Seasonal Habitat Use and Early Marine Ecology of Juvenile Pacific Salmon in Southeastern Alaska

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Abstract: Habitat use and early marine ecology of juvenile (age-.0) Pacific salmon (*Oncorhynchus* spp.) were studied monthly at inshore, strait, and coastal habitats along a seaward migration corridor in southeastern Alaska from May through October 1997–99. A total of 31,853 fish from 40 taxa were captured with 283 surface trawl hauls; juvenile salmon made up 61% of the total catch. Predation on juvenile salmon was observed in 4 of 19 fish species examined, and occurred in 33 (5%) of the 661 predators examined. Juvenile salmon catches typically peaked in June and July and in strait habitats, where two Alaska hatchery chum salmon (*O. keta*) stocks made up > 50% of the chum salmon sampled. Of the juvenile chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) stocks of known origin, marine migration rates averaged 1 and 3 km/d for Alaska stocks and 19 and 29 km/d for Columbia River Basin stocks. Our results imply that seasonal habitat use patterns of juvenile salmon are related to favorable temperatures and zooplankton abundance and are also linked to species and stock of salmon. Long-term ecological monitoring of key juvenile salmon stocks is needed over varying environmental conditions to understand relationships among habitat use, marine growth, year-class strength, and ocean carrying capacity.

INTRODUCTION

Increasing evidence for relationships between Pacific salmon (*Oncorhynchus* spp.) production and shifts in climate has renewed interest in processes governing year-class strength in salmon (Beamish 1995). However, actual links tying salmon production to climate change are poorly understood. Synoptic time series of ocean conditions and salmon life-history characteristics are needed to adequately identify mechanisms linking production to climate change (Pearcy 1997). In addition, the presence of mixed stocks with different life-history characteristics confounds research attempts to assess marine growth, survival, distribution, migration, and ocean carrying capacity.

The ocean's carrying capacity for salmon is related to their tolerance for environmental change, density, food supply, and the density of competitors and predators. In their review of implications for stock enhancement of salmonids in the North Pacific Ocean, Cooney and Brodeur (1998) argued that much more knowledge about the distribution of forage resources and the interactions of predators is needed if enhancement of selected species is to proceed without risk of deleterious

effects. An understanding of the spatial, temporal, and ecological overlap between stocks and species of salmon, habitat characteristics, juvenile salmon condition, prey resources, and predators is required to understand factors governing the marine survival and production of salmon.

An ocean survey of juvenile salmon was initiated in 1997 to monitor the early marine ecology of juvenile salmon along a primary migration corridor in the northern region of southeastern Alaska (Orsi et al. 1997). We report three years of findings on habitat use, migration, and growth of juvenile salmon in the region, as well as physical and biological habitat characteristics, fish species composition, and predation on juvenile salmon.

MATERIALS AND METHODS

Study Area

Twenty four stations in inshore, strait, and coastal habitats were sampled at approximately monthly intervals in marine waters of the northern region of southeastern Alaska from May through October 1997–99

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(Fig. 1). Stations were located along a seaward migration corridor used by juvenile salmon extending 250 km from inshore waters within the Alexander Archipelago along Chatham Strait and Icy Strait, through Cross Sound, and to offshore waters in the Gulf of Alaska (Orsi et al. 1998). All sampling occurred during daylight, between 07:00 and 20:00 hours.

Sampling stations were selected based on 1) the existence of historic data in the region, 2) the necessity to sample multiple habitat types along the migration corridor transited by juvenile salmon, and 3) vessel and sampling gear constraints. Historical biological and oceanographic data were available for Auke Bay Monitor (ABM), False Point Retreat (FPR), Lower Favorite Channel (LFC), and Icy Strait (Bruce et al. 1977; Mattson and Wing 1978; Ziemann and Fulton 1990). The Taku Inlet (TKI) station represents conditions near a large glacial river system of large wild stock production along the mainland. The Chatham Strait transect represents a mixing area of two major stocks of chum salmon (O. keta) entering the strait habitat from the south (Hidden Falls hatchery) and north (Douglas Island Pink and Chum (DIPAC) hatchery). The Cross Sound, Icy Point, and Cape Edward transects represent coastal habitats adjacent to and in the Gulf of Alaska.

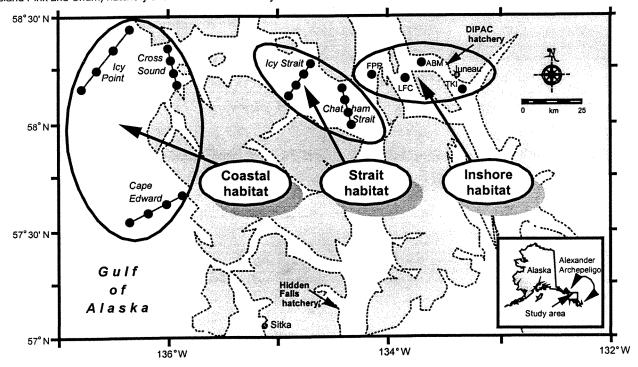
Vessel and sampling gear constraints limited operations to distances ≥ 1.5 and ≤ 65 km offshore, and ≥ 75 m depths; as a result, no trawling occurred at the ABM station. Sea conditions of < 2.5 m and winds < 12.5 m/sec were necessary to operate the sampling gear safely.

Oceanography and Fish Sampling

Physical and biological oceanographic sampling at each station included thermosalinograph data taken at 2 meters (m) and one 20 m vertical plankton haul. Surface temperature and salinity data were collected at 1-minute intervals with a SeaBird¹ SBE-21 thermosalinograph. One shallow (20 m) vertical haul was done using a conical NORPAC plankton net (50 cm diameter frame, 243 µm mesh), the standard for previous zooplankton sampling programs in the region.

Fish were sampled with a Nordic 264 rope trawl modified to fish the surface water directly astern of the NOAA ship *John N. Cobb*, a 29 m research vessel. The trawl was 184 m long, with a mouth opening of 24 m \times 30 m (depth \times width), and was spread apart by a pair of 3 m foam-filled Lite trawl doors, each weighing 544 kg (91 kg submerged). Earlier gear trials with this vessel

Fig. 1. Stations sampled monthly in inshore, strait, and coastal marine habitats of the northern region of southeastern Alaska, May—October 1997–99. Up to 24 stations were sampled: four stations (ABM: Auke Bay Monitor, FPR: False Point Retreat, LFC: Lower Favorite Channel, TKI: Taku Inlet) in inshore habitats, two transect lines (four stations each) in strait habitats, and three transect lines (four stations each) in coastal habitats. Localities of the two primary salmon hatcheries in the region are identified: DIPAC (Douglas Island Pink and Chum) hatchery and Hidden Falls hatchery.



¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

and trawl indicated the actual fishing dimensions of the trawl to be 24 m vertical (head rope to foot rope) and 24 m horizontal (wingtip to wingtip). Trawl mesh sizes from the jib lines aft to the cod end ranged from 162.6 to 10.1 cm over the 129.6 m meshed portion of the rope trawl and a 6.1 m long, 0.8 cm knotless liner was sewn into the cod end. For each haul, the trawl was fished 20 min at 1.5 m/sec (3 knots), covering approximately 1.9 km (1.0 nautical mile) across a station. The effective sampling volume of water swept by the rope trawl during one haul was estimated to be $1.07 \times 10^6 \,\mathrm{m}^3$. This volume was calculated by multiplying the cross section of the trawl mouth opening (576 m²) by the horizontal distance covered by one trawl haul (1,852 m), and dividing by a factor of four to account for surface orientation of juvenile salmonids (i.e., the top 6 m). Overwater trawl speed was usually monitored from the vessel using an electromagnetic current meter (Marsh McBirney, Inc., Model 2000-21). Station coordinates were targeted as the midpoint of the trawl haul; however, current, swell, and wind conditions dictated the direction of the trawl haul.

After each haul, fish were anesthetized, identified, enumerated, measured, labeled, bagged, and frozen. Fish were measured to the nearest millimeter (mm) fork length (FL) with a Limnotera FMB IV electronic measuring board (Chaput et al. 1992). All salmon were screened for coded-wire tags (CWTs). Juvenile salmon were poured through a portable CWT detector, and larger salmon were examined for missing adipose fins. After the juvenile salmon in each haul were processed, the stomachs of potential predators of juvenile salmon were examined.

Laboratory Processing and Data Analysis

Zooplankton settled volumes (ZSV) from the 20 m vertical tows were estimated by quantifying the amount of zooplankton settled for 24 hours in an Imhof 1,000 ml cone. Mean ZSV from all stations within a habitat was averaged, summarized by month, and pooled across years.

Apparent growth rates of pink salmon (O. gorbuscha) and chum salmon between June and July in the strait habitats were estimated by subtracting the average FL in July from that in June and dividing by the number of days between sampling periods. The number of days between sampling periods was estimated by subtracting the weighted date of sampling for July by the weighted date of sampling from June, with weights supplied by the number of each species of juvenile salmon captured and measured each day of sampling. Growth rate variance was estimated by summing the FL variance during each period and dividing by the squared number of days between sampling periods. Otolith marks were used to determine stock-specific growth rates for DIPAC and Hidden Falls hatchery chum salmon in 1997 and 1998.

Methods used to estimate stock-specific growth rates were similar to those described above.

Origin information was obtained for chinook salmon (O. tshawytscha), coho salmon (O. kisutch), and chum salmon from CWTs (Jefferts et al. 1963) or thermally induced otolith marks (Hagen and Munk 1994). Independent tag readers verified all CWT codes and otolith marks. Release data for CWT codes and otolith marks were obtained from regional mark coordinators. Release and recovery data enabled migration rates to be determined by dividing marine distances traveled by the number of days at sea.

RESULTS

Seasonal Habitat Characteristics

From 1997 through 1999, data were collected from 319 surface thermosalinograph readings, 335 vertical zooplankton hauls, and 283 rope trawl hauls (Table 1). After 1997, limited rope trawling occurred in May due to the absence of juvenile salmon, but oceanographic data were collected. Inclement weather, particularly in coastal habitats, restricted sampling opportunities, thereby reducing the number of stations sampled some months.

Seasonal patterns were apparent in the temperature and salinity data (Fig. 2). Average surface temperatures ranged from 6.9 to 13.4°C and differed among habitats by up to 2.5°C monthly. Seasonal temperature patterns were consistent among habitats. Each year, temperatures were lowest in May, increased to a peak in July or August, then declined to near the spring minimum by October. Inshore habitats generally warmed first in spring, and coastal habitats cooled last in fall. Average surface salinities ranged from 16.7 to 31.8 PSU and differed among habitats by up to 19 PSU monthly. Seasonal salinity patterns were similar in inshore and strait habitats, but differed in coastal habitats. At inshore and strait habitats, salinity declined from May to July, then increased by October. In coastal habitats, salinities were relatively constant each month and year. Salinities were lowest in inshore habitats and highest in coastal

Interannual differences in the environment among habitats were also observed (Fig. 2). Lower temperatures prevailed in 1999 than in the two prior years, particularly in coastal habitats. Between years, annual peak temperature varied < 1°C in inshore and strait habitats and \sim 2°C in coastal habitats. Minimum salinities for all habitats occurred later in 1999 (August) than in 1997–98 (July).

Mean ZSV varied seasonally and among habitats (Fig. 3), ranging between 0 and 50 ml at the individual stations. In May, ZSV was similar at all three habitats, ~15 ml. However, seasonal patterns differed by habitat type from June through August. In inshore and strait

Table 1. Number of thermosalinograph*, zooplankton, and rope trawl samples collected monthly at inshore (I), strait (S), and coastal (C) habitats in marine waters of the northern region of southeastern Alaska, May–October 1997–99.

| | | The | rmosalinog 2 m depth | | Zooplankton | | | | Rope trawl)–24 m dep | Rope trawl 24 m depth |
|----------|------|-----|-------------------------|-----|-------------|-----|-----|----|--------------------------|--------------------------|
| Month | Year | ı | S | С | 1 | S | С | I | S | С |
| May | 1997 | 4 | 8 | 8 | 4 | 8 | 8 | 3 | 8 | 8 |
| | 1998 | 4 | 9 | 1 | 7 | 8 | 1 | 2 | 9 | 0 |
| | 1999 | 4 | 8 | 4 | 6 | 8 | 4 | 0 | 4 | 0 |
| June | 1997 | 4 | 8 | 8 | 4 | 8 | 8 | 3 | 8 | 8 |
| | 1998 | 4 | 8 | 12 | 7 | 8 | 12 | 3 | 8 | 12 |
| | 1999 | 4 | 8 | 11 | 6 | 8 | 11 | 3 | 8 | 11 |
| July | 1997 | 5 | 9 | 8 | 4 | 8 | 8 | 3 | 8 | 8 |
| • | 1998 | 4 | 12 | 16 | 6 | 12 | 16 | 3 | 12 | 16 |
| | 1999 | 4 | 8 | 11 | 6 | 8 | 11 | 3 | 8 | 11 |
| August | 1997 | 4 | 9 | 8 | 4 | 8 | 8 | 3 | 8 | 8 |
| | 1998 | 6 | 12 | 8 | 8 | 12 | 7 | 4 | 12 | 8 |
| | 1999 | 4 | 12 | 8 | 6 | 12 | 8 | 3 | 12 | 8 |
| SeptOct. | 1997 | 4 | 5 | 8 | 7 | 5 | 12 | 3 | 4 | 7 |
| • | 1998 | 4 | 4 | 7 | 7 | 4 | 7 | 3 | 4 | 7 |
| | 1999 | 4 | 8 | 8 | 6 | 8 | 8 | 3 | 8 | 8 |
| Total | | 63 | 128 | 128 | 88 | 125 | 122 | 42 | 121 | 120 |

^{*}Thermosalinograph data from 2 m depth; zooplankton data from 20 m vertical hauls, 50 cm diameter frame, 243 µm mesh conical net; rope trawl data from 0–24 m depth, 20 min. haul.

Fig. 2. Surface (2 m) temperatures and salinities from inshore, strait, and coastal marine habitats, May-October 1997–99.

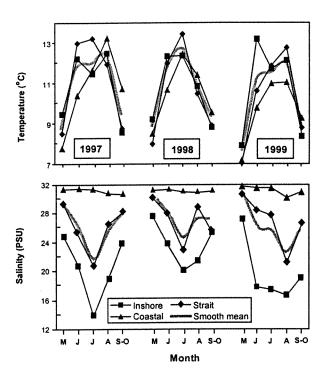
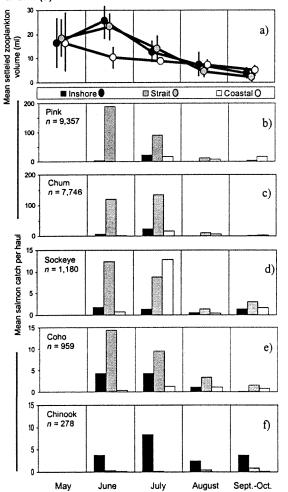


Fig. 3. Mean settled volumes of zooplankton from 20 m vertical hauls (a) and mean catch per rope trawl haul of juvenile salmon (b-f) from inshore, strait, and coastal marine habitats, May-October 1997–99. One standard deviation about the mean is shown (a).



habitats, ZSV increased to ~ 25 ml in June and also remained 5–15 ml higher than in coastal habitats through July, declining sharply from June through August. At coastal habitats, ZSV declined slowly from May through October. In October, ZSV was similar again at all three habitats, ~ 5 ml.

Catch and Ecological Interactions

A total of 31,853 fish from 40 taxa were captured, including all five species of juvenile Pacific salmon and steelhead (*O. mykiss*); salmonids made up 61% of the total catch (Table 2). Of the 19,521 salmonids sam-

pled, over 98% were juveniles: 9,357 pink salmon, 7,746 chum salmon, 1,180 sockeye salmon (*O. nerka*), 959 coho salmon, and 278 chinook salmon; only 129 were immatures (125 chinook salmon, 3 chum salmon, 1 sockeye salmon) and 144 were adults. Non-salmonid species making up > 1% of the catch included 4,992 sablefish (*Anoplopoma fimbria*), 2,849 capelin (*Mallotus villosus*), 2,671 Pacific herring (*Clupea harengus*), and 406 squid (Gonatidae). Juvenile pink and chum salmon were typically the primary catch components each year. Interannual differences in catch composition occurred, notably as the large catches of juvenile sablefish in 1997 and juvenile pink salmon in 1998.

Table 2. Catches of fishes and squid sampled with 283 rope trawl hauls, May-October 1997-99

| | | | | Number caught | | | | | | |
|-------------------------|--------------------|---------------------------------------|--------|---------------|-------|---|----|--|--|--|
| Common name | Life-history stage | Scientific name | 1997 | 1998 | 1999 | Total | % | | | |
| Pink salmon | J | Oncorhynchus gorbuscha | 1,107 | 7,267 | 983 | 9,357 | 29 | | | |
| | Α | | 5 | 14 | 74 | 93 | (| | | |
| Chum salmon | J | O. keta | 3,565 | 2,748 | 1,433 | 7,746 | 24 | | | |
| J. Carriori | Ĵ+ | | 0 | 1 | 2 | 3 | (| | | |
| | Α | | 0 | 11 | 0 | 11 | (| | | |
| Sockeye salmon | J | O. nerka | 237 | 434 | 509 | 1,180 | | | | |
| ockeye sannon | J+ | 5. | 1 | 0 | 0 | . 1 | | | | |
| | Ä | | 0 | 1 | 3 | Total 9,357 93 7,746 3 11 1,180 | | | | |
| Salan andaran | J | O. kisutch | 215 | 371 | 373 | 959 | | | | |
| Coho salmon | Ä | O. KISUICH | 5 | 18 | 12 | | | | | |
| | | 0 4-6 46- | | 104 | 61 | | | | | |
| hinook salmon | J | O. tshawytscha | 113 | | | | | | | |
| | J+ | | 29 | 58 | 38 | | | | | |
| iteelhead | J | O. mykiss | 1 | 0 | 0 | | | | | |
| | Α | | 0 | 1 | 0 | 1 | | | | |
| ablefish | J | Anoplopoma fimbria | 4,795 | 196 | 1 | | • | | | |
| | J+ | • • | 0 | 5 | 161 | 166 | | | | |
| apelin | J-A | Mallotus villosus | 399 | 550 | 1,900 | 2,849 | | | | |
| acific herring | J-A | Clupea pallasi | 599 | 783 | 1,289 | 2,671 | | | | |
| quid | Ĵ | Gonatidae | 231 | 166 | 9 | 406 | | | | |
| /alleye Pollock | J-A | Theragra chalcogramma | 100 | 47 | 102 | 249 | | | | |
| oft Sculpin | J-A | Psychrolutes sigalutes | 27 | 40 | 106 | 173 | | | | |
| piny dogfish | A | Squalus acanthias | 10 | 81 | 10 | 101 | | | | |
| rested sculpin | J-A | Blepsias bilobus | 46 | 28 | 14 | 88 | | | | |
| acific spiny lumpsucker | J-A | Eumicrotremus orbis | 45 | 11 | 9 | 65 | | | | |
| /olf-eel | j | Anarrhichthys ocellatus | 1 | 57 | 2 | 60 | | | | |
| acific sand lance | J | Ammodytes hexapterus | 53 | 0 | 2 | 55 | | | | |
| acific sandfish | J-A | Trichodon trichodon | 12 | 24 | 17 | 53 | | | | |
| rowfish | J-A | Zaprora silenus | 9 | 5 | 20 | 34 | | | | |
| reenling | J | Hexagrammos spp. | 0 | 18 | 0 | 18 | | | | |
| tockfish | J | Sebastes spp. | 13 | 5 | 0 | 18 | | | | |
| igmouth sculpin | J | Hemitripterus bolini | 5 | 3 | 3 | 11 | | | | |
| tarry flounder | Α | Platichthys stellatus | 2 | 4 | 4 | 10 | | | | |
| hree-spined stickleback | J-A | Gasterosteus aculeatus | 1 | 4 | 1 | | | | | |
| lack rockfish | Α | Sebastes melanops | 0 | 4 | 1 | | | | | |
| mooth lumpsucker | . A | Aptocyclus ventricosus | 3 | 1 | 1 | | | | | |
| rrowtooth flounder | J | Atheresthes stomias | 5 | 0 | 0 | | | | | |
| olly Varden | Α | Salvelinus malma | 0 | 0 | 3 | | | | | |
| ngcod | J | Ophiodon elongates | 0 | 1 | 2 | | | | | |
| lue shark | Α | Prionace glauca | 0 | 1 | 1 | | | | | |
| almon shark | Α | Lamna ditropis | 1 | 1 | 0 | | | | | |
| oacher | J | Agonidae | 1 | 1 | 0 | | | | | |
| latfish | J | Pleuronectidae | 0 | 2 | 0 | | | | | |
| ilverspotted sculpin | J-A | Blepsias cirrhosus | 0 | 0 | 2 | | | | | |
| nknown fish | j | _ ` | 0 | 2 | 0 | | | | | |
| acific saury | Α | Cololabis saira | 0 | 1 | 0 | | | | | |
| ack mackerel | Α | Trachurus symmetricus | 1 | 0 | 0 | | | | | |
| acific pomfret | Α | Brama japonica | 1 | 0 | 0 | • | | | | |
| ulachon | j | Thaleichthys pacificus | 0 | 0 | 1 | - | | | | |
| Quillfish | Ĵ | Ptilichthys goodei | 1 | 0 | 0 | | | | | |
| acific cod | Ĵ | Gadus macrocephalus | 0 | 0 | 1 | 1 | | | | |
| otal | | · · · · · · · · · · · · · · · · · · · | 11,633 | 13,069 | 7,151 | 31,853 | 10 | | | |

^{*}J = Juvenile age-0+ fish, first year at sea; J+ = age-1+ fish one ocean-winter old; A = adult of spawning age; J-A = inclusive of all life history stages.

Predation on juvenile salmon was low. They were eaten by 4 of the 19 fish species examined for predation, and occurred in 33 (5%) of 661 stomachs (Table 3). The four fish species identified as predators of juvenile salmon were age 1+ sablefish, adult coho salmon, adult Pacific sandfish (*Trichodon trichodon*), and adult spiny dogfish (*Squalus acanthias*). Of these, age 1+ sablefish and adult coho salmon were the primary predators.

Habitat Use and Growth of Juvenile Salmon

Habitat use by juvenile salmon differed by month and species (Fig. 3). Seasonally, catch rates of juvenile salmon were lowest in May and highest in June and July. All species were most abundant in strait habitats except chinook salmon, which were found primarily in inshore habitats. Pink and coho salmon were most abundant in June, whereas chum, sockeye, and chinook salmon were most abundant in July. Average densities of juvenile salmon were highest in strait habitats during June and July (i.e., 1.1 fish per 1,000 m³); with a peak single catch density of 5.6 fish per 1,000 m³. Both juvenile salmon abundance and ZSV volume in strait habitats seasonally declined from July to August (Fig. 3).

Offshore distribution across the Icy Point transect in the coastal habitat reflected the width of the coastal migration band of juvenile salmon in the Gulf of Alaska (Fig. 4). Data from the Cape Edward offshore transect were not used because it was not sampled in 1997, nor

consistently sampled monthly in 1998-99. Offshore distribution of juvenile salmon was generally < 25 km from shore. Catches of all five species generally declined with distance offshore; however, a higher proportion of pink and chum salmon than the other three species were closer to shore.

Apparent growth of juvenile pink and chum salmon was compared to surface temperature and ZSV in the strait habitats in June and July (Fig. 5). From 1997 through 1999, apparent growth (mean mm per day) of both species declined from ~ 1.6 to < 1 mm/d, as mean temperature declined from ~ 13 to 11.5°C, and as mean ZSV declined from 24 to 13 ml. In 1997 and 1998, stock specific growth rates for the DIPAC and Hidden Falls hatchery chum salmon were similar to the mixed stock growth rate estimates. Although mixed stock estimates of growth rate had higher variances, no obvious bias appeared to be present. The similarity between the mixed stock and stock specific growth rates may be due to the high proportion (50%) of the DIPAC and Hidden Falls stocks in our samples during June and July.

Stock-specific Distribution and Migration

Recoveries of 1,575 otlolith-marked juvenile chum salmon provided information on stock composition and stock-specific migration (Table 4). Hatchery chum salmon stocks made up 44–55% of the catch in June and July, whereas unmarked fish made up 75–100% of the catch in August through October. In 1997 and

Table 3. Number of potential predators of juvenile salmon examined (n_{ex}) and the actual number of those predators observed (n_{obs}) to have eaten juvenile salmon as a prey item from samples collected by rope trawl, May–October 1997–99.

| | Life- history | 1997 | | | 1998 | | | 1999 | | | Total | | |
|------------------|------------------|-----------------|------|------|-----------------|------|------|-----------------|------|------|-----------------|------|------|
| Predator species | stage* | n _{ex} | nobs | % |
| Sablefish | J+ | 0 | 0 | 0.0 | 4 | 1 | 25.0 | 66 | 24 | 36.3 | 70 | 25 | 35.7 |
| Coho salmon | Α | 6 | 0 | 0.0 | 18 | 2 | 11.1 | 12 | 2 | 16.7 | 36 | 4 | 11.1 |
| Pacific sandfish | Α | 8 | 2 | 25.0 | 3 | 0 | 0.0 | 16 | 0 | 0.0 | 27 | 2 | 7.4 |
| Spiny dogfish | Α | 10 | 0 | 0.0 | 80 | 1 | 1.3 | 10 | 1 | 10.0 | 100 | 2 | 2.0 |
| Walleye Pollock | Α | 42 | 0 | 0.0 | 31 | 0 | 0.0 | 65 | 0 | 0.0 | 138 | 0 | 0.0 |
| Chinook salmon | J+ | 29 | 0 | 0.0 | 52 | 0 | 0.0 | 42 | 0 | 0.0 | 123 | 0 | 0.0 |
| Pink salmon | Α | 5 | 0 | 0.0 | 14 | 0 | 0.0 | 81 | 0 | 0.0 | 100 | 0 | 0.0 |
| Sablefish | J | 17 | 0 | 0.0 | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 17 | 0 | 0.0 |
| Pacific herring | Α | 14 | 0 | 0.0 | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 14 | 0 | 0.0 |
| Starry flounder | Α | 3 | 0 | 0.0 | 3 | 0 | 0.0 | 4 | 0 | 0.0 | 10 | 0 | 0.0 |
| Chum salmon | Α | 0 | 0 | 0.0 | 8 | 0 | 0.0 | 0 | 0 | 0.0 | 8 | 0 | 0.0 |
| Black rockfish | Α | 0 | 0 | 0.0 | 4 | 0 | 0.0 | 1 | 0 | 0.0 | 5 | 0 | 0.0 |
| Sockeye salmon | Α | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 4 | 0 | 0.0 | 4 | 0 | 0.0 |
| Dolly Varden | Α | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 3 | 0 | 0.0 | 3 | 0 | 0.0 |
| Chum salmon | J+ | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 | 1 | 0 | 0.0 |
| Salmon shark | Α | 0 | 0 | 0.0 | 1 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 |
| Blue shark | Α | 0 | 0 | 0.0 | 1 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 |
| Jack mackerel | Α | 1 | 0 | 0.0 | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 |
| Pacific promfret | Α | 1 | 0 | 0.0 | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 |
| Pacific cod | Α | 0 | 0 | 0.0 | 0 | 0 | 0.0 | 1 | 0 | 0.0 | 1 | 0 | 0.0 |
| Total | | 136 | 2 | 1.5 | 219 | - 4 | 1.8 | 306 | 27 | 8.8 | 661 | 33 | 4.9 |

^{*}J = juvenile age-0+ fish, first year at sea; J+ = age-1+ fish, one ocean-winter old; A = adult of spawning age.

Table 4. Sample size (n) and stock composition of juvenile chum salmon examined for otolith marks in straits, June–October 1997–98. Estimates of stock composition have been corrected for the unmarked Hidden Falls hatchery component (60% of the Hidden Falls stock were marked; 100% of Douglas Island Pink and Chum (DIPAC) stock were marked).

| Year | Month | n | Unmarked (%) | DIPAC (%) | Hidden Falls (%) | Total (%) |
|------|----------|-----|-----------------|--------------|---------------------|--------------|
| 1997 | June | 50 | 46 | 49 | 5 | 100 |
| | July | 258 | 51 | 12 | 37 | 100 |
| | August | 215 | 75 | 10 | 15 | 100 |
| | SeptOct. | 11 | 100 | 0 | 0 | 100 |
| 1998 | June | 354 | 45 | 36 | 19 | 100 |
| | July | 378 | 56 | 19 | 25 | 100 |
| | August | 2 | 100 | 0 | 0 | 100 |
| | SeptOct. | 7 | 81 | 0 | 19 | 100 |

Fig. 4. Mean catch per rope trawl haul of juvenile salmon related to distance offshore along the Icy Point transect, June–October 1997–99.

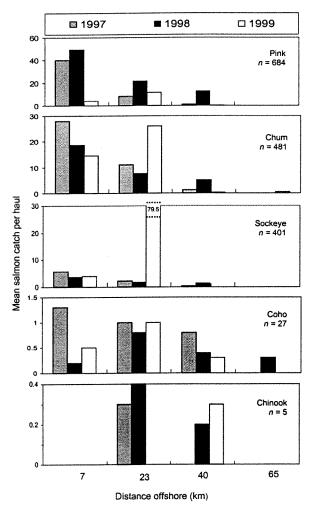
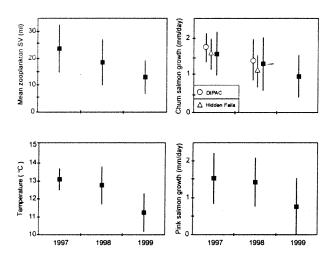


Fig. 5. Relationships between temperature and zooplankton to apparent growth rates of juvenile pink and chum salmon stocks in the strait habitats, June–July 1997–99. Stock-specific growth rates from otolith mark recoveries are included for DIPAC and Hidden Falls hatchery chum salmon stocks. One standard deviation about the mean is shown.



1998, DIPAC chum salmon migrated 1.9 and 1.6 km/d and were present predominantly in June, whereas Hidden Falls chum salmon migrated 2.2 and 2.4 km/d and were present predominantly in July.

Recoveries of 68 CWT chinook and coho salmon indicated differences in habitat use by species, stock, and ocean-age group (Table 5). CWT chinook salmon (33) were recovered primarily in inshore habitats, whereas CWT coho salmon (35) were recovered primarily in strait habitats. Alaska stocks were recovered primarily in inshore and strait habitats, whereas, Columbia River Basin (CRB) stocks were recovered exclusively in coastal habitats. By ocean-age group, age 1.0 juvenile chinook salmon (26) were present in all habitats and older, age 0.1, 1.1, 1.2, and 1.3 immature chinook salmon (7) were present exclusively in strait and coastal habitats.

Of the 61 CWT juvenile chinook and coho salmon (age 1.0) recovered, temporal occurrence within habitat differed by stock and species (Table 5). Alaska stocks of chinook salmon were present from June through October, principally in inshore habitats in July. Their average migration rate was 1.3 km/d. Alaska stocks of coho salmon were present from June through October, principally in strait habitats in June. Their average migration rate was 3.2 km/d. In contrast, CRB stocks of chinook salmon (4) and coho salmon (1) were recovered exclusively in coastal habitats in June and July; their average migration rates were 19.1 and 28.6 km/d.

DISCUSSION

The initial marine stage of juvenile salmon ecology has been studied in Canada and Alaska (LeBrasseur and Parker 1964; Healey 1967; Bailey et al. 1975; Cooney et al. 1978; Mortensen et al. 2000). Our study examined the next marine stage, the migration of juvenile salmon from littoral waters to the neritic waters farther offshore, involving routes through complex and highly diverse habitats. The patterns and timing of seaward dispersal are influenced by many factors, including natal stream localities, shoreline and basin bathymetry, current patterns, biological and oceanographic conditions, and a host of physiological and behavioral changes. According to Sheridan (1962), migration timing of juvenile salmon to the open ocean is keyed to take advantage of optimal water temperatures, salinities, and food availability. In our study, before juvenile salmon arrived in the habitats, temperatures were relatively low, but their arrival at successive habitats along the migration corridor corresponded with peaking temperatures. Additionally, in spring as juveniles arrived at inshore and strait habitats, ZSV increased and was soon at a seasonal peak. In contrast, when most juvenile

salmon reached the coastal habitat later in the season, the ZSV were already declining. However, by that time juvenile salmon rely on neustonic fauna and fish prey, taxa different from and larger than those captured in our small-mesh zooplankton samples (Landingham et al. 1998). Consequently, our low estimates of ZSV in the coastal habitats may not have been indicative of food supplies for arriving salmon. Therefore, in most habitats we studied, the timing of seaward migration of juvenile salmon coincided with seasonal peak periods of temperature and zooplankton.

In our study, the spatial and temporal occurrence of juvenile salmon in the marine waters of southeastern Alaska was relatively consistent between years and habitats, with peak salmon abundance in June and July. Juveniles were absent from these habitats in May because at that time in their life history they are distributed in shallow, littoral habitats (Jaenicke et al. 1985; Mortensen and Wertheimer 1988; Wertheimer and Celewycz 1996). Mortensen et al. (2000) found that peak emigration of pink and chum salmon fry from Auke Bay, Alaska, occurred in April and May; even late emigrants with the longest residencies were virtually absent by mid-July. In our study, juvenile salmon abundance peaked in most habitats in June and July, and declined in August through October. Thus, juvenile salmon migrate in the northern region of southeastern Alaska from littoral to neritic habitats from May to June and disperse to offshore habitats or travel outside the study area from July to August.

Adaptations of salmonids to oceanographic and feeding conditions are important because environmental conditions vary widely over their geographic range. Food requirements and fish behavior change with the physical and biological characteristics of habitat. Neither sea surface temperatures nor salinities have been found to consistently determine the distribution patterns

Table 5. Age and origin of recovered coded-wire tagged chinook and coho salmon sampled by rope trawl, May-October 1997-99.

| | | | Number of coded-wire-tagged fish recovered | | | | | | | |
|--------------|----------|-------------------------|--|---------|------|--------|-------------|-------|--|--|
| Species | Age* | Origin | May | June | July | August | SeptOct. | Total | | |
| | | | Inshore | habitat | | | | | | |
| Chinook | 1.0 | Southeastern Alaska | : | 5 | 9 | 4 | 3 | 21 | | |
| Coho | 1.0 | Southeastern Alaska | | 3 | 2 | - | | 5 | | |
| | | | Strait I | nabitat | | | | | | |
| Chinook | 1.0 | Southeastern Alaska | | | 1 | _ | - | 1 | | |
| | 1.1 | Southeastern Alaska | 3 | | 1 | | | 4 | | |
| | 1.2 | Southeastern Alaska | 1 | | - | | _ | 1 | | |
| | 1.3 | Southeastern Alaska | _ | | | 1 | - | 1 | | |
| Coho | 1.0 | Southeastern Alaska | _ | 17 | 7 | 3 | 1 | 28 | | |
| | | | Coastal | habitat | | | | | | |
| Chinook | 1.0 | Columbia River Basin | _ | 4 | | | | 4 | | |
| | 0.1 | Olympic Pen. Washington | | 1 | _ | | | 1 | | |
| Coho | 1.0 | Columbia River Basin | _ | _ | 1 | - | _ | 1 | | |
| | 1.0 | Southeastern Alaska | _ | | 11 | | | 1 | | |
| Total for al | habitats | | 4 | 30 | 22 | 8 | 4 | 68 | | |

^{*}European age notation: number preceding decimal point denotes the number of freshwater winters and the number following the decimal point denotes the number of ocean winters.

of salmon (Groot and Margolis 1991), yet differences in thermal tolerance among species have been noted. Coho and chinook salmon are most tolerant of high temperatures, sockeye salmon prefer cooler water, and pink and chum salmon show the least tolerance for high temperature (Brett 1952; Groot and Margolis 1991; Groot et al. 1995). Although salmon do not necessarily optimize their distribution within the range of physical environments they traverse, the physical environment affects their physiology and metabolism (Groot et al. 1995). For example, temperature significantly influences the rate of digestion in juvenile salmon and other fish (e.g., Brett and Higgs 1970; Bailey et al. 1975). In a laboratory study, Brett et al. (1969) demonstrated that optimal growth of juvenile sockeye occurred at 15°C under high rations and at 5°C under low rations. This shift to lower temperatures for optimum growth at lower rations occurred because the efficiency of food conversion improved, even though absolute growth rates also declined with temperature. Brett's experimental temperature range of 5-17°C brackets average temperatures observed in our study. Fish growth and tolerance for low temperatures were also influenced by water salinity (Brett 1952; Brett et al. 1969), and juvenile salmon are known to occupy waters of "sub-optimal" quality when motivated by food availability (Birtwell et al. 1999).

Predation on juvenile salmon observed in our study was estimated at 5%. This rate may have been artificially high because the trawl concentrated predators and prey. However, we observed predation in only 4 of the 19 species of salmon predators examined, so if netinduced predation was prevalent, other predator species should have been implicated. For example, walleye pollock (Theragra chalcogramma) have been identified as a major predator on juvenile salmon in Prince William Sound, Alaska (Willette et al. 1999), yet out of the 138 we examined over three years, none ate juvenile salmon. Strong year classes of key predators, such as sablefish, adult coho salmon, and spiny dogfish, may also impact salmon survival. Other studies have also identified predation on juvenile salmon by adult coho salmon (Wing 1985) and spiny dogfish (Beamish et al. 1992). The latter study noted that only a small percentage of predators actually preyed on salmon, but the resulting salmon mortality was believed to be high because of the large numbers of predators in the area. The availability of alternative prey resources may also buffer the effect of predation on salmon (Willette et al. 1999), and predation in other habitats or by avian predators (Scheel and Hough 1997) may be significant.

Density-dependent effects commonly indicate that carrying capacity has been exceeded. During the 1970s and 1980s, unprecedented hatchery production of salmonids occurred around the Pacific rim (Heard 1995). Coincident with this production were changes in forage fish communities, indicating environmental change. Declines in lipid-rich forage species, such as capelin,

and increases in lipid-poor species, such as gadids and flatfish, were correlated with trophic shifts and population declines among piscivorous seabirds (Anderson et al. 1997; Duffy 1998; Anderson et al. 1999) and with decadal-scale shifts in the Gulf of Alaska (GOA) oceanographic regime (Piatt and Anderson 1996). Evidence also exists for long-term changes in the prey resources of salmon and planktivorous forage fish (e.g., Brodeur and Ware 1992; Frost and Bollens 1992; Cooney et al. 1994; Tanasichuk 1998a, b; Aydin et al. 1999). If oceanographic regime shifts caused changes in GOA fish communities, coincident with increased hatchery production of salmon and decreased production of zooplankton prey resources, fish trophic interactions could have influenced food supplies. Abundance of competing planktivores is an important aspect of carrying capacity (Sturdevant 1999). Possible densitydependent food limitation among salmon has been documented in diminished size and older age of maturity of salmon stocks from numerous localities (Bigler et al. 1996). Studies focusing on the estimation of carrying capacity in southeastern and southcentral Alaska showed little impact of salmon on availability of their prey (Bailey et al. 1975; Cooney 1993). In contrast, studies off British Columbia and Washington indicated juvenile salmon cropped prey resources, which initiated emigration (Healey 1982; Simenstad and Salo 1982). Our results suggest that declining ZSV from July to August contributed to the emigration of juvenile salmon. This is consistent with Healy's (1982) proposal that poor feeding conditions in mid-summer resulted in the emigration of juvenile pink and chum salmon from the Strait of Georgia. Simenstad and Salo (1982) also suggested that foraging success and the availability of preferred prey items in Hood Canal, Washington, were related to migration rates of juvenile salmon out of estuarine and nearshore areas. They calculated a neritic carrying capacity for juvenile chum salmon of 10 to 70 fish per 1,000 m³ (Simenstad and Salo 1982). Our highest estimated densities for all species of juvenile salmon ranged from 1.1 to 5.6 fish per 1,000 m³, although further analysis of the diet and available prey fields of juvenile salmon in our region is needed to estimate its carrying capacity, and to link the spatial and temporal occurrence of salmon with localized feeding conditions.

The offshore distribution pattern of our juvenile salmon in coastal waters was similar to that found in other studies. Along the Icy Point coastal transect, most of our juvenile salmon occurred < 25 km of shore in all years; few occurred > 40 km. Off the coast of Oregon and Washington, Miller et al. (1983) found concentrations of juveniles only < 28 km of shore. Hartt and Dell (1986) characterized the coastal migration of juvenile salmon as a 37 km-wide band of fish off the coast of southeastern Alaska, where the continental shelf is narrow, and the band extends farther offshore in the north-

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ern Gulf of Alaska where the shelf widens. Distribution of juvenile salmon off the coast of southeastern Alaska has been documented to at least 74 km offshore in August (Jaenicke and Celewycz 1994).

Apparent growth of fish in our strait habitats tracked interannual changes in temperature and ZSV. Both stock-specific and mixed stock estimates of chum salmon growth showed a similar decline with temperature and ZSV. In Auke Bay, Mortensen et al. (2000) found that water temperature was the main factor determining growth of juvenile pink salmon during their early marine period, but prey limitation was also implicated. Mortensen et al. (2000) showed that early spring emigrants exposed to 5-7°C had lower growth rates than later emigrants exposed to 9-11°C. We found interannual temperature declines on the order of 2°C coincident with declining growth rates in strait habitats in June and July. Therefore, our findings for slightly older iuvenile pink and chum salmon in strait habitats support the conclusions of Mortensen et al. (2000).

Stocks of juvenile chinook and coho salmon appear to have marine migration rates differing by origin and species. We determined migration rates for Alaska stocks to be 1.3 km/d for chinook salmon and 3.2 km/d for coho salmon, whereas migration rates for CRB stocks of these species were 19.1 and 28.6 km/d. Off the coast of Oregon and Washington, Fisher and Pearcy (1994) found chinook salmon stocks (primarily CRB) migrating 4.4 km/d and Pearcy and Fisher (1988) found northward-migrating coho salmon stocks traveling 11.0 km/d within 10 days of release. Off southeastern Alaska, Orsi and Jaenicke (1996) found stream-type (age 1.0) chinook salmon of Alaska stocks migrating 0.3 km/d, British Columbia stocks migrating 0.9 km/d, and CRB stocks migrating 6.9 km/d. Thus, it appears juvenile chinook salmon migrate slower than coho salmon, and CRB stocks of both species migrate rapidly along the Alaska coast.

CWT juvenile stream-type chinook salmon from the CRB captured off southeastern Alaska in June have important implications to the life-history strategies of these stocks, many of which are threatened or endangered. Our recoveries of CRB juvenile chinook salmon in June are significant because previous recoveries of these fish off Alaska have occurred only in September and October (Hartt and Dell 1986; Orsi and Jaenicke 1996). Our documented 3-4 month earlier occurrence of these stocks off Alaska indicates they may have a critical marine-entry period. Therefore, any natural or artificial impediments delaying entry of these stocks to the estuary could jeopardize their opportunities to initiate ocean migration at the proper time, thereby minimizing their access to suitable marine habitat and impacting survival.

Our results suggest juvenile salmon have seasonal habitat use patterns synchronous with environmental changes, and display distinct species- and stockdependent migration patterns. A long-term seasonal monitoring program during the early marine life-history stage of juvenile salmon enables researchers to adequately identify complex stock-specific information and trophic interaction necessary to understand relationships among habitat use, marine growth, year-class strength, and ocean carrying capacity.

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