juveniles was conducted in Puget Sound. Upon release, hatchery chum salmon juveniles in inside waters (Hood Canal, Puget Sound, Washington) actively disperse, many across open waters to the opposite shore, and then passively migrate close to shore at rates that vary annually and seasonally (4–14 km•day^{-1}) depending on residual surface-water outflows (Bax 1982, 1983a).

Juvenile coastal cutthroat and steelhead trout are distributed in coastal waters off the Oregon and Washington coasts in early summer (Pearcy et al. 1990; Brodeur et al. 2003). Juvenile cutthroat trout tend to be distributed closer to shore (9.4–27.8 km) than steelhead trout, but occasionally catches of both species are highest well offshore (37.2–46.3 km) in May and June. Juvenile cutthroat trout have been caught as far as 66 km offshore, and some make substantial alongshore movements (> 250 km). By September, most cutthroat and steelhead trout juveniles have left coastal waters, with cutthroat trout returning to freshwater and most steelhead trout migrating far offshore (see sections below on Timing and Speed of Movement and High Seas Work). Juvenile coastal cutthroat trout in Puget Sound, Washington, are usually distributed in shallow (< 3 m deep) water, and may not migrate more than 50 km from their natal stream (see review by Johnston 1982). Columbia River steelhead trout juveniles migrate northward and farther offshore than most chinook and coho salmon juveniles from the Oregon-Washington region (Miller et al. 1983).

Southeast Alaska

Southeast Alaska juvenile salmon rear in the inside waters of the Alexander Archipelago before moving to outside coastal waters, where they migrate northward along the coast or move progressively offshore (e.g., Hartt and Dell 1986; Jaenicke and Celewycz 1994; see review by Heard et al. 2001). Pink salmon are usually the most abundant species of juvenile salmon in research catches in this region, and are often associated with juvenile chum salmon and to a lesser extent with sockeye salmon, which are also abundant. The distributions of Southeast Alaska juvenile pink, chum, and sockeye salmon in research catches tend to be highly aggregated or patchy compared to those of coho and chinook salmon (e.g., Hartt and Dell 1986; Jaenicke and Celewycz 1994).

In March to early June, most Southeast Alaska salmon juveniles are distributed in littoral, inside-water habitats (e.g., Jaenicke et al. 1985; Mortensen and Wertheimer 1988). Peak abundance of juvenile salmon in neritic habitats is in June and July (Orsi et al. 2000). Migrations of juvenile salmon in coastal waters off Southeast Alaska peak in August (Hartt and Dell 1986; Jaenicke and Celewycz 1994). A substantial portion of coho salmon juveniles in Southeast Alaska, however, resides in inside waters until late fall (Orsi et al. 1987; Jaenicke and Celewycz 1994).

Along the outer coast, juvenile salmon are generally concentrated within 25 km of shore, and catches of all species decline with distance offshore, although pink and chum salmon tend to be distributed closer to shore than other species (e.g., Hartt and Dell 1986; Murphy et al. 1999; Orsi et al. 2000). Hartt and Dell (1986) described outer coastal migrations of juvenile salmon as a "band" of fish, only 37 km wide in areas off Southeast Alaska, where the continental shelf is narrow, and extending farther offshore in the northern Gulf of Alaska, where the shelf is wider. In August, Jaenicke and Celewycz (1994) caught juvenile salmon as far as 74 km offshore of Southeast Alaska. In some years, the majority of juvenile salmon in research catches off Southeast Alaska in August are in waters beyond the continental shelf, indicating that annual and seasonal changes in the Alaska coastal current affect offshore distribution (Jaenicke and Celewycz 1994).

Peak movements of Southeast Alaska pink salmon juveniles to coastal waters are in late July–early August, and variation in migration rates (5.5–22.2 km•day^{-1}) corresponds to seasonal and annual changes in net transport by wind-induced surface currents (Martin 1966). Royce et al. (1968) estimated that all species of juvenile salmon and steelhead trout migrate from Dixon Entrance to Yakutat Bay at a rate of about 18.5 km•day^{-1}. Sakagawa (1972) estimated that northward migration rates of pink salmon ranged from 10 km•d^{-1} to 45 km•day^{-1} (average of 17 km•day^{-1}), that about 17 km•day^{-1} of the speed is due to the coastal current, and that the maximum speed of active migration of pink salmon is 28 km•day^{-1}.

Sakagawa (1972) developed a conceptual model of juvenile salmon movements from Cape Flattery, Washington to Yakutat Bay, Alaska. In inside waters, movements of juvenile salmon are influenced by tidal currents, but net movement is outward to the open coast (outside waters). Along the open coast, net movement of most juvenile salmon is northward (in outside waters). Some juvenile salmon move back and forth between inside and outside waters while migrating northward, and a few move southward. Some juvenile salmon do not migrate and remain in inside waters. Catch per unit effort (with purse seines fishing to a depth of approximately 40 m) is not significantly affected by time of day. Most of the northerly migration of juvenile salmon in the Gulf of Alaska can be accounted for by ocean current transport. High variability in nearshore currents and possibly in fish behavior, however, tends to obscure any direct relationship between migration speed and calculated transport in the Alaska Coastal Current.

Research by the NMFS (OCC and SECM) indicates that distribution and migration rates of juvenile salmon in neritic habitats off Alaska in May–October differ by species, stock, and habitat (Farley and Munk 1997; Carlson et al. 2000; Orsi et al. 2000). This research has provided some of the first stock-specific information on migration rates of Alaska hatchery salmon juveniles (determined by recoveries of thermally otolith-marked or coded-wire tagged fish). Recoveries of thermally otolith-marked hatchery fish show that by late July–early August, southeast Alaska hatchery pink salmon juveniles are distributed northwest along the continental shelf from Cape Spencer (off Southeast Alaska) to an area offshore from the Kenai Peninsula in the northern Gulf of Alaska (Farley and Munk 1997; Carlson et al. 2000). In inside waters off Southeast Alaska, juvenile chum salmon released from a hatchery near Juneau were caught primarily in June and migrated at 1.9 (June) and 1.6 (July) km•day^{-1}. Juvenile chum salmon released from another hatchery were caught primarily in July and migrated at speeds of 2.2 (June) and 2.4 (July) km•day^{-1} (Orsi et al. 2000). Along the outer coast in late July, hatchery chum salmon juveniles were distributed northwest along the continental shelf from Cape Spencer, Southeast Alaska, to Cape Hinchinbrook, Prince William Sound (Farley and Munk 1997; Carlson et al. 2000).

Southeast Alaska chinook and coho salmon juveniles are caught in inside waters from June through October; however, chinook salmon catches are highest in July in inshore habitats (average migration rate of 1.3 km•day^{-1}), and coho salmon catches are highest in June in strait habitats (average migration rate of 3.2 km•day^{-1}; Orsi et al. 2000). An earlier study within the Alexander Archipelago and adjacent coastal waters showed that stream-type Southeast Alaska chinook salmon juveniles in inside waters migrate slower (0.3 km•day^{-1}) than British Columbia (0.9 km•day^{-1}) and Columbia River Basin (6.9 km•day^{-1}) stocks in outside waters (Orsi and Jaenicke 1996).

Experimental fishing with commercial trolling gear at five depth intervals (0.1–7.5 m, 7.6–15.0 m, 15.1–22.5 m, 22.6–30.0 m, and 30.1–37.5 m) indicates that in September juvenile coho salmon are caught in significantly shallower water than juvenile chinook salmon, and that juvenile chinook salmon move progressively deeper with increasing age and size (Orsi and Wertheimer 1995). Surface gillnet catches of juvenile coho salmon are highest at night (Jaenicke et al. 1984).

Prince William Sound, Cook Inlet, and Kodiak Island

In April and May, juvenile pink and chum salmon enter Prince William Sound, Alaska, and are distributed in shallow, littoral habitats (Cooney et al. 1978; Wertheimer and Celewycz 1996; Boldt 2001). When they reach approximately 60–70 mm in length, they move to neritic habitats, and by mid-August, most have moved through southwest passages of Prince William Sound to outside waters, where they migrate westward over the continental shelf of the Gulf of Alaska (Cooney et al. 2001).

Recoveries of thermally otolith-marked hatchery fish show that by late July–early August most Prince William Sound hatchery pink salmon juveniles are distributed in the vicinity of the Kenai Peninsula and Kodiak Island (Gore Point and Marmot Island), and that their range extends to areas off the south side of the Alaska Peninsula and as far west as Mitrofania Island (750 km west of Prince William Sound) (Farley and Munk 1997; Carlson et al. 2000). Pink salmon juveniles released from one hatchery in southwest Prince William Sound may move directly to the Gulf of Alaska in July without rearing in inside waters (Boldt 2001). By October a few Prince William Sound hatchery pink salmon juveniles remain over the continental shelf along the Seward hydrographic transect (approximately 90 km from Prince William Sound) (Boldt 2001).

Emigration of pink and chum salmon juveniles into Cook Inlet begins in late May and peaks in June, substantially later than these species enter Prince William Sound (Moulton 1997). Pink salmon is the most abundant species in June, and chum salmon is the most abundant species in July. Pink, sockeye, coho, and chinook salmon apparently move quickly through northern Cook Inlet, while chum salmon juveniles remain in this region longer than the other species. Pink and chum salmon juveniles form small aggregations (10–50 fish) near the surface, with peak fish densities usually in the 15–20-m depth range. The highest and most diverse catches of all species of juvenile salmon are associated with tide rip lines or floating debris (Moulton 1997).

Large numbers of juvenile salmon (estimated annual average production > 0.5 billion; peak production > 1.5 billion) enter coastal waters throughout the Kodiak region (Stern 1976). In late May and late

June, both pink and chum salmon juveniles are abundant in littoral habitats around Kodiak Island (Tyler 1972; Gosho 1977; Harris and Hartt 1977). By late July, as they increase in size, most Kodiak Island pink and chum salmon juveniles move to neritic habitats. Outmigration of juvenile pink salmon from Kodiak Island bays, fjords, and channels peaks in August, although large diurnal schools of juvenile pink and chum salmon can be found in intertidal areas of Kodiak Island bays in August (Harris and Hartt 1977). Post-smolt sockeye salmon remain in Chignik Lagoon (south side of Alaska Peninsula) for about four to six weeks, initially occupying littoral areas and gradually moving into deeper waters of the lagoon before moving to outside waters (Dahlberg 1968; Phinney 1968). In August, local stocks of juvenile salmonids of all species are caught in outside waters of the Kodiak region (Hartt and Dell 1986). In addition, by late August the distribution of juvenile sockeye salmon from as far south as the Fraser River and juvenile coho and chinook salmon and steelhead trout from as far south as Oregon extends to the highly productive marine waters of Cook Inlet-Kodiak region (Hartt and Dell 1986; Myers et al. 1996). The small size of juvenile salmon distributed in the Shelikof Strait, between Kodiak Island and the mainland, in August indicates that they may be primarily from local (Kodiak region) stocks (Farley et al. 2000b, 2001b).

Eastern Bering Sea and Aleutian Islands

Most of the U.S. data on ocean distribution and migration patterns of juvenile salmon in the eastern Bering Sea pertain to Bristol Bay sockeye salmon (Straty 1974; Straty and Jaenicke 1980; Straty 1981; Hartt and Dell 1986; Isakson et al. 1986; Farley et al. 1999, 2000a, 2001a, c). Bristol Bay sockeye salmon usually spend one or two years in freshwater before migrating to the ocean. Sockeye smolts (approximately 4–15 g in weight) leave freshwater rearing areas from mid May to mid July, and throughout much of the summer are found in concentrated schools around the perimeter of Bristol Bay and along the north side of the Alaska Peninsula (most within 93–111 km of shore) (Hartt and Dell 1986). In general, movements from the river mouths are nearshore along the southeast and south side of Bristol Bay to Port Moller, and offshore beyond Port Moller. Tidal currents appear to influence direction of movement, which is variable (Hartt and Dell 1986). In cold years juvenile sockeye salmon distribution may be restricted to warmer waters around the margins of Bristol Bay, and in warm years they may be distributed in cooler waters farther offshore (Straty 1974; Farley et al. 1999, 2000a, 2001c). The southwestward extent of distribution of juvenile sockeye salmon along the north side of the Alaska Peninsula in July, August, and September may also be influenced by sea temperatures, with fish moving farther southward (west of Port Moller) earlier in the year in warm years (Straty and Jaenicke 1980; Hartt and Dell 1986; Isakson et al. 1986; Farley et al. 1999, 2000a, 2001a, c). Migration routes through Bristol Bay seem to correspond to areas with the steepest salinity gradients (Straty 1974; Straty and Jaenicke 1980; Straty 1981). Juvenile sockeye salmon in the eastern Bering Sea appear to be most abundant at or near the surface (upper 1 m at night, 2-m depth during the day) (Straty 1974). Juvenile sockeye salmon are scarce or absent in summer (June–October) sampling in neritic waters off the Aleutian Islands (Hartt and Dell 1986; Carlson et al. 1996, 1997).

Gradual offshore movements of juvenile sockeye salmon, northwestward into the Bering Sea, may continue through fall before salmon move southward through the Aleutian Passes into the North Pacific Ocean. The northwestward extent of their distribution in the Bering Sea in fall and winter is not known. Overwintering of juveniles in the Bering Sea may occur in some years (see section on High Seas Work). The area where juvenile sockeye salmon are distributed at the end of their first winter at sea may be different for individual stocks or populations, and also may be the approximate location from which maturing salmon begin their return migrations (Rogers 1988).

Historical marking studies indicate some separation in major stocks of juvenile Bristol Bay sockeye salmon as far seaward as Port Moller (Straty 1974). Differences that may contribute to stock-specific distributions include time of outmigration, travel distance from the lake system of origin, age, and size. Annual variation in time of outmigration is caused by time of ice breakup, water temperature, and wind action in nursery lakes. All Bristol Bay stocks have early, middle, and late components, but the average time of outmigration is earliest for Ugashik and Egegik smolts, intermediate for Kvichak (later in cold than in warm years), and latest for Naknek and Wood River smolts (Rogers 1988). There is substantial annual variation in the abundance and distribution of sockeye salmon juveniles in Bristol Bay on a given date, which is caused by annual variation in smolt production and migration timing in each lake system and spring weather conditions that affect the beginning of outmigration (Rogers 1977). Due to differences in migration timing, the distributions of Egegik and Ugashik smolts may not overlap those of the majority of smolts from the Naknek and Kvichak rivers, and may be well separated from the Nushagak stocks, and the separation may be greater in cold years because of greater delay in Kvichak and Wood River migrations (Rogers 1988). For example, Ugashik or Egegik River smolts may arrive at the outer boundary of Bristol Bay in mid-July, whereas Wood

River fish may not arrive there until the end of September (Bax 1985; Rogers 1988). By the time they reach Port Moller, juvenile Bristol Bay sockeye salmon stocks may be well mixed. Estimated travel rates of Bristol Bay sockeye salmon juveniles in the Bering Sea between Port Moller and Unimak Island (3.9–6.7 km•d^{-1}) are slower than those of British Columbia stocks migrating northward in the Alaska coastal current (Skeena River, 6.5–13.9 km•day^{-1}; Fraser River, 14.1–26.7 km•day^{-1}) (Hartt and Dell 1986).

Hartt and Dell (1986) provided limited information on the distribution of other species of juvenile salmon in the eastern Bering Sea and Aleutian Islands. Most of their sampling was done from late June to September 1964–1968 in neritic waters beyond the 46-m depth contour with fine-mesh purse seines. Pink and chum salmon fry (less than 1 g in weight) begin to migrate into Bristol Bay in July (Rogers 1977). Hartt and Dell (1986) had only small catches of juvenile chum salmon in July in the eastern Bering Sea and Aleutians, which were probably composed of local stocks, but these catches increased in August in the eastern Bering Sea. Pink salmon juveniles were scarce or absent in their catches throughout the region. Juvenile coho salmon were caught in small numbers in the eastern Bering Sea in July, August, and September. Juvenile chinook salmon first appeared in eastern Bering Sea catches in late June, and were caught in all subsequent time periods. The westernmost catches of juvenile chinook salmon were south of the central Aleutian Islands during July. Data were inadequate for inferring migration patterns between juvenile and age .1 stages, but indicated that western Alaskan stocks migrated farther offshore than stocks from other North American production areas to the south. The mixing of juvenile age .0 and immature age .1 chinook salmon in both coastal and offshore waters appeared to be unique compared to other Pacific salmon species. There was no evidence of overlap in distribution of Bering Sea and Gulf of Alaska salmon stocks at the juvenile stage for any species. The direction of local movements of all species of salmon juveniles in the eastern Bering Sea was variable, apparently influenced by strong tidal currents and rich feeding conditions.

OCC research in the eastern Bering Sea in July–September indicates substantial annual, seasonal, and spatial variation in distribution by species and life history stage of juvenile chum, pink, coho, and chinook salmon (Farley et al. 1999, 2000a, 2001a, c). No juvenile salmon were caught during extensive research trawl surveys in neritic waters off the Aleutian Islands in July–August 1996–1997 (Carlson et al. 1996, 1997). There are no reported catches of steelhead trout juveniles in the eastern Bering Sea and Aleutian Islands, although steelhead trout populations occur in some streams along the north side of the Alaska Peninsula and eastern Aleutian Islands (see review by Burgner et al. 1992).

Martin et al. (1986) provides limited information on coastal movements of Yukon River salmon juveniles. The peak outmigration of juvenile chinook salmon probably occurs during or shortly after ice breakup (early June), and there is no indication that juvenile chinook salmon utilize littoral coastal habitats in the vicinity of the Yukon Delta. Outmigration of juvenile pink salmon peaks before mid June, and pink salmon juveniles seem to move rapidly through delta habitats to the delta front. Outmigration of juvenile chum salmon peaks in late June, and juvenile chum salmon use coastal habitats and the delta front from June through early August. Similar movements of juvenile chum salmon were observed in Norton and Kotzebue Sound (see review by Martin et al. 1986). Millions of juvenile chum salmon are dispersed by high river discharges through numerous distributary channels into coastal habitats surrounding the Yukon delta, and catches in coastal habitats decreased as water temperatures increased to 18–21°C in mid-July.

In conclusion, while general information on broad-scale and regional movements of juvenile salmon in U.S. coastal waters is probably sufficient, better field data on local, stock-specific movements is needed in almost every region. At the limits of coastal distribution of juvenile salmon (California, Arctic–Yukon–Kuskokwim, and Aleutian Islands), even the most basic information on juvenile salmon movements is sometimes lacking. Coastal field investigations in many U.S. regions have been conducted only in summer in neritic habitats, and for most species and stocks we do not have any information on October–December movements. There are few or no data on movements of small juvenile salmon in littoral habitats along most of the outer U.S. coastline. Better field data on spatial and temporal variation in stock-specific movements, distribution, migration routes and rates of juvenile salmon in marine habitats both on and off the continental shelf will improve our ability to estimate their abundance, growth, and survival.

DIET IN COASTAL WATERS

A substantial body of literature has accumulated on the food habits and feeding ecology of juvenile salmon in coastal waters of the U.S. Some of this information is presented by species and life history stage in Brodeur (1990). These studies fall into the broad categories of food habits, feeding selectivity, daily ration, and food consumption.

Food items preyed upon by juvenile salmon have been studied extensively in protected areas such as southeast Alaska and Puget Sound. Pink and chum salmon near shore feed on a variety of plankton but copepods predominate (Bailey et al. 1975). Simenstad et al. (1982) summarized diet information for juvenile salmonids from 16 different estuaries in Puget Sound and along the Washington coast. Juvenile pink salmon were found to feed almost exclusively on small zooplankton such as copepods and larvaceans. Juvenile chum showed a more diverse diet including epibenthic crustaceans (harpacticoid copepods) and emergent insects, and switch to planktonic prey at a larger size. Chum salmon juveniles appear to be more selective than pink salmon. Juvenile sockeye salmon consume larger zooplankton prey (e.g., euphausiids, juvenile shrimp, and decapod larvae). Because of their larger size when entering the estuaries, juvenile coho salmon forage on large planktonic or small nektonic prey, including decapod larvae, fish larvae and juveniles, and euphausiids. Finally, juvenile chinook salmon utilize a broad trophic spectrum due to their extended residence in some estuaries, ranging from insects, amphipods, mysids, and nekton. Other estuarine and nearshore food studies have documented the diversity of prey items in relation to fish size, seasonality, and various habitats (e.g. Landingham and Mothershead 1988; Murphy et al. 1988; Landingham et al. 1998).

The general diets of juvenile salmon in coastal waters are fairly well known for all salmon species in much of the continental shelf region off the West Coast and Alaska (Table 4). Quantitative studies of the diet of juvenile salmonids in the California Current include those by MacFarlane and Norton (2002) and Norton (2002) for California; Peterson et al. (1982), Emmett et al. (1986), Loch and Miller (1988), Brodeur and Pearcy (1990), Pearcy et al. (1990), Brodeur (1991), and Schabetsberger et al. (2003) for Oregon and Washington; Andrews (1970), Jaenicke et al. (1984), Landingham et al. (1998), and Auburn and Ignell (2000) for outside waters of Southeast Alaska; Cooney et al. (1981), Sturdevant et al. (1996), Moulton (1997), and Boldt (2001) for northern Gulf of Alaska; and Straty (1974) and Carlson (1976) for the Bering Sea. These studies find some intraspecific differences in type and size of prey consumed by salmonids with coho and chinook salmon and cutthroat trout tending to be mainly piscivorous, steelhead trout more omnivorous, and pink, chum, and sockeye salmon more planktivorous. Diet composition changes markedly with ontogeny toward larger and more evasive prey in later juvenile stages (Brodeur 1991; Boldt 2001). Interannual and seasonal differences in prey availability can lead to major differences in diet composition (Brodeur and Pearcy 1990).

Quantitative examination of feeding selectivity, daily ration, and food consumption are less common and even completely lacking for juvenile salmon in several systems. Feeding selectivity has been addressed by Brodeur et al. (1987), Brodeur (1989), and Schabetsberger et al. (in press) for juvenile coho and chinook salmon off Oregon and Washington. They found that juvenile salmon are highly opportunistic in their feeding habits but tend to select the most visually obvious prey within the suitable size range. These studies, along with that of Landingham et al. (1998), show that salmon often consume prey associated strictly with the near surface neustonic layer.

Brodeur and Pearcy (1987) estimated the daily ration of juvenile coho salmon based on the diel trajectory of stomach content weight and laboratory-derived evacuation rates. Coho salmon juveniles were found to feed primarily at the crepuscular (dawn and dusk) periods. These ration estimates (2.4–3.7% body weight per day depending on the temperature) were found to yield similar estimates of food consumption compared with estimates made using bioenergetic models (Brodeur et al. 1992). Studies of the overall consumption of juvenile salmon utilizing bioenergetic models suggest very little if any food limitation in coastal waters. Brodeur et al. (1992) found that juvenile chinook and coho salmon have the potential to easily exhaust the available fish prey resources during anomalous low-productivity years (e.g. during the 1983 El Niño), but generally they consume substantially less than 1% of the total production during normal years. Based on bioenergetic consumption estimates, juvenile pink salmon in Prince William Sound, Alaska were also estimated to have consumed less than 1% of the total annual zooplankton production in the sound (Boldt and Haldorson 2002). However, their impact may be more severe (up to 8.2%) in a restricted geographic nearshore area where pink juveniles generally reside in the sound. Also, if standing stocks of zooplankton were assumed to be stable over a 10-day period, consumption of some key zooplankton groups such as large calanoid copepods and hyperiid amphipods ranged from 15–19% of the standing stock in Prince William Sound (Boldt and Haldorson 2002).

MARINE PREDATION

Predation is likely to be the major source of mortality for most juvenile salmon when they first enter the marine environment. Juvenile salmon may be preyed upon by a variety of predators in the estuarine and coastal environments, including adult salmon, other fishes, seabirds, and marine mammals (Fresh 1997). In some cases, introduced species such as striped bass (*Morone saxatilis*) in the Coos Bay Estuary in Oregon have been estimated to consume many juvenile and adult salmonids (Johnson et al. 1992). However, despite some extensive studies examining potential predation on juvenile salmon, there have been relatively few documented examples of large numbers of juveniles being consumed in marine

Table 4. Studies on juvenile salmon feeding habits conducted in U.S. coastal waters.

Geographic Region	Species	Month	Year	Number Examined	Main Prey	Source
California	chinook	May–Sept.	1995–1999	146	fishes, decapods, euphausiids, copepods	Norton (2002)
Washington/ Oregon	coho	June	1979	220	fishes, euphausiids, amphipods	Peterson et al. (1982)
	chinook			146	fishes, euphausiids, amphipods	
	chum			41	euphausiids, amphipods, decapods	
	chinook	May–Sept.	1980	174	fishes, decapods, amphipods	Emmett et al. (1986)
	coho			137	fishes, euphausiids, amphipods, pteropods	
	cutthroat	May–June	1980	17	fishes, mysids, decapods	Loch and Miller (1988)
	coho	June–Sept.	1984	217	fish, decapods, euphausiids, insects	Brodeur (1989)
	chinook			118	fish, decapods, euphausiids, copepods	
	cutthroat	May–Aug.	1981–1985	67	fish, decapods, euphausiids	Pearcy et al. (1990)
	steelhead			98	fish, decapods, euphausiids, amphipods	
	coho	May–Sept.	1980–1985	1652	fish, decapods, euphausiids, pteropods	Brodeur and Pearcy (1990)
	chinook			844	fish, decapods, euphausiids, amphipods	
	chum			109	euphausiids, fish, chaetognaths, copepods	
	sockeye			32	euphausiids, fish, amphipods, copepods	
	chinook	June	2000	249	amphipods, fish, decapods, euphausiids	Schabetsberger et al. (2003)
	coho			98	amphipods, fish, euphausiids	
SE Alaska	sockeye	NA	1967–1968	996	euphausiids, fish larvae, pteropods, copepods	Andrews (1970)
	coho	July	1982	45	fish, euphausiids, amphipods, decapods	Jaenicke et al. (1984)
	chum			17	euphausiids, amphipods, copepods	
	pink			14	euphausiids, amphipods, copepods	
	sockeye			5	euphausiids, amphipods, copepods	
	pink	July–Aug.	1983–1984	452	amphipods, fish, euphausiids, tunicates	Landingham et al. (1998)
	chum			210	tunicates, fish, amphipods	
	sockeye			279	fish, amphipods, euphausiids, copepods	
	coho			127	fish, decapods	
	pink	Oct. –Nov.	1995	227	pteropods, fish, hyperiids, euphausiids	Sturdevant et al. (1997)
	chum			120	larvaceans, euphausiids, hyperiids	
	coho			70	fish, euphausiids, hyperiids	
	sockeye			10	euphausiids, pteropods, gelatinous	
	pink	July	1996	130	euphausiids, hyperiids, calanoids, fish	Auburn and Ignell (2000)
	sockeye			120	euphausiids, calanoids, fish, hyperiids	
	chum			112	euphausiids, hyperiids, calanoids, fish	
	coho			147	fish, euphausiids	
N. Gulf of Alaska/ Aleutian Islands	pink	July–Aug.	1996	110	euphausiids, hyperiids, pteropods, fish	Auburn and Ignell (2000)
	sockeye			99	euphausiids, fish, decapods	
	chum			80	hyperiids, euphausiids, fish	
	coho			80	fish, euphausiids, decapods	
	pink	July–Oct.	1998	104	pteropods, hyperiids, larvaceans, copepods	Boldt (2001)
Bering Sea	sockeye	June–Sept.	1969–1970	>1200	fish, euphausiids, copepods, pteropods	Straty (1974)
	sockeye	June–Sept.	1966–1967	160	copepods, fish, decapod larvae	Carlson (1976)

waters (e.g., Buckley 1999). However, because of the high abundance of some potential predators, a relatively low incidence of predation over a long period of time can lead to a high cumulative mortality on some populations.

Pearcy (1992) reviewed what was known about predators on juvenile salmon along the U.S. West Coast. Few marine fish predators have been identified, but those that were identified as predators include salmonids (Fresh et al. 1981; Stuart and Buckman 1985; Brodeur et al. 1987; Pearcy et al. 1990) and non-salmonids such as rockfish (*Sebastes* spp.) and Pacific whiting (*Merluccius productus*) (Brodeur et al. 1987; Emmett et al. 2001). However, many of these studies were done in coastal waters, and much of the predation could be occurring in the very nearshore region and in river mouths, where predators may be attracted to large pulses of migrants, particularly in systems with hatcheries (Emmett 1997; Peterson and Brodeur 1997).

Documenting bird and marine mammal predation may be even more problematic because of the difficulties in collecting specimens for stomach analysis. Common murres *Uria aalge* have been shown to aggregate and actively feed during release periods of a hatchery near the mouth of Yaquina Bay (Bayer 1986). Salmonids were an important part of the diet of common murres collected in coastal waters offshore of several estuaries along the Oregon Coast (Mathews 1983). Based on the occurrence of PIT tags at a single colony on a man-made island in the lower Columbia River, Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*) were estimated to consume more than 50,000 juvenile salmon and steelhead trout (Collis et al. 2001). The annual consumption of juvenile salmon by terns alone has been estimated to be 8.1 million (1997) and 12.4 million (1998) fish, based upon bioenergetic modeling (Roby et al. 2003). Pinnipeds such as harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*) appear to be the major marine mammal predators on salmon in the Pacific Northwest (Everitt et al. 1981; Brown and Mate 1983; Zamon 2001; Laake et al. 2002), although much of the impact is on returning adult runs in estuaries.

In Alaskan waters, there have also been a number of studies on predation on juvenile salmon. Early observations of predators upon juvenile salmon in estuaries or nearshore ocean waters include Dolly Varden char (Lagler and Wright 1962), Pacific herring *Clupea harengus* (Thorsteinson 1962) and walleye pollock *Theragra chalcogramma* (Armstrong and Winslow 1968). Wing (1985) found juvenile salmon in troll-caught adult coho salmon in Southeast Alaska. Dolly Varden char, great sculpin, *Myoxocephalus polyacanthocephalus,* Pacific staghorn sculpin, *Leptocottus armatus* and buffalo sculpin, *Enophrys bison,* were all found to prey on juvenile salmon (Mortensen et al. 2000). As a component of a multiyear study analyzing salmon habitats in Southeast Alaska, Orsi et al. (2000) examined diets of 19 potential fish predators and found only four species consumed juvenile salmon. Only sablefish *Anoplopoma fimbria* and adult coho salmon were found to be important predators.

Probably one of the most concerted efforts to examine predation on juvenile salmon in U.S. waters has been accomplished as part of the SEA program in Prince William Sound (Willette et al. 2001). The target species in this study was juvenile pink salmon, a species that is released by the millions from hatcheries each year, in addition to the substantial wild production. Based on field estimates of predator abundance and diet, these authors were able to estimate the consumption of juvenile pink salmon by key predators. They found that Pacific herring and walleye pollock were the dominant piscivorous fish predators. Willette et al. estimated that nine fish and avian predator groups consumed approximately half of the annual production of pink salmon in the Sound. Finally, predation pressure appears to be less in the nearshore environment than offshore in the Sound. In one of the most quantitative estimates of predation impact by seabirds, Scheel and Hough (1997) estimated that seabirds foraging near a hatchery in Prince William Sound consumed between 1.1 and 2.4% of the hatchery production of pink salmon during their study period. Willette (2001) suggests that the seasonal availability of prey such as copepods in inshore regions influenced the offshore migration and subsequent consumption of juvenile salmon. Populations of marine birds and mammals are fairly high throughout much of Alaska, and a number of important salmon predators, including several seals, whales, eagles, gulls, and terns, have been identified (Straty 1974; Meachum and Clark 1979).

GROWTH AND MORTALITY PATTERNS IN ESTUARIES AND COASTAL OCEANS

Juvenile salmon generally exhibit little growth in most estuaries. For example, Reimers (1973) found that juvenile chinook salmon in the Sixes River Estuary in southern Oregon grew at a rate of 0.07 $mm \bullet day^{-1}$ in the summer which was attributed to food limitation. Growth rates of juvenile chinook salmon were estimated to be relatively low (0.18 $mm \bullet day^{-1}$) in the San Francisco Estuary but increased rapidly (0.6 $mm \bullet day^{-1}$) in the coastal ocean (MacFarlane and Norton 2002). Estimates of yearling chinook salmon growth rate in the Columbia River estuary and coastal ocean based on CWT recoveries were on the order of 1.05 mm•day^{-1} in length and 1% body weight•day^{-1} (Fisher and Pearcy 1995). Fisher and Pearcy (1988) observed substantial variability in marked and unmarked juvenile coho salmon growth rates over five years of sampling (range 0.36–2.20 mm•day^{-1} in length). They showed that coho salmon survival is positively correlated to early (March–June) upwelling, even in low upwelling years, but growth of smolts caught in coastal waters was not. Growth rates of coho salmon jacks returning after one summer at sea were related to the cumulative upwelling strength for the whole summer (March–September) and showed substantial differences between poor and moderate upwelling years. In juvenile coho salmon maturing after more than one summer at sea captured off Oregon and Washington from 1998 to 2000, growth rates ranged from 0.63 to 1.61 mm•day^{-1} in length, with the highest growth rates occurring in fish caught off southern Oregon (Brodeur et al. 2003). Overall, growth rates of CWT coho salmon during their first four months at sea were between 1.8 and 2.5% BW•day^{-1}, which may be close to their predicted physiological maximum rates, but they decreased to about 0.6% BW•day^{-1} by the second summer of life (Fisher and Pearcy, unpublished manuscript, available from J. Fisher, Oregon State University, Corvallis). Mathews and Buckley (1976) found growth rates of 1.7% BW•day^{-1} for Puget Sound coho salmon during their first summer at sea.

Juvenile salmon grow rapidly in the marine environment. Larger pink salmon move from the nearshore habitats to the middle of the bay (Mortensen and Wertheimer 1988). Mortensen et al. (2000) documented that greater early growth in juvenile pink salmon resulted in higher survival to adults. This higher survival resulted from less predation. Taylor et al. (1987) showed that the earliest emigrants from Auke Creek stayed longer in Auke Bay than did later emigrants from the stream. Murphy et al. (1999) sampled juvenile salmon with a rope trawl in May, June, July, August, and October in northern southeast Alaska. They found that the mean length of coho salmon increased more each month than the other species. Mean length of sockeye salmon showed the lowest rate of increase, and pink and chum salmon showed similar size increases and were intermediate in growth rate between coho and sockeye salmon.

In Prince William Sound, Willette et al. (2001) found that juvenile pink salmon that have higher sustained growth rates shortly after entering the marine environment tend to suffer lower predation rates. They also showed that the growth rates of hatchery fish are directly related to the density of zooplankton available to them, especially during years when the total release from the hatchery was > 20 million fish. This suggests that there is density-dependent growth limitation in the system and Willette et al. suggest that these juveniles may adopt foraging strategies that maximize their growth rates.

ENVIRONMENTAL CORRELATES WITH SURVIVAL AND LIFE HISTORY

Population models indicate that long-term survival prospects of most salmon stocks are dependent on both freshwater and ocean conditions (Lawson 1993). Perhaps the most intensely studied population of salmon with respect to ocean environmental conditions relating to survival has been that of coho salmon in the Oregon Production Index (OPI) area from southern Washington to northern California. Early studies had suggested that the magnitude of the coastal upwelling, or factors associated with upwelling early in the summer during smolt outmigration, have an effect on the return of adult OPI coho salmon the following year (Scarnecchia 1981; Nickelson and Lichatowich 1984; Anderson and Wilen 1985; Nickelson 1986). Nickelson (1986) showed that there was a threshold level of upwelling intensity below which marine survival of hatchery coho salmon was always low (< 5%) but above which survival was high. Contrary to previous observations, he found that the smolt-to-adult relationship was linear for wild, public hatchery and private hatchery fish analyzed separately, thus implying that a density-independent relationship existed. However, more recent work extending the time series of OPI into the 1980s and 1990s shows that this relationship has disintegrated (Lawson 1997) and, in fact, there has been an inverse, but insignificant, relationship between upwelling and OPI survival from 1982–1992 (Pearcy 1997).

Cole (2000) examined sea surface temperatures (SST) available from satellite data and found that OPI coho salmon survival was enhanced during cool years in their first spring, but warm temperatures during their first winter negatively affected survival. A recent study by Logerwell et al. (2003) looked at four uncorrelated environmental factors hypothesized to be important in the early life history of OPI coho salmon. These include (1) climate conditions as the smolts enter the ocean, (2) the spring transition between downwelling and upwelling, (3) ocean conditions during the spring upwelling, and (4) winter conditions at the end of the first year at sea. They found that their model predicted a substantial amount of the variability in OPI survival, and suggest that the model may have utility in predicting ocean survival.

Recent work has used the extensive coded-wire database to examine survival at the individual stock level and determine environmental factors related to these survival levels. Coronado and Hilborn (1998) examined the geographic patterns in survival of coho salmon from Oregon to Alaska based on CWT returns. They found that large-scale regions had similar patterns of survival that most likely are related to where the smolts first enter the ocean. However, these authors did not attempt to relate these survival patterns to marine variables. Ryding and Skalski (1999) used CWT data from hatcheries on or near the U.S. west coast to isolate marine effects. They found that some variables (June SST, spring transition timing) were not linearly related to survival, implying that some optimal conditions exist for these variables. Hobday and Boehlert (2001) examined a large number of coho salmon stocks (225 river systems) throughout this species' range in North America and six environmental variables calculated on spatial and temporal scales appropriate for early ocean influences of each stock. These authors found that survival was influenced most by environmental conditions occurring in late summer, and that these conditions most affected salmon in the southern region, followed by those of the northern region and then Puget Sound. Mixed-layer depth was found to be the most critical variable affecting juvenile salmon survival and size of jacks and adults. Koslow et al. (2002) examined salmon survival relative to a large suite of environmental variables specific to certain regions of the ocean and collapsed the data using Principal Component Analysis. These relationships were examined for both early marine residence and the winter-spring period prior to spawning migrations. They were able to identify components of the environment that accounted for a substantial part of variability in hatchery and wild coho salmon survival. Included among these were upwelling, cool surface temperatures, strong wind mixing, deep mixed layer, and strong transport of the California Current. In contrast to the results of Ryding and Skalski (1999), all relationships with survival were found to be linear. More recent studies have addressed the effects of ocean climate variables on Columbia River chinook salmon populations (Levin 2003).

There have been surprisingly few studies of this type looking at the relationship between salmon survival and environmental variables outside of the Pacific Northwest. Kope and Botsford (1990) examined the relationship between chinook salmon recruitment in central California and variables such as upwelling, sea surface height and temperature and found better relationships with survival in the final ocean year than the first summer. Botsford and Lawrence (2002) examined patterns of covariability in coho and chinook salmon and Dungeness crab (*Cancer magister*) catch rates throughout the California Current in relation to environmental data collected at the same spatio-temporal scales. Coho salmon were found to vary synchronously from Northern Washington to Central California on annual time scales whereas chinook salmon vary on longer time scales with population-specific patterns. Attempts at correlating salmon recruitment and climate in Alaskan waters have shown some correlations but generally at lags that seem difficult to associate with direct causal mechanisms (e.g., Quinn and Marshall 1989; Adkinson et al. 1996; Downton and Miller 1998). Clearly more studies could be done as time series of survival and environmental conditions attain sufficient length for suitable analyses.

STUDIES OF HATCHERY VERSUS WILD FISH INTERACTIONS

Mahnken et al. (1998) reviewed annual production trends (1900–1992) and survival trends (1970–1990) for hatchery salmon in the Pacific Northwest (Washington, Oregon, Idaho, and California) and Alaska. Despite a long history of concerns about hatchery and wild stock interactions (predation, competition), there have been few field investigations focusing directly on this issue (Fresh 1997; Heard 1998), perhaps largely because of the difficulty in identifying the hatchery or wild origin of individual fish in mixed-stock catches at sea.

In the Pacific Northwest, concerns about declining salmon survival rates, rapidly expanding public and private sea ranching operations, and intensive shoreline development and pollution have prompted numerous field investigations of the estuarine and early marine life history of juvenile salmon since the 1960s (e.g., Sims 1970; Johnson 1973; Reimers 1973; Moore et al. 1977; Schreiner 1977; Myers 1978; Rasch and O'Conner 1979; Myers 1980; Simenstad et al. 1980; Bax 1982; Durkin 1982; Kjelson et al. 1982; Myers and Horton 1982; Pearce et al. 1982; Simenstad and Salo 1982; Bax 1983b; Miller et al. 1983; Pearcy 1984a, b; Dawley et al. 1985a, b; Fisher and Pearcy 1988; Pearcy and Fisher 1988; Pearcy et al. 1989; Fisher and Pearcy 1990; Pearcy and Fisher 1990; Pearcy et al. 1990). Although the focus of most studies was not to evaluate hatchery and wild stock interactions, many provide at least some data pertinent to this issue.

A variety of techniques have been used to identify hatchery or wild stocks or both in mixed-stock catches (e.g., tags, fin clips, dye marks, scales, hatchery species and release dates, external parasites, visceral fat, fish size, and fin erosion). Evidence from these and other similar studies demonstrates overlap in spatial and temporal distribution and food habits of hatchery and wild juvenile salmon in estuarine and coastal habitats, and sometimes predation of larger hatchery juveniles on smaller hatchery or wild juveniles. Species, time, and size (age, growth rate) at marine entry, and distribution and abundance of prey appear to be the most important factors influencing the overlap in utilization of marine habitats by hatchery and wild juvenile salmon. The potential for negative effects (decreased growth and survival) from hatchery and wild stock interactions exists, if prey resources are limited or foraging success is poor.

In Alaska, an increasing percentage of hatchery salmon releases have had thermal marks placed on their otoliths since the mid-1990s (approximately 60% in 2000) (Scott et al. 2001). A number of NMFS Auke Bay Laboratory field investigations have demonstrated that thermally-marked hatchery salmon releases are sufficient to enable recoveries in inland, coastal, and high seas salmon surveys (e.g., Farley and Munk 1997; Carlson et al. 2000; Farley and Carlson 2000; Orsi et al. 2000; Farley et al. 2001d; Orsi et al. 2001b). These studies are providing valuable new information on the ocean distribution, migration, growth, and abundance of juvenile hatchery salmon (see section on coastal movements); however, differentiation of unmarked hatchery fish and wild fish in mixed-stock catches is still problematic.

Over the past decade a system of major hatcheries in Prince William Sound have produced 70–80% of large pink salmon returns to that region (averaging 27 million fish per year). This development has created controversy over potential impacts of hatchery production on local wild stocks. These hatcheries have released over 650 million juvenile pink salmon into Prince William Sound annually (McNair 2002) and some scientists have suggested that this number of hatchery fry can have a deleterious impact on smaller numbers of wild fry probably through density-dependent interactions in early marine life history stages. Hilborn and Eggers (2000) examined a series of factors and argued that pink salmon hatchery production in Prince William Sound has essentially replaced wild stock production that would have occurred in the absence of hatcheries. These authors also believe that the large hatchery program was reducing the basic productivity of local wild stocks. Wertheimer et al. (2001), however, analyzed the same data sets and concluded that hatcheries were supplementing wild stock production with a net gain of 17.5–23.7 million pink salmon to fisheries annually in the region. A further detailed modeling study that examined a broad series of bio-environmental variables (Wertheimer et al. in press) concluded that variable regional conditions in the marine environment, rather than numbers of hatchery fry, best explain the changes over time in wild stock production of pink salmon in Prince William Sound.

Pioneering research by the University of Alaska in Prince William Sound where 100% of hatchery releases are thermally otolith-marked, found no significant differences in caloric content of wild and thermally otolith-marked hatchery juvenile pink salmon caught at the same geographic locations (Boldt 2001). Significant geographical differences in caloric content of both hatchery and wild stock groups indicated extended periods of local mixing of hatchery and wild juveniles, and low caloric content at some locations may have been related to local prey depletion (Boldt 2001). Since the late 1990s, U.S. GLOBEC and many other programs have focused their research efforts on climate and physical and biological oceanographic effects on the distribution, growth, and survival of juvenile salmon in coastal waters (see overview of major field research programs). Pearcy (1997) predicted that a change to less favorable ocean conditions would result in more evidence of density-dependent interactions between hatchery and wild salmon stocks.

MOVEMENT TO THE HIGH SEAS, TIMING AND SPEED OF MOVEMENT

Broad syntheses of catch, biological, and stock identification data by Canadian, Japanese, and U.S. scientists of the INPFC provided conceptual models of the movements of juvenile salmonids to the high seas (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981; Hartt and Dell 1986; Burgner et al. 1992). Among salmonid populations known to migrate to the high seas, those of juvenile steelhead trout appear to move offshore relatively soon after ocean entry in the spring or early summer, whereas those of juvenile Pacific salmon move offshore later in the fall or early winter following ocean entry. As described in our overview of major field investigations, however, most U.S. research on juvenile salmonids has emphasized spring and summer (April–September) work in inside and coastal waters (mainly within 200 km from the shoreline). There has never been a comprehensive U.S. field research effort to determine the timing and extent of movements of juvenile salmon and steelhead trout from coastal waters to the high seas (international waters, beyond the U.S. 200-mile zone). Among all U.S. geographical regions, salmonid species, and populations, western Alaska salmon (sockeye, chum, pink, coho, and chinook salmon) and Pacific Northwest steelhead trout seem to make the most extensive high seas migrations as juveniles. Juvenile salmon from many U.S. populations may never migrate far offshore, but nevertheless make extensive migrations to inside and coastal waters distant from their rivers of origin (see section on movements in coastal waters). The proportions of U.S. salmonids migrating to the high seas and those remaining in coastal waters are not known.

The most comprehensive U.S. research on movements of western Alaska juvenile salmon to the high seas has focused largely on Bristol Bay sockeye salmon. Investigations by the NMFS Auke Bay Laboratory in the eastern Bering Sea from the mid 1960s to the early 1970s, indicated that juvenile Bristol Bay sockeye salmon begin their seaward movements in mid-August from the area along north side of the Alaska Peninsula beyond Port Moller (Straty 1974; Carlson 1976; Straty and Jaenicke 1980; Straty 1981). The timing of seaward movements of juveniles coincides with the departure from the high seas of major runs of adult sockeye salmon to Bristol Bay and adult pink salmon to eastern Kamchatka Peninsula. By mid-September large numbers of juvenile sockeye salmon are distributed to at least 167 km offshore in the eastern Bering Sea (east of 166°W). Pioneering winter high-seas gillnet research by the NMFS Northwest and Alaska Fisheries Science Center from 1962–1970 indicated that by January and early February relatively few juvenile sockeye salmon remain in the Bering Sea, and that they are broadly distributed across the central and eastern North Pacific (north of 46°N, between at least 175°E to 150°W) (French and McAlister 1970; Bakkala 1971; Bakkala and French 1971; French and Bakkala 1974). Estimated migration routes of juvenile Bristol Bay sockeye salmon from the Bering Sea to the North Pacific are through the Aleutian passes, and their winter high seas distribution in the North Pacific extends southward to at least about 46°N in the central North Pacific and 48–51°N south of the Alaska Peninsula. Their migrations cover an estimated horizontal distance of 1,300–1,850 km at a rate of at least 14.8–18.5 km•day^{-1} (French and Bakkala 1974). These and other estimates of travel rates (Table 3) are probably conservative because a cooperative Japan-U.S.-Canada high-seas trawl survey in 1992 found that juvenile sockeye salmon are distributed in international waters of the central and eastern North Pacific early in December, which would require much faster migration rates for some individuals (Nagasawa et al. 1994). A field research program on juvenile Bristol Bay sockeye salmon initiated by Auke Bay Laboratory in 1999 is providing additional information on the extent of their seaward movements in July–September (see section on coastal movements) (Farley et al. 1999, 2000a, 2001c).

In the eastern North Pacific Ocean in summer (through August), most juvenile salmon are concentrated in coastal and inland waters, but opportunistic sampling has shown that juvenile coho and chinook salmon occur in small numbers in high seas areas as early as July and August, and that some juvenile steelhead trout move to the high seas as early as June (e.g., Hartt and Dell 1986; Burgner et al. 1992). A few coded-wire tagged juvenile steelhead trout released from U.S. Pacific Northwest coastal and Columbia River hatcheries in April have been recovered in July in the international waters of the eastern North Pacific during cooperative Japan–U.S. tagging programs (Pearcy and Masuda 1982; Myers et al. 2001b). These data, however, are insufficient to estimate exact timing, migration speeds, and migration routes of juvenile steelhead trout to the high seas. A cooperative Japan–U.S.–Canada high-seas trawl survey in 1992 found that juvenile sockeye, chum, pink, coho, and chinook salmon were distributed in international waters of the Gulf of Alaska in December (Nagasawa et al. 1994). Fall and winter research in this region has been inadequate to indicate the exact migration routes and precise travel rates of juvenile salmon moving offshore.

HIGH SEAS WORK

High-seas salmon research, which focused primarily on investigations of the distribution of immature and adult salmon in spring and summer (April–September), was conducted as part of the U.S. research commitment to the INPFC (see annual reports of U.S. research in International North Pacific Fisheries Commission (INPFC) 1955–1992). Tagging and fine-mesh purse-seine fishing operations by FRI in 1964–1968, designed to study movements of juvenile salmon, were conducted primarily in coastal waters, where juveniles are concentrated in summer (see section on coastal movements) (Hartt and Dell 1986). High-seas tagging operations by FRI with longlines in the Gulf of Alaska, 1964–1966, were coordinated with similar operations by Canada and Japan, and provided some information on high seas distributions of juvenile salmon. Research by the NMFS Northwest Fisheries Science Center with multi-meshed gill-nets in winter (January–March 1962–1970) provided partial information on the high-seas distribution of juvenile salmon during their first winter at sea (French and Mason 1964; French et al. 1969; French and McAlister 1970; see INPFC Annual Reports, 1962–1970). Fisheries-oceanographic research by the U.S. Fish and Wildlife Service defined major oceanographic features and related them to the high-seas distribution of salmon (see INPFC Annual Reports, 1959–1971). A comprehensive analysis by FRI of Canadian and U.S. (1955–1990), Russian (1983–1990), and Japanese (1981–1989) research vessel data provided some information on the high-seas distribution and growth of juvenile steelhead (Burgner et al. 1992). The results of international cooperative NPAFC winter research on juvenile salmon in the 1990s, during trans-Pacific cruises of the Japanese R/V *Kaiyo maru*, are summarized by Mayama and Ishida (this volume).

Historically, most work by NMFS on the high seas emphasized research on Bristol Bay sockeye salmon. To capture juvenile sockeye salmon in winter, net panels with small meshes (508 mm and 635 mm stretched mesh) were added to a standard string of panels with larger meshes for capturing older immature and adult salmon. These small-mesh panels, however, may not have been fine enough to capture the smallest size groups of juvenile salmon. The gillnet survey data showed that juvenile sockeye salmon are distributed over a broad oceanic region in January–March (170°E–145°W, 45–57°N). Occurrence in winter of juvenile sockeye salmon in the Bering Sea and western North Pacific Ocean (near 170°E) was relatively low, and major concentrations were in the central (near 46°30'N) and eastern (48–51°N, 165–155°W) North Pacific (French and Bakkala 1974). In the Bering Sea, juvenile sockeye salmon were distributed farther south than older sockeye salmon, but experimental fishing to the north beyond the northern stations where sockeye salmon were caught was not possible because of sea ice (French and Mason 1964). There was considerable annual variation in the average size of juvenile sockeye salmon in winter, and fish caught in the Bering Sea tended to be larger than those caught in the North Pacific (French 1966). French and Bakkala (1974) concluded from age composition data that many of the juvenile sockeye salmon in their winter high seas catches were of Bristol Bay stocks. These fish migrated to the northeastern Pacific Ocean by January and February of their first year at sea, and predominated in winter catches eastward from 175°E to about 160°W and possibly to 155°W in years of high abundance. Estimated migration routes of juvenile Bristol Bay sockeye salmon from the Bering Sea to the North Pacific were through the Aleutian passes, between 179°E and 169°W (see above section on movements to the high seas) (Royce et al. 1968; French and Bakkala 1974).

In winter, juvenile sockeye salmon were generally not caught in the Bering Sea or North Pacific Ocean at extremes of cold or warm SSTs. The largest catches were at 3.5°–5.5°C SST (French and Bakkala 1974). In the North Pacific Ocean, catches of juvenile sockeye salmon were often associated with a specific water mass, called the Oyashio Extension (originating as western Subarctic water and extending eastward to about 150°W in the Gulf of Alaska). This water mass was characterized by low salinities, a weak eastward current, and a 200 to 400 m deep core of cold (< 3.6°C) water (French and McAlister 1970; Bakkala 1971). In some years, however, when this water mass (combined with eastward flowing Subarctic Current waters and called the Western Subarctic Intrusion) shifted northward, juvenile salmon remained at about the same latitudes (near or south of 50°N) in the Transition area waters, which are characterized by relatively warm temperatures of 4–9°C at 200 m (French and Bakkala 1974). In addition to looking at the effects of large water masses, the importance of local, transient oceanographic features, e.g., the sharp temperature-salinity fronts where salmon were sometimes concentrated, were also investigated (e.g., Favorite et al. 1971, 1972). Synoptic, repetitive high seas fishing and oceanographic sampling at fixed locations was often not possible, but an important conclusion from this work was that proper interpretation of high-seas catch statistics requires data on short-term changes in local environmental conditions (Favorite et al. 1972). This type of intensive fisheries-oceanographic field research to define high-seas salmonid habitats is beyond the scope of any U.S. high-seas salmon research since conducted.

The U.S. high-seas data for other species of juvenile salmon are even more limited than for sockeye salmon. What little information is available has been summarized in INPFC joint comprehensive reports on distribution and origin of salmon in offshore waters by Canada, Japan, and the United States (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981). Few juvenile chum salmon were caught during U.S. winter surface gillnet and longline surveys, perhaps because of their small size or other factors related to gear selectivity, feeding behavior, or vertical distribution (Neave et al 1976). Tagging data show that some West Coast and Alaska populations of pink and coho salmon make extensive high-seas migrations (Myers et al. 1996). United States and Canadian longline catches of pink salmon in the Gulf of Alaska showed that by November at least some juvenile pink salmon are distributed offshore, and that by January and February pink salmon, averaging 30 cm long, are broadly distributed across the southern Gulf (45–51°N, 133–156°W) (Royce et al. 1968; Hartt and Dell 1986). High-seas catch data from areas west of 180° W longitude in January–March showed that both pink and coho salmon were distributed south of 46°N (Godfrey et al. 1975; Takagi et al. 1981). Catch data have also shown that in January–March coho salmon are distributed in the central Gulf of Alaska (50°N, 150–160°W) (Godfrey et al. 1975). NMFS observer data indicated that in December at least some juvenile chinook salmon are distributed in the international waters of the central Bering Sea (Florey 1975).

Juvenile steelhead trout first appear in high seas catches in June, and in the Gulf of Alaska from spring through fall, their numbers decrease in coastal catches and increase in high seas catches (Pearcy and Masuda 1982; Hartt and Dell 1986; Burgner et al. 1992). Hartt and Dell (1986) and others have hypothesized that steelhead trout migrate directly offshore from the point of ocean entry, but there are no data on migration routes and travel rates (see section above on movements to the high seas). Most juvenile steelhead trout from U.S. basins probably remain in the Gulf of Alaska throughout their first summer and fall, although the known westward range of juvenile steelhead trout in summer extends to 180° longitude in the central North Pacific Ocean (Burgner et al. 1992). There are too few samples of juvenile steelhead trout from high seas surveys to describe their winter distribution. By the following spring, their high-seas range extends across the North Pacific (125°W–155°E), and has shifted southward (generally south of 52°N in the Gulf of Alaska and south of 48°N in the central North Pacific; Burgner et al.

1992). Japan–U.S. research gillnet surveys in the central Gulf of Alaska in summer 1993–2000 showed that juvenile steelhead trout were distributed at all latitudes sampled from 49°N to 56°N (8–13°C SST), and were most frequent in catches at 52°N (10°C SST) (Myers et al. 2001b). In this region, mesoscale (200–300 km) and small (< 200 km) eddies may influence primary productivity and the distribution of juvenile steelhead trout and their prey (primarily small fish and squid) (Onishi et al. 2000; Myers et al. 2001b).

Evidence from high-seas tagging studies has shown that the ocean ranges of many U.S. salmonid stocks from California to arctic Alaska extend into international waters of the North Pacific Ocean and Bering Sea (Myers et al. 1996). There are little or no stock-specific data, however, on juvenile salmon in high-seas areas from September through March. Future high-seas investigations should be coordinated with investigations of coastal juvenile salmon so that we can determine the relative importance of both habitats to the growth and survival of specific stocks of juvenile salmon during their first fall and winter at sea.

RECOMMENDATIONS FOR FUTURE STUDIES

The studies described in this paper, together with those conducted by other nations in the North Pacific Rim, have significantly advanced our understanding of where and when juvenile salmon occur in coastal waters, and have substantially augmented our knowledge of the biology of these juveniles. All the studies described have attempted to sample the physical and biotic environment where juvenile salmon were caught, in an attempt to determine habitat preferences. This has had somewhat limited utility, especially in the early marine life stages of salmon shortly after leaving their river systems, since they may have to traverse less preferred and perhaps even unfavorable areas to arrive at their optimal habitats. These measurements need to be continued and perhaps broadened to include finer-scale and depth-stratified oceanographic and biological dynamics that may be sensed by these juveniles.

An enormous amount of information has been gathered on the movement patterns of juvenile salmon in coastal waters. Much of the early information was based on tagging at sea (Hartt and Dell 1986; Myers et al. 1996). In recent years, the proliferation of releases of coded-wire tagged (Pearcy and Fisher 1988) and thermally-marked (Farley and Munk 1997) hatchery salmon has provided a wealth of information on where fish from different stocks reside in coastal waters, as well as rough estimates of growth and migration speeds. Directional purse seines and fine-mesh gillnets provide some information on direction of movements. New advances in miniaturization allow widespread application of acoustic and data-storage tags on juvenile salmon as they enter the ocean (Boehlert 1997; Walker et al. 2000). Promising new technology is being developed for moored arrays of listening devices in coastal waters for detecting the presence of juvenile salmon and monitoring their movements and behavior (Boehlert 1997; Klimley et al. 1998).

Determining early ocean mortality factors and rates may continue to be elusive for several years to come. Unique individual tagging of all hatchery fish will add much information on the timing and direct causes of mortality. It will also aid in understanding wild and hatchery salmon interactions in the coastal environment. In the future, we hope to see greater U.S. research emphasis on local interactions between hatchery and wild juvenile salmon and their prey resources, possible density-dependent interactions, and the influence of these early marine interactions on adult salmon production in changing ocean regimes (Noakes et al. 2000; Levin and Williams 2002).

Logistic complications and safety concerns have generally limited most coastal sampling at sea to daytime and late spring through early fall collections of juvenile salmon. More information is needed on the nocturnal depth distribution, aggregation, and movement patterns of juvenile salmon. More winter sampling will help determine whether there exists a second 'critical period' in the life of salmon (Beamish and Mahnken 2001), or at least whether their habitat preferences change at this time of the year.

Obviously, juvenile salmon are not alone in the coastal environment, and in many cases, they may play a minor role in the ecosystem relative to other more plentiful fishes and invertebrates. However, the juveniles themselves may be critically affected by what happens around them, especially by the abundance of predators, competitors, and prey. As described in this review and elsewhere (Brodeur 1990), much is known about the feeding habits and food preferences of juvenile salmon, although more research is clearly needed on consumption rates relative to food availability so that some estimation of the carrying capacity of the coastal environment for juveniles is achieved (Cooney 1984; Cooney and Brodeur 1998). Similarly, competitors and predators of juvenile salmon have been identified (Fresh 1997), but their impact on juvenile salmon survival has seldom been measured. Understandably, such measurements are difficult to accomplish in the field. It may be that these data gaps can be filled by simulation modeling, perhaps by either individually-based bioenergetics models or general ecosystem models focussing on juvenile salmon. However, the models are generally wanting for appropriate field data in some areas at the present time.

At present, there has been little or no U.S. research on changes in abundance and body size of salmon caused by rapid global warming from the combined effects of man-made greenhouse gas emissions (e.g., carbon dioxide, methane, nitrous oxide and the fluorocarbons) and the Arctic Oscillation, a natural climate phenomenon that has been in its warm phase for the past 30 years (Thompson and Wallace 1998). Global warming is likely to affect marine distribution, growth, and survival, and is likely to affect the amount of ocean habitat available to juvenile and adult salmon (Welch et al. 1998). Because the effects of global climate change on salmon will differ between oceanic regions, as well as among salmon species and stocks, new U.S. research on both regional and trans-oceanic scales is highly recommended.

Recent years have seen the expansion of several studies as well as the initiation of new studies examining juvenile salmon in the ocean. In fact, the last several years have probably witnessed more sampling activity in U.S. waters over a broader geographic and temporal scale than in any previous period. The future looks equally promising with many new programs starting up (e.g., U.S. GLOBEC; BASIS), but a continuation of the effort already in place is necessary if we are to make critical advances in our knowledge of juvenile salmon distribution, behavior, and ecology when they first enter the ocean.

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