

Abstract—Juvenile chinook salmon, *Oncorhynchus tshawytscha*, from natal streams in California's Central Valley demonstrated little estuarine dependency but grew rapidly once in coastal waters. We collected juvenile chinook salmon at locations spanning the San Francisco Estuary from the western side of the freshwater delta— at the confluence of the Sacramento and San Joaquin Rivers— to the estuary exit at the Golden Gate and in the coastal waters of the Gulf of the Farallones. Juveniles spent about 40 d migrating through the estuary at an estimated rate of 1.6 km/d or faster during their migration season (May and June 1997) toward the ocean. Mean growth in length (0.18 mm/d) and weight (0.02 g/d) was insignificant in young chinook salmon while in the estuary, but estimated daily growth of 0.6 mm/d and 0.5 g/d in the ocean was rapid ($P \leq 0.001$). Condition (K factor) declined in the estuary, but improved markedly in ocean fish. Total body protein, total lipid, triacylglycerols (TAG), polar lipids, cholesterol, and nonesterified fatty acids concentrations did not change in juveniles in the estuary, but total lipid and TAG were depleted in ocean juveniles. As young chinook migrated from freshwater to the ocean, their prey changed progressively in importance from invertebrates to fish larvae. Once in coastal waters, juvenile salmon appear to employ a strategy of rapid growth at the expense of energy reserves to increase survival potential. In 1997, environmental conditions did not impede development: freshwater discharge was above average and water temperatures were only slightly elevated, within the species' tolerance. Data suggest that chinook salmon from California's Central Valley have evolved a strong ecological propensity for a ocean-type life history. But unlike populations in the Pacific Northwest, they show little estuarine dependency and proceed to the ocean to benefit from the upwelling-driven, biologically productive coastal waters.

Manuscript accepted 23 August 2001.
Fish. Bull. 100:244–257 (2002).

Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California*

R. Bruce MacFarlane
Elizabeth C. Norton

Santa Cruz Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
110 Shaffer Road
Santa Cruz, California 95060

E-mail address (for R. B. MacFarlane): Bruce.MacFarlane@noaa.gov



Estuaries are considered important in the development of juvenile salmon. In the Pacific Northwest, estuaries have been shown to provide nursery and rearing conditions for juveniles emigrating from streams of birth to the ocean (Reimers, 1973; Healey, 1982; Levy and Northcote, 1982; Myers and Horton, 1982; Simenstad et al., 1982; McCabe et al., 1986). The San Francisco Estuary is the largest estuary on the West Coast and is a segment in the migration corridor for chinook salmon (*Oncorhynchus tshawytscha*) from natal streams in the watersheds of the Sacramento and San Joaquin Rivers, known as California's Central Valley. The Central Valley is unique by having four runs of chinook salmon which constitute a significant socioeconomic resource. Ocean harvest south of Pt. Arena (estimated as 85–95% from Central Valley stocks) and spawning escapement range between 0.5 and 1.3×10^6 chinook salmon per year (1970–98) and represent about \$60 million (U.S.) in personal income annually (PFMC¹). Beyond the direct value of Central Valley chinook salmon, their demography and welfare significantly affect the financial and societal aspects of water rights decisions.

Chinook salmon populations migrating through the San Francisco Estuary are at the southern limit of the species' geographical range and are subject to the impacts of a highly urbanized, industrialized, and agricultural freshwater and estuarine system (Nichols et al., 1986). All chinook salmon runs originating in the Central Valley are in jeopard-

dy. Before 1900, spawning runs were estimated at 2×10^6 adults (Fisher, 1994), but in 1998 only an estimated 0.25×10^6 returned of which about 30% were of hatchery origin (PFMC¹). The Sacramento River winter-run chinook was the first Pacific salmonid species listed under the U.S. Endangered Species Act of 1973 (ESA). Originally categorized as threatened in 1989, its status was changed to endangered in 1994. Chinook salmon of the Central Valley spring run, once forming the dominant chinook race in California (Clark, 1929), were listed as threatened in 1999. Even the fall run, by far the dominant run today (92% of all Central Valley spawners, 1990–98 [PFMC¹]), has uncertain status and is an ESA candidate. Hatchery production supports the natural fall run, and the other runs to a much lesser degree. Annually, about 35 million chinook salmon are produced by state and federal hatcheries in the Central Valley; the fall run comprises 95% (Mills et al., 1997).

California and federal water development projects, such as dams and water diversions, have clearly played a role in the decline of Central Valley salmon (Moyle, 1994), but other factors may al-

* Contribution 114 of Santa Cruz Laboratory, National Marine Fisheries Service, NOAA, Santa Cruz, CA 95060.

¹ PFMC (Pacific Fishery Management Council). 1999. Review of 1998 ocean salmon fisheries. Pacific Fisheries Management Council, Portland, OR, 65 p. PFMC, 2130 SW Fifth Ave., Suite 224, Portland, OR 97201.

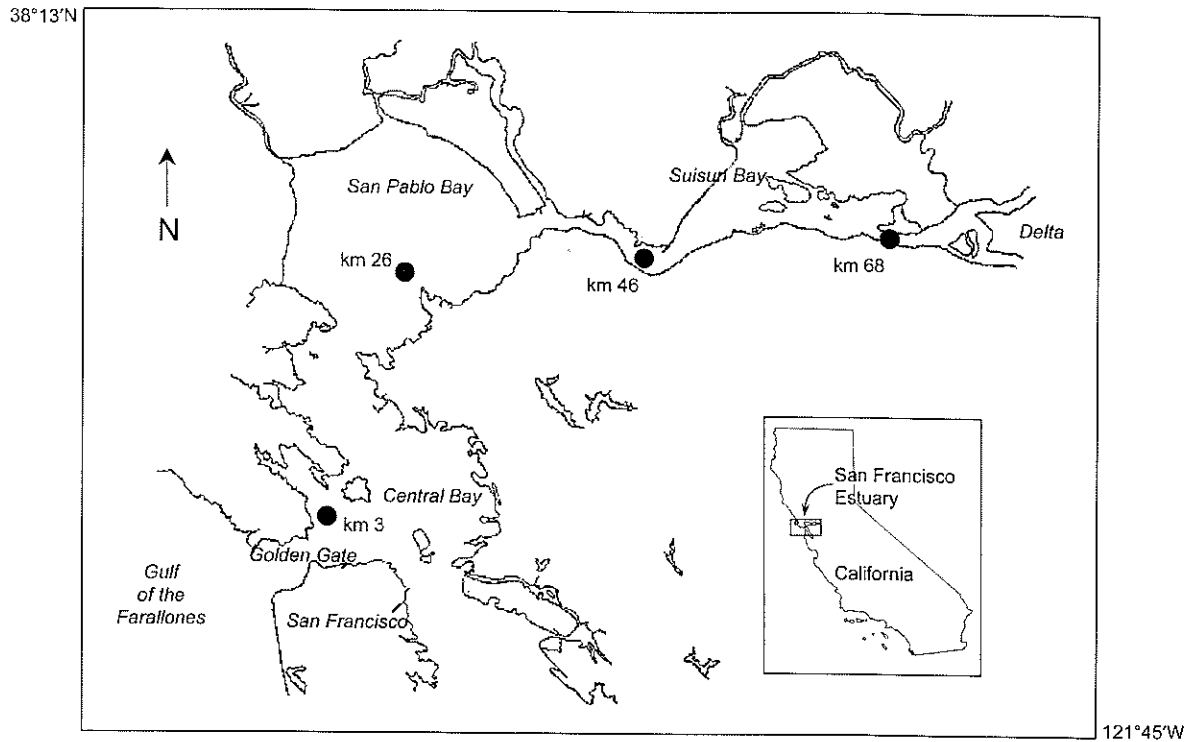


Figure 1

The northern portion of the San Francisco Estuary and nearshore Gulf of the Farallones. Juvenile salmon collection locations are denoted as km (e.g. km 26) from the estuary exit at the Golden Gate. Juvenile salmon were collected throughout the nearshore area in the Gulf of the Farallones, not at specific locations.

so be involved. Migration through the highly impacted San Francisco Estuary and early residence in a marine environment at the southern margin of the species' distribution may impair physiological development that could lead to direct mortality or, indirectly, to reduced survival potential during the oceanic phase.

Although some data exist on abundance, growth, and feeding for chinook salmon migrating through estuaries in southeastern Alaska and British Columbia (Healey, 1980b, 1982; Levy and Northcote, 1982; Landingham et al., 1998); Washington and Oregon (Reimers, 1973; Myers and Horton, 1982; Simenstad, et al. 1982; McCabe et al., 1986; Fisher and Pearcy, 1996); and the Klamath River estuary in northern California (Wallace and Collins, 1997), the only data available for Central Valley emigrants are those of Kjelson et al. (1982). In that paper, life history descriptions were presented for fall-run juveniles, but the emphasis was on fry (≤ 70 mm fork length) in the freshwater delta at the head of the estuary. Almost nothing is known of juvenile chinook biology in the larger saline portions of the San Francisco Estuary.

Knowledge of juvenile chinook salmon biology during their first year in the marine environment is even more limited, and nonexistent for the area south of the California-Oregon border. Healey (1980a) presented distribution, growth, and feeding information on first ocean-year chinook salmon in the Strait of Georgia, British Colum-

bia. Similar data have been presented for juvenile chinook from the Columbia River drainage off the Oregon and Washington coasts (Miller et al., 1983; Brodeur and Pearcy, 1990; Fisher and Pearcy, 1995).

The purpose of this study was to describe juvenile chinook salmon physiological development during their emigration through the San Francisco Estuary and early residence in the coastal waters of central California. Residence time, age, growth, condition, lipid classes and protein concentrations, and feeding data are presented to characterize the significance of habitat utilization at the southern limit of the species' distribution. The information presented here can serve as a basis for comparison with other year classes from the Central Valley and with populations from more northerly estuaries, as well as for assessments of the influences of natural and anthropogenic perturbations on salmon habitat.

Methods

Study area

Juvenile salmon leaving California's Central Valley pass through the San Francisco Estuary, a series of embayments, before entering the ocean in the Gulf of the Farallones (Fig. 1). The delta, a freshwater network of channels and leveed

islands at the confluence of the Sacramento and San Joaquin Rivers, forms the eastern boundary. Measurable salinity (>1 psu) occurs on the western side of the delta in Suisun Bay. Water flows through Suisun Bay into San Pablo Bay, then into the Central Bay of San Francisco Bay before exiting the estuary at the Golden Gate. The estuary has a surface area of about 1100 km² and is fringed on the northern shore with marshes, which have shrunk by more than 90%, to 125 km², since 1850 (Conomos, 1979). Most of the estuary shoreline is urban, suburban, and industrial development, however. The Gulf of the Farallones, a relatively broad expanse of the continental shelf extending from Pt. Reyes (38°00'N, 123°01'W) to Pillar Pt. (37°30'N, 122°30'W) to the Farallon Islands (Southeast Farallon Island- 37°42'N, 123°00'W) on the edge of the continental shelf, ranges to 90 m but is mostly 20 to 50 m deep. This hydrodynamically complex area is influenced by the cool southerly flowing California Current; freshwater discharge from the San Francisco Estuary; and seasonally strong coastal upwelling (spring and summer) and a northerly flowing countercurrent, the Davidson Current (winter).

Field sampling

Juvenile chinook salmon in this study were collected from the fall run, as determined by the daily length criteria used to discriminate juveniles among the four runs (Johnson et al., 1992). Because salmon from the four runs are phenotypically indistinguishable, to target fall-run juveniles we used daily length criteria and collected fish during the period when fall-run chinook salmon dominate the migration toward the ocean.

We collected juvenile chinook salmon at four locations spanning the San Francisco Estuary (Fig. 1): at km 68, the west side of the delta at the confluence of the Sacramento and San Joaquin Rivers; km 46, the exit from Suisun Bay; km 26 in San Pablo Bay; and several sites within a 1-km radius of km 3 for greater coverage of the estuary exit at the Golden Gate and to avoid ship traffic. Two multiday surveys of the estuary were completed starting at km 68 and proceeding through successive downstream locations to the Golden Gate. The first sampling date was 30 April 1997 at km 68; the last was 15 July 1997 at km 3.

Collections were made in the estuary with a midwater trawl towed at 2-3 knots for 15-30 min. The trawl was made of nylon mesh with a 10-m headrope and footrope, 10-m height at the mouth, and 20-m length. Mesh size was 1.6 cm at the headrope and decreased to 0.4 cm before the codend. The codend was fitted with a 1.27-cm knotless mesh liner. The net was kept open by aluminum spreaders and depressors. For most tows, the spreaders were visible at the surface, confirming that the net fished the upper layer of the water column.

Juvenile chinook salmon were also obtained from the coastal ocean in the Gulf of the Farallones. Stations where salmon were caught were within 15 km of the Golden Gate in waters 18 to 36 m deep. A high-speed midwater rope trawl was towed at 3-4 knots for 15-30 min at each site. The net had a 53-m headrope and footrope with a 1.27-cm mesh codend liner (Dotson and Griffith, 1996). Tempera-

ture-depth recorders attached to the footrope and headrope indicated that the net fished 5-10 m below the surface with a vertical opening of 13 m.

Fish were removed from the net as soon as practicable and placed in labeled plastic zip-top bags. Juveniles captured within the estuary were kept under ice; those from the ocean were stored at -80°C, until returned to the laboratory.

We collected hydrologic data during all field trips. Within the estuary, a Hydrolab H20® Multiprobe connected by cable to a Surveyor 3® data logger (Hydrolab Corp., Austin, TX) was used to record vertical profiles of temperature, salinity, dissolved oxygen, pH, and turbidity. In the Gulf of the Farallones, a SeaCat SBE 19-03® (Sea-Bird Electronics, Inc., Bellevue, WA) conductivity-temperature-depth sonde (CTD) recorded profiles of temperature and salinity in a grid of stations spaced at 2' latitude and longitude intervals encompassing the salmon fishing sites.

Laboratory analyses

In the laboratory, we examined, measured, and dissected fish, usually within 24 h of capture. Fork length and total body weight were recorded. The peritoneal cavity was opened by incision along the ventral side from vent to opercular isthmus. The stomach and its contents were removed and stored in 10% buffered formalin for subsequent analysis of prey. Sagittal otoliths were removed, cleaned of membranes, rinsed in deionized water, and stored for subsequent aging. The remaining portion of the fish was placed in a Whirl® bag, purged with N₂, and stored at -80°C for lipid and protein analyses.

Heads of juvenile salmon containing coded-wire tags, evident by a missing adipose fin, were removed and sent to the U.S. Fish and Wildlife Service, Stockton, CA, to obtain data on the location and time of release of each fish.

Concentrations of lipid classes and total protein were determined in 15 fish randomly chosen from each location. Heads, fins, and stomachs were removed to limit analyses to body constituents. Frozen bodies were minced with a knife, then homogenized in a blender for about 30 sec to a uniform paste. We extracted lipids from a 1g- to 3g-aliquot by using the method of Bligh and Dyer (1959). Total lipid was quantified by thin-layer chromatography with flame-ionization detection with an Iatroscan TH-10 Mark V® (Iatron Laboratories, Inc., Tokyo, Japan) according to procedures published previously (MacFarlane et al., 1990, 1993). Total lipid was separated into steryl or wax ester, triacylglycerols, nonesterified fatty acids, cholesterol, and polar lipid classes and quantified according to methods in MacFarlane and Norton (1999). We estimated total protein concentration by the Lowry method, using bovine serum albumin as a standard (Lowry et al., 1951). All lipid and protein values are expressed as wet weight (mg/g).

Fish ages were estimated from otolith analysis (Brothers, 1987). Sagittae were embedded in epoxy, then ground and polished on the distal surface to a mid-sagittal section. Otolith concentric bands were counted under oil immersion with transmitted polarized light illumination into a video microscopy system at a monitor magnification

of 1500x. Counts representing daily increments of growth were made from the otolith margin (dorsal edge) to a posterior primordium. Each otolith was counted at least two times by the same reader. Data are presented as age, in days, between the hatching check and the otolith margin.

Stomach contents were identified and quantified according to methods of Hobson and Chess (1976). Prey were identified to the lowest possible taxa, enumerated, and their relative volume and size distribution recorded. The derived parameter, index of relative importance (IRI), was used to determine the importance of specific taxa to juvenile salmon at each sampling location. The IRI was computed by the equation

$$IRI = (N + V)FO,$$

where N , V , and FO = the percent number, volume, and frequency of occurrence, respectively, of a taxon in the stomach contents (Pinkas et al., 1971).

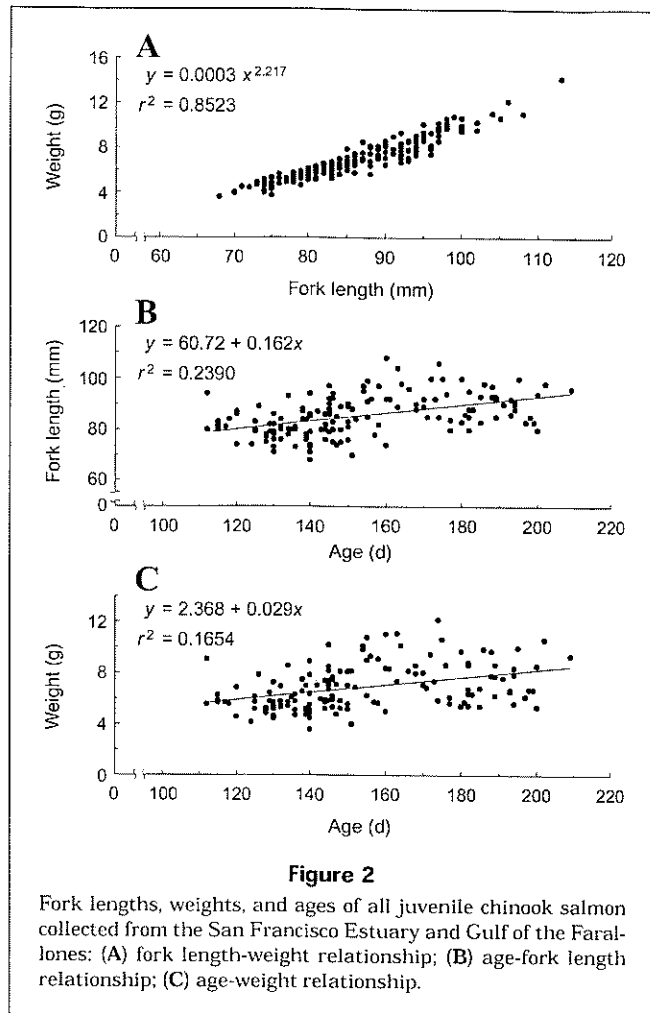
Size, age, condition, lipids, and protein data were analyzed for variability among locations by means of the general linear model of analysis of variance. Differences among specific locations were determined with Tukey's studentized range test, set at $\alpha = 0.05$, which controls for MEER (maximum experimentwise error rate) under complete or partial null hypotheses. All statistical procedures were performed with SAS software (SAS Institute, Inc., 1994).

Results

We collected and evaluated 310 subyearling chinook salmon from the 1996-97 year class. The catch consisted of naturally spawned and hatchery-produced fish of unknown proportions because less than 3% were marked (by adipose fin clips and coded wire tags) and there were no morphological features to distinguish hatchery from naturally produced salmon. Mean fork length (FL) was 89 mm and ranged from 68 to 113 mm. Total body weights ranged from 3.59 to 14.62 g, with a mean of 7.58 g. A power function was fitted to the relationship between FL and weight (Fig. 2A). Ages were determined for 156 juveniles and ranged from 112 to 209 days after hatching. The relationship of FL or weight to age was not as well fitted as that for weight on FL (Fig. 2, B and C); however, length and weight were positively correlated to age ($P < 0.0001$).

Each sampling location within the estuary was visited more than once on successive surveys through the 30 April-15 July period of juvenile emigration. There were no statistically significant trends in size, age, lipid, and protein variables by sampling date at any location; therefore we combined data for each location from both surveys through the estuary.

While in the estuary, juvenile chinook salmon grew little in length or weight; but in coastal waters, they grew



rapidly (Fig. 3). Juveniles entering the estuary at km 68 had a mean (\pm SE) FL of 82.8 ± 0.7 mm and weight of 6.36 ± 0.21 g. At the exit of the estuary (km 3), mean FL and weight of cohorts were 89.5 ± 1.1 mm and 7.23 ± 0.30 g, representing mean gains of about 7 mm and 0.9 g. Size changes within the estuary were not statistically significant ($P > 0.05$). Year-class cohorts in the coastal waters of the Gulf of the Farallones were significantly longer and heavier than those from the estuary (FL, $P < 0.0001$; weight, $P < 0.001$). Ocean-caught juveniles were 8.2 mm longer and weighed 6.5 g more than fish collected near the estuary exit.

Juvenile salmon spent about 40 d migrating along the 65-km length of the estuary, according to otolith increment counts (Fig. 3C). Mean age at the entry to the estuary was 136 ± 2 d; at the exit it was 176 ± 3 d. Juveniles aged from the Gulf of the Farallones were 156 ± 5 days old, indicating a shorter freshwater or estuarine residence than that for those captured from the Golden Gate area.

Daily growth rates in the estuary can be calculated from differences in mean size over the 40-d estimated time of

transit. According to this technique, mean daily growth was about 0.18 mm/d and 0.02 g/d.

Because we aged only a subset of fish from each sampling location, mean age of all fish obtained at each site could be estimated with the FL-on-age regression equation for age (Fig. 2B). Results of that computation revealed close agreement with measured ages at all locations except the Gulf of the Farallones (Fig. 3C), where calculated age was 189 ± 8 d. Both methods of age determination indicated that juveniles caught in coastal waters were from the same year class.

The average migration rate through the estuary was estimated at 1.6 km/d on the basis of the difference between mean ages of juvenile salmon sampled at the estuary entry and exit (i.e. 65 km/[176 d at km 3 - 136 d at km 68]). Data from coded-wire-tagged fish caught within the estuary and the Gulf of the Farallones revealed a wide range of migration rates (Table 1). For those captured within the estuary (17 of 24), the mean migration rate was 4.0 ± 0.9 km/d. Most tagged-recaptured salmon had rates ≤ 2.6 km/d

but were from two releases within the estuary, thus representing migration rates in the lower estuary only. Juveniles released farther upstream in the rivers and caught in the lower estuary had somewhat faster migration rates ($\bar{x}=9.1 \pm 2.5$ km/d, $n=4$).

Not only did juvenile chinook salmon grow slowly while in the estuary, their condition declined as they proceeded to the Golden Gate (Fig. 4). There was a significant decrease in Fulton's condition factor (K) between fish entering the estuary and those departing ($P<0.001$). Once the fish were in coastal waters, however, their condition improved markedly.

Body constituents and energy reserves varied little while migrating fish were in the estuary, but total lipid was depleted in fish from the Gulf of the Farallones (Fig. 5A). Total body protein concentrations were approximately 150 mg/g, wet weight, in fish from all locations, and did not vary significantly. Total lipid also did not vary in fish within the estuary but was significantly lower in salmon caught in the ocean ($P<0.0005$). Mean lipid concentration for fish in the estuary was about 30 mg/g, or 15% of dry weight, and decreased to 17.7 ± 1.6 mg/g in the ocean. The decline in lipids in fish from the Gulf of the Farallones was attributed to decreased concentrations of triacylglycerols (TAG), the dominant lipid class (Fig. 5B). TAG levels increased from 14.8 ± 2.5 mg/g in fish entering the estuary to about 18 mg/g in estuarine salmon and were depleted to 4.3 ± 1.4 mg/g in coastal fish. The concentration of polar lipids, composed primarily of phospholipids, remained unchanged through the estuary and in the ocean. Other lipid classes- cholesterol and nonesterified fatty acids- were found at much lower concentrations and did not vary significantly during the emigration. Steryl or wax esters were absent or at very low levels in most individuals and showed no differences related to location.

We examined feeding and prey selectivity in juvenile chinook salmon migrating through the estuary and in coastal waters. A lesser proportion of fish leaving the rivers contained food items compared with those within the estuary. Fifty percent of juvenile salmon had stomach contents at Chipps Island (km 68, 21 of 42 sampled). In contrast, more than 80% from Carquinez Strait (km 46, 8 of 10 samples) and San Pablo Bay (km 26, 20 of 23 samples) had prey in their stomachs. A lower percentage (70%) from the Central Bay (km 3, 9 of 13) had fed recently, but in the Gulf of the Farallones, 82% (23 of 28) of the juveniles contained food.

The relative importance of prey items varied as juvenile salmon migrated through the estuary and entered the ocean (Table 2). Stomachs of juveniles leaving the rivers contained primarily gammaridean amphipods *Corophium* sp., and lesser amounts of crab megalopae, dipteran insects, other malacostracan crustaceans, and other insects. After the salmon passed through Suisun Bay (km 46), their stomachs contained mostly the hemipteran *Hesperocorixa* sp., the calanoid copepod *Eucalanus californicus*, the mysid *Acanthomysis* sp., fish larvae, and other insects. Cumaceans were clearly dominant in juvenile salmon in San Pablo Bay (km 26), but

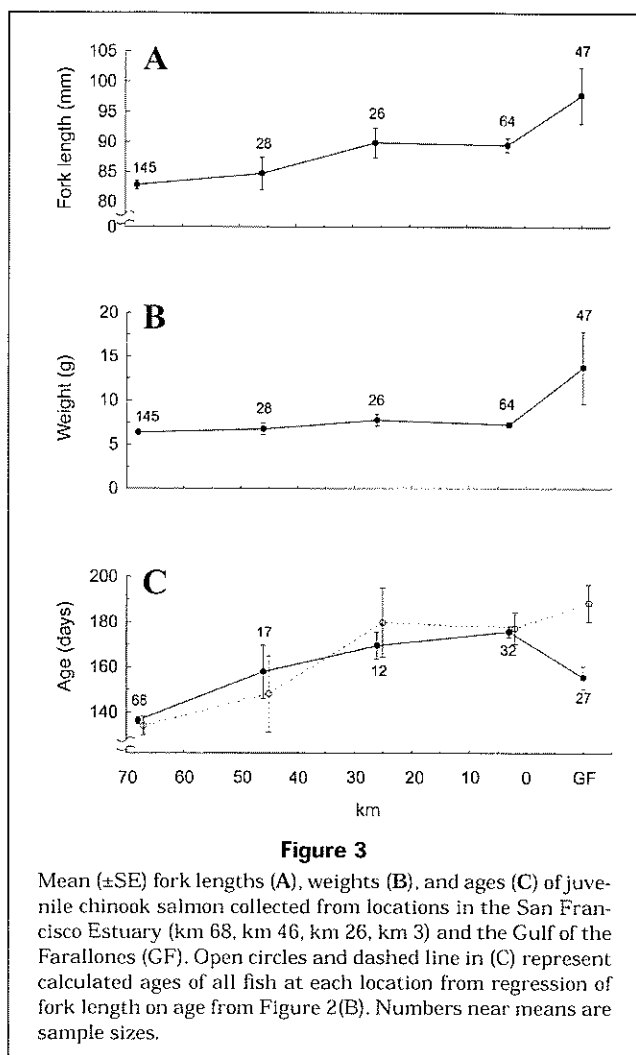


Table 1
Minimum distance traveled by coded-wire tagged juvenile chinook salmon between marking and recapture.

Release			Capture			Km traveled	Days free	Km/d traveled
Date	Location	km	Date	Location	km ¹			
1 Apr 1997	Battle Creek	470	12 May 1997	Gulf of Farallones	- 19	489	41	11.93
15 Apr 1997	West Sacramento	157	9 May 1997	Gulf of Farallones	- 19	176	24	7.33
16 Apr 1997	Battle Creek	470	11 May 1997	Gulf of Farallones	- 17	487	25	19.48
24 Apr 1997	Gridley Boat Ramp	244	29 May 1997	Pt. San Pablo	17	227	35	6.49
24 Apr 1997	San Pablo Bay	37	10 May 1997	Gulf of Farallones	- 22	59	16	3.69
24 Apr 1997	Gridley Boat Ramp	244	11 May 1997	Gulf of Farallones	- 20	264	17	15.53
28 Apr 1997	Mossdale	150	12 May 1997	Gulf of Farallones	- 20	170	14	12.14
29 Apr 1997	Dos Reis Park	146	27 May 1997	Carquinez Strait	46	100	28	3.57
29 Apr 1997	Dos Reis Park	146	11 May 1997	Gulf of Farallones	- 20	166	12	13.83
14 May 1997	Hatfield State Park	221	29 May 1997	Pt. Pinole	26	195	15	13.00
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. Pinole	26	17	10	1.70
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
19 May 1997	Benicia	43	29 May 1997	Pt. San Pablo	17	26	10	2.60
30 May 1997	Woodbridge Dam	149	Jun 10 1997	Golden Gate	0	149	11	13.55

¹Negative km data represent distance captured seaward of the Golden Gate.

insects were still important. In the Central Bay, the final embayment before the estuary exit, fish larvae were the dominant forage item. *Ampelisca abdita*, a gammaridean amphipod, and cumaceans were important as well. Fish larvae continued to be the most important prey of juvenile chinook salmon in the coastal waters of the Gulf of the Farallones, but euphausiids and decapod early life stages were also consumed in significant numbers.

Discussion

Chinook salmon from California's Central Valley streams have a largely ocean-type life history although perhaps a few spring and late-fall run juveniles overwinter in freshwater and migrate to the ocean as yearlings (Fisher, 1994; Myers et al., 1998). Fry (<70 mm FL) are abundant in the freshwater delta from February to April. They leave as smolts (>70 mm FL) and enter the San Francisco Estuary, primarily in May and June. Kjelson et al. (1982) reported that few juveniles were present in the delta or estuary

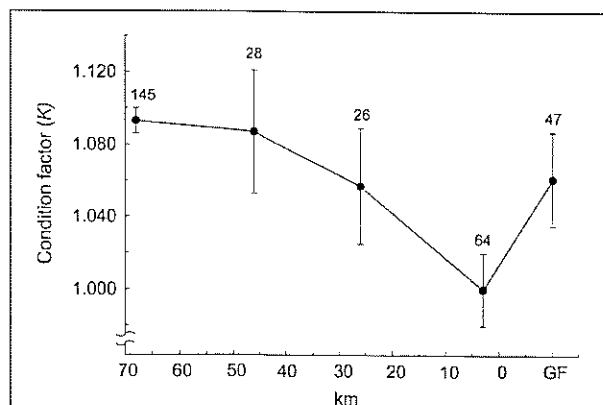


Figure 4

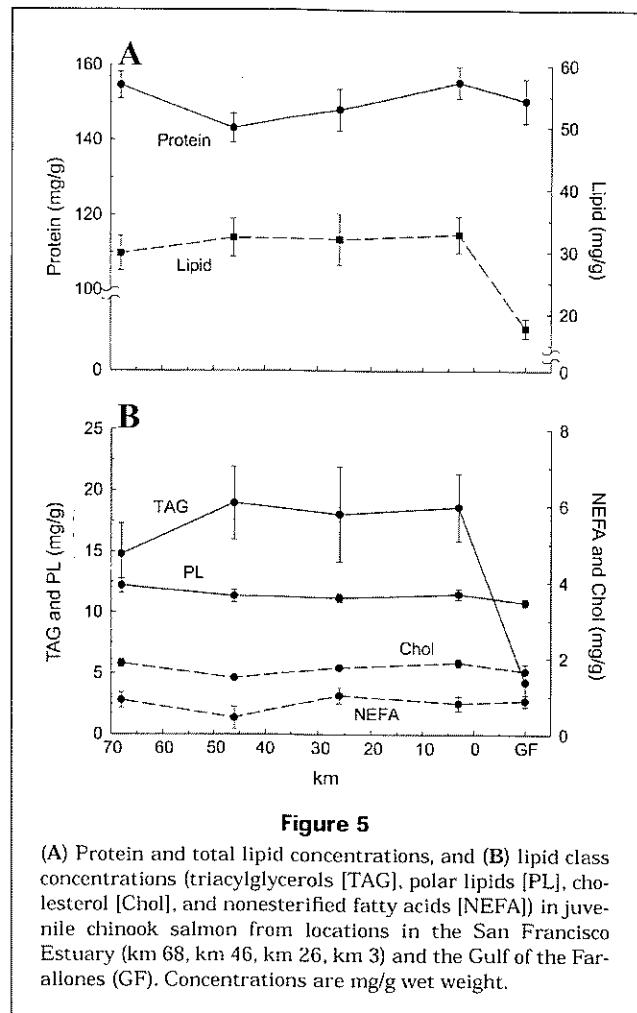
Changes in mean (\pm SE) Fulton's condition factor (K) of juvenile chinook salmon from locations in the San Francisco Estuary (km 68, km 46, km 26, km 3) and the Gulf of the Farallones (GF). Numbers above means are sample sizes.

after June. Our findings concur: the smallest salmon we caught was 68 mm FL, and we caught no fish after 27 June. Juveniles were approximately 4.5 months old (after hatching) when they entered the San Francisco Estuary. They spent about 40 days there, migrating at 1.6 km/d, based on mean age differences of fish entering the estuary and fish leaving at the Golden Gate. This is probably a minimum estimate of migration rate, because data from tagged fish caught within the estuary showed rates of 1.70 to 13.55 km/d, representing residence times of 38 to 5 days. A previous mark-recapture study also found higher migration rates (10 to 18 km/d), although the data were for passage through the upstream delta (Kjelson et al., 1982).

Studies in the Pacific Northwest suggest that juveniles of ocean-type chinook salmon make extensive use of estuaries, spending as much as 6 to 9 months in them feeding and growing (Myers and Horton, 1982; Simenstad et al., 1982; Healey, 1991). In the Columbia River estuary, subyearling chinook salmon were present throughout the year, although most abundant in May to September (McCabe et al., 1986). Fall-run juveniles entered the Sixes River estuary in the spring and were abundant from June through August (Reimers, 1973). Juvenile chinook salmon resided in Washington estuaries for 6 to more than 29 weeks, but some individuals were present for up to 189 d (Simenstad et al., 1982). Even in northern California's Klamath River estuary, juvenile fall-run chinook salmon remained from June to September (Wallace and Collins, 1997). The relatively short period of abundance in the San Francisco Estuary and emigration rates presented here suggest that juvenile chinook from the Central Valley may derive less benefit from estuarine residence than do more northerly populations.

Juvenile chinook salmon grew little while in the San Francisco Estuary. Though growth was not statistically significant, on average they increased in size by 7 mm FL and 0.9 g, representing daily growth of 0.18 mm/d and 0.02 g/d. These estimates indicate slower growth than has been reported for juvenile chinook in most estuaries to the north. In five estuaries on Vancouver Island and the Fraser River, juveniles grew 0.21 to 0.62 mm/d (Levy and Northcote, 1982; Healey, 1991). Growth measurements from population sampling and from following marked fish produced similar results in the Sixes River estuary, where daily growth ranged from 0.07 mm/d in summer to 0.9 mm/d in spring (Reimers, 1973). Reimers speculated that the very slow growth during summer was due to food limitation caused by high salmon abundance.

Growth can also be inferred by the change in size of fish collected at the same locations from the beginning to the end of the emigration period. We found no significant increase in size at given locations within the estuary during the May-June emigration season. Kjelson et al. (1982) also found no change in smolt size in the delta from April to June. In contrast, the mean size of juvenile chinook salmon in the Columbia River estuary increased from March to December, suggesting substantial growth or immigration of larger fish during the season.



Although little growth occurred during estuarine residence, growth was rapid in the coastal waters of the Gulf of the Farallones. Juvenile ocean cohorts were 10% longer in mean FL and 90% heavier than those from the estuary, although size varied more in ocean residents than in chinook salmon within the estuary. Faster growth rates of juvenile chinook salmon in coastal waters than in estuaries have been reported from British Columbia (Healey, 1980a), and Oregon and Washington (Miller et al., 1983; Fisher and Pearcy, 1995), with rates of 1 mm/d and more. Daily growth rates of juveniles in the Gulf of the Farallones were difficult to determine because the mean age of the subset aged by otolith analysis was less than the mean age of fish at the estuary exit. But if the calculated age of ocean juveniles (from the regression of age on FL) is used, during the calculated 13 d of ocean residence they grew at about 0.6 mm/d and 0.5 g/d, well above rates while in the San Francisco Estuary.

Growth rate estimates from the regressions of FL or weight on age for all juveniles from both the estuary and gulf were 0.16 mm/d and 0.029 g/d. These results agree

Table 2

Stomach contents of juvenile chinook salmon. %N is the numerical percentage; %V is the percent relative volume; %FO is the frequency of occurrence percentage; and IRI is the index of relative importance, $(\%N + \%V)\%FO$.

Location and prey species	%N	%V	%FO	IRI	Location and prey species	%N	%V	%FO	IRI
km 68, Chipps Island (n=21)					km 26, San Pablo Bay (n=20) <i>continued</i>				
Malacostraca					Malacostraca				
Decapoda					Decapoda				
Caridean shrimp	2.6	5.7	4.8	39.3	Crab megalopae	0.5	0.3	35.0	28.0
Crab megalopae	7.7	10.0	19.0	336.3	Mysidacea				
Mysidacea					Unidentified	0.5	0.5	5.0	5.0
Unidentified	7.7	4.6	14.3	175.9	Cumacean				
Amphipoda					Unidentified	61.7	17.9	50.0	3980
Gammaridea	2.6	5.7	4.8	39.8	Amphipoda				
<i>Corophium</i> spp.	30.8	26.4	33.3	1905	Gammaridea				
Eusirdae unidentified	2.6	5.7	4.8	39.8	<i>Ampelisca abdita</i>	1.6	1.2	10.0	28.0
Isopoda					<i>Corophium</i> spp.	3.6	23.2	5.0	134.0
<i>Gnorimosphaero luta</i>	2.6	0.6	4.8	15.4	<i>Corophium spinicorne</i>	0.5	4.2	5.0	23.5
Insecta					<i>Maera</i> spp.	0.5	1.5	5.0	10.0
Hymenoptera					Unidentified	1.0	1.3	3.6	8.3
Unidentified	2.6	5.7	4.8	39.8	Cirripedia				
Homoptera					Thoracic				
Aphid	2.6	0.3	4.8	13.9	Barnacle cirri	1.6	1.3	10.0	29.0
Diptera					Insecta				
Flies unidentified	2.6	1.1	4.8	17.8	Coleoptera				
Culicidae	2.6	2.6	4.8	25.0	Unidentified	1.0	1.1	5.0	10.5
Unidentified	7.7	6.3	19.0	266.0	Hemiptera				
Unidentified	10.3	9.7	14.3	286.0	Unidentified	0.5	0.5	5.0	5.0
Algae					Homoptera				
Unidentified	5.2	11.4	9.5	157.7	Flatidae	0.5	0.3	5.0	4.0
Unidentified	7.7	4.0	4.8	56.2	Diptera				
km 46, Carquinez Strait (n=8)					Unidentified	1.6	1.0	15.0	39.0
Malacostraca					Lepidoptera	1.3	1.0	5.0	11.5
Mysidacea					Orthoptera	0.5	0.3	5.0	4.0
<i>Acanthomysis</i> spp.	3.9	17.0	12.5	257.5	Unidentified	10.4	12.7	25.0	577.5
Unidentified	2.0	6.0	12.5	100.	Polychaeta				
Amphipoda					Phyllodocida				
Gammaridea	3.9	3.0	12.5	86.3	Nereidae	1.0	4.7	10.0	57.0
Cumacea	5.9	5.0	12.5	136.3	Unidentified	1.6	8.2	15.0	147.0
Copepoda					Pisces				
Calanoida					Unidentified larvae	0.5	2.4	5.0	14.5
<i>Eucalanus californicus</i>	5.9	15.0	12.5	261.3	Unidentified	0.5	1.6	5.0	10.5
Insecta					Algae				
Coleoptera					Unidentified	8.8	8.7	30.0	10.5
Unidentified	2.0	14.0	12.5	200.0	Unidentified	0.5	0.3	5.0	4.0
Hemiptera					km 3, Central Bay (n=10)				
<i>Hesperocorixa</i> spp.	72.5	1.0	12.5	918.8	Crustacean				
Unidentified	2.0	20.0	12.5	275.0	Unidentified	-	1.2	10.0	-
Pisces					Malacostraca				
Unidentified	2.9	19.0	12.5	273.8	Decapoda				
km 26, San Pablo Bay (n=20)					Crab megalopae	1.2	0.1	10.0	13.0
Crustacean									
Unidentified	-	2.9	5.0	-					

continued

Table 2 (continued)

Location and prey species	%N	%V	%FO	IRI	Location and prey species	%N	%V	%FO	IRI
km 3, Central Bay (n=10) continued					Gulf of the Farallones (n=23) continued				
Cumacean					Crab megalopae	2.1	7.3	21.7	204.0
Unidentified	45.1	11.1	20.0	1124	Crab zoea	6.8	6.6	26.0	348.4
Amphipoda					Caridean shrimp	0.9	1.2	13.0	27.3
Gammaridea					Euphausiacea				
<i>Ampelisca abdita</i>	20.7	8.6	60.0	1758	<i>Thysanoessa gregaria</i>	6.2	2.6	13.0	114.4
Copepoda					Unidentified	24.9	18.5	47.8	2075
Siphonostomatoidea	1.2	1.2	10.0	24.0	Amphipoda				
Cirripedia					<i>Caprella californica</i>	0.3	-	4.3	-
Thoracica					Insecta				
Barnacle cirri	1.2	1.2	10.0	24.0	Coleoptera				
Insecta					Unidentified	0.3	0.3	8.7	5.2
Unidentified	8.5	1.2	20.0	194.0	Hymenoptera				
Polychaeta					Unidentified	2.1	1.2	8.7	2.3
Phyllodocida					Homoptera				
Nereidae	1.2	2.5	10.0	37.0	Aphid	2.1	0.9	17.4	52.2
Unidentified	1.2	3.7	10.0	49.0	Diptera				
Pisces					Culicidae	0.3	0.1	4.3	1.7
Unidentified larvae	14.6	55.4	60.0	4200	Unidentified	5.3	3.7	21.7	195.3
Unidentified	1.2	10.5	10.0	117.0	Arachnida				
Algae					Araneae				
Unidentified	3.7	3.1	10.0	68.0	Unidentified	0.3	0.2	4.3	2.2
Gulf of the Farallones (n=23)					Polychaeta				
Gastropoda	0.3	0.2	4.3	2.2	Phyllodocida				
Malacostraca					Nereidae	0.3	0.5	4.3	3.4
Decapoda					Pisces				
<i>Cancer magister</i> (juv)	1.5	6.9	26.0	218.4	Unidentified larvae	46.3	49.9	70.0	6545

well with growth estimated by differences in mean values at the entrance and exit of the estuary.

Further evidence that residence in the San Francisco Estuary was not beneficial to juvenile salmon was their decline in condition (K -factor) while migrating through the estuary. But, along with faster growth, condition improved markedly in juveniles in coastal waters. Changes in K can be due to several causes, including stomach fullness and metabolic state. In an associated study of contaminants, the weight of stomach contents was measured at the same locations and dates as the ones described here. Stomach contents were $0.5\% \pm 0.1\%$ of body weight in fish with food in their stomachs at both the entrance and exit of the estuary (MacFarlane, unpubl. data). Further, a greater proportion of fish contained food at the estuary exit, where K was the lowest. Thus, differences in stomach fullness were not the cause of lower condition. Changes in metabolic equilibria, reflected in altered body composition of protein and lipids, can change body density, as shown by Brett et al. (1969) for juvenile sockeye salmon (*Oncorhynchus nerka*) and thus affect condition. In juveniles in the San Francisco Estuary, body protein and total lipid concentrations were similar at all sampling locations, so chang-

es in body density were unlikely contributors to reduced condition. However, metabolic costs of smoltification can cause changes in length - weight relationships. During the transformation, salmon can become more slender due to depleted energy reserves (Hoar, 1988), especially TAG (Henderson and Tocher, 1987). It is possible that decreased lipid and protein content, and not changes in relative concentrations, caused by catabolism for seawater adaptation, resulted in juveniles leaving the estuary at a lower weight for a given length than when they first entered. However, in a study conducted in 1999, gill Na^+ , K^+ -ATPase activity, an indicator of seawater adaptation, was greater in juvenile chinook salmon caught at the entrance to the estuary (km 68) compared with that of those sampled within the rivers leading into the estuary, but was not increased further in those collected at locations within the San Francisco Estuary.² This suggests that adaptation was largely completed by the time of estuary entrance and may not be the primary contributor to the body lower condition of fish

² Alonzo, J. J., and R. B. MacFarlane. 1999. Unpubl. data. Santa Cruz Laboratory, Southwest Fish. Sci. Ctr. NMFS, NOAA. 110 Shaffer Road, Santa Cruz, CA 95060.

leaving the estuary. Further, Zaugg and McLain (1972) showed that condition was either unchanged or declined for several months after stabilization of higher Na^+ , K^+ -ATPase levels in salmonids undergoing parr-smolt transformation. The increase in K -factor in fish captured in the coastal waters of the Gulf of the Farallones argues against smoltification as the main cause of lower condition in juvenile salmon leaving the estuary.

Although total lipid concentrations were unchanged in juveniles within the estuary, they declined greatly in salmon in the Gulf of the Farallones. Most of the decrease was due to depletion of TAG. It appears that the rapid growth of juveniles in the ocean was fueled by TAG energy reserves acquired during downstream migration. Growth seems to take precedence over maintenance of energy reserves. Increased body lipid (presumably TAG) at the time of ocean entry has been shown to improve juvenile chinook survival (Burrows, 1969; Higgs et al., 1992); thus a lack of substantial TAG accumulation while in the estuary may compromise early ocean survival should prey be scarce.

There was little difference in protein concentrations in juveniles from the estuary and the gulf. This is not surprising; protein appears to be conserved except during periods of starvation. Protein levels in juvenile salmonids have been shown to be unaffected by ration, growth, environmental variation (Shearer et al., 1997; Edsall et al., 1999), or locomotion (Alsop and Wood, 1997).

As juvenile chinook salmon migrated through the San Francisco Estuary, their feeding changed progressively from invertebrates to fish larvae. Young salmon leaving the freshwater delta had recently eaten primarily *Copepoda*, which seems also to be a major prey of juvenile chinook in Oregon estuaries (Reimers, 1973; McCabe et al., 1986). In 1979-80, juvenile chinook in the delta preyed primarily on cladocerans and dipterans (Kjelson et al., 1982). Over the past several decades, the zooplankton community in the delta and estuary has changed dramatically because of water diversions and introductions of many exotic species (Kimmerer and Orsi, 1996; Cohen and Carlton, 1998). The change in prey found in our study may be a result of anthropogenic alterations in the ecosystem.

There was greater diversity in feeding in the upper bays- Suisun and San Pablo- where insects, copepods, mysids, and cumaceans formed a major portion of young chinook salmon diet. These embayments are bordered by the last remaining extensive brackish and salt marshes in the northern estuary. Additionally, Suisun Bay includes the mixing zone of fresh and salt water, a well-known locale of high plankton abundance. Thus the high biological productivity of these habitats could be expected to provide diverse food items. The composition of the diet here was similar to that found in more northerly estuaries (Healey, 1991) and provided further evidence that juvenile chinook salmon feed on about the same prey types in these habitats throughout their range.

Chinook salmon are highly piscivorous. Fish larvae were clearly the dominant prey in central San Francisco Bay and in the Gulf of the Farallones. Typically young chinook eat mostly fish larvae as they grow and enter marine environments (McCabe et al., 1986; Fisher and Pearcy, 1996;

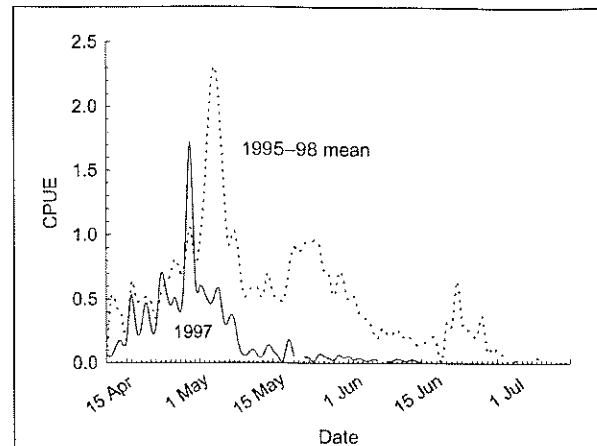


Figure 6

Juvenile chinook salmon catch by midwater trawl at the entrance to the San Francisco Estuary (km 68) in 1997 compared with 1995-98 mean. Catch per unit of effort (CPUE) is presented as the number of salmon/1000 m^3 water. Data from U.S. Fish and Wildlife Service, Stockton, CA.

Landingham et al., 1998). In the coastal waters of the Gulf of the Farallones, juvenile chinook salmon fed on early life stages of euphausiids and decapods as well, but to a lesser extent than on fish. Fish, euphausiids, and decapods were the major prey in coastal ecosystems from Oregon to southeastern Alaska (Brodeur and Pearcy, 1990; Landingham et al., 1998).

Once juvenile chinook entered the ocean, feeding intensity appeared to increase. Whereas stomach contents were 0.5% of body weight in the estuary, in the gulf they were $0.9\% \pm 0.1\%$ of body weight. The rapid growth rate found in young salmon shortly after ocean entry seemed to result from greater feeding activity in combination with the utilization of lipid reserves to fuel the synthesis of formed tissues.

To understand the context of data on juvenile salmon physiological ecology, it is helpful to know the relative abundance of these fish and the environmental conditions in 1997. Emigrating juvenile salmon abundance is monitored at the estuary entrance (km 68) by a consortium of California and federal research agencies (Interagency Ecological Program). Data for 1997 indicated that abundance was lower and migration to the ocean occurred earlier than the 1995-98 average (Fig. 6). Mean daily catch per unit of effort (1 January to 30 June 1997) was 0.132 ± 0.02 juveniles/(10³/m³ water), about 80% less than in 1996 and 1997 and 50% less than in 1998. Freshwater outflow from the delta into the estuary in 1997 was categorized by California Department of Water Resources as "above normal" and peak flows occurred in January, earlier than typical (Fig. 7). Hydrologic conditions in the estuary during May and June 1997 were similar to long-term means, but water temperatures and salinities were statistically higher ($P < 0.0001$, Table 3). Water temperatures were 18.4°C ,

Table 3

Mean hydrologic characteristics of the water column in the San Francisco Estuary and the coastal Gulf of the Farallones during juvenile chinook salmon migration toward the ocean in 1997 compared with long-term means. Data are means (\pm SE) of surface to bottom for May and June. Years for long-term mean were 1989-97, except for turbidity and pH, which were 1995-98. (Long-term data for estuary are from U. S. Geological Survey, Menlo Park, CA, and for gulf from Groundfish Population Analysis, Santa Cruz Laboratory, NMFS, Santa Cruz, CA). NTU = nephelometric turbidity units.

Variable	Estuary		Gulf	
	1997	Long-term	1997	Long-term
Temperature(°C)	18.4 (0.1) ¹	17.5 (0.0)	10.6 (0.0) ¹	10.1 (0.0)
Salinity (‰)	16.7 (0.5) ¹	14.7 (0.2)	33.6 (0.0)	33.6 (0.0)
Dissolved O ₂ (mg/L)	7.98 (0.03) ²	7.91 (0.02)		
Turbidity (NTU)	36.0 (3.0)	35.1 (2.8)		
pH	7.58 (0.01) ¹	7.62 (0.00)		
Chl <i>a</i> (µg/L)	3.19 (0.05)	3.11 (0.03)		

¹ *P* (probability of no difference from long-term mean) <0.0001.

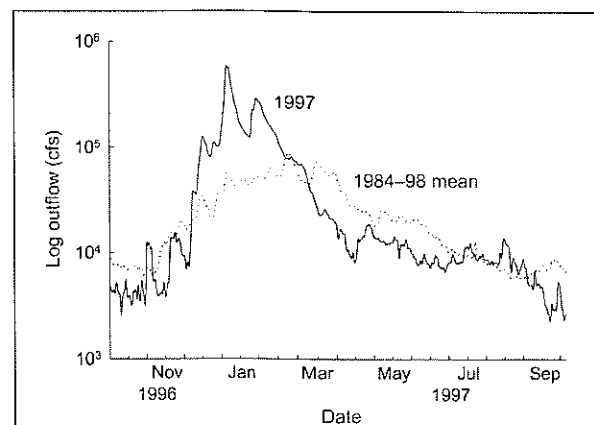
² *P*<0.05.

about 1°C warmer than long-term means, although well within the tolerance limits for the species at these latitudes (Baker et al., 1995). This temperature has been shown to allow growth rates of about 1% body weight/day in juvenile chinook salmon under simulated field feeding conditions (Weatherley and Gill, 1995).

Water flows and temperature are two primary environmental variables affecting the distribution and development of fishes; thus it is reasonable to assume that the timing of the emigration in 1997 was a function of that year's hydrology. Flow and temperature were believed to influence the migration and distribution of juvenile chinook salmon in the Sacramento and San Joaquin Rivers (Kjelson et al., 1982) and other systems (Cramer and Lichatowich, 1978; Healey, 1980b; Wallace and Collins, 1997). In fact, higher water temperatures of the Central Valley drainage may be a factor in the early emigration and physiological development seen in California chinook salmon in contrast to northerly populations (Healey, 1991). Mean water temperature between 1988 and 1997 at the estuary entrance (km 68) was 19.9°C in June and 21.7°C in July,³ within the range of predicted 10% mortality estimated with a fitted model (Baker et al., 1995). Temperatures within the Central Bay through July, however, remained below 18°C.

The strongest El Niño of the century began in 1997 and may have influenced the physiology and ecology of salmon in the coastal waters of the Gulf of the Farallones. Water temperatures in the gulf were 0.5°C above the mean

³ Bayliss, J. I., J. L. Edmunds, J. L. Cole, and J. E. Cloern. 1998. Studies of the San Francisco Bay, California estuarine ecosystem: regional monitoring program results, 1997. U. S. Geological Survey Open-File Report 98-168, 194 p. [Available from U. S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025.]

**Figure 7**

Freshwater outflow into the San Francisco Estuary from the Sacramento River-San Joaquin River Delta in 1997 compared with 1984-98 mean. Outflow data are mean daily cubic feet per second (cfs) from California Department of Water Resources, Sacramento, CA.

for May and June, 1989-97. Although temperatures were within the preferred range for chinook salmon in the ocean (Weatherley and Gill, 1995), altered oceanographic conditions may have changed the composition of the prey community, affecting the feeding of juveniles.

Among Pacific salmon, chinook salmon display the greatest variability of life history patterns, including time spent in fresh and brackish water before ocean entry, growth rates, the proportion maturing each year, and fecundity (Healey, 1991). Populations from the Central Valley of California are at the extreme southern end of the species' dis-

tribution and, like many populations at the edges of their distribution, may differ in their early life history from more centrally located stocks. Certainly, Central Valley chinook salmon are known to have unique characteristics such as unusually high fecundity, larger size at age (Healey, 1991), and large population size (PFMC¹). Lesser estuarine dependence may be another unique trait of these southerly populations. Our data suggest that juvenile chinook salmon derive little benefit from their time spent in the San Francisco Estuary. There was little growth, depleted condition, and no accumulation of lipid energy reserves during the relatively limited time the fish spent transiting the 65-km length of the estuary. Extensive use of estuaries, especially by ocean-type chinook juveniles, seems more typical for populations to the north. Rearing and rapid growth have been characteristic of northerly stocks during extended periods of residence (Reimers, 1973; Healey, 1982; Simenstad et al., 1982; Percy, 1992) but were not evident in the San Francisco Estuary (Kjelson et al., 1982; our study).

Emigrating juvenile chinook salmon may not have always used the San Francisco Estuary as they do now. Extensive modification and degradation of the estuary by human activities in the past century or so may have altered the life history pattern of Central Valley chinook salmon populations. Loss of habitat, changes in prey communities, water-flow alterations and reductions, etc. may have contributed to less use of the estuary than previously.

Because Central Valley juvenile chinook salmon exhibit little estuarine dependence, they appear to benefit from expedited ocean entry. The rapid growth seen in the Gulf of the Farallones may confer potential for greater survival. Other chinook salmon studies have determined that larger juveniles are more likely to survive in the ocean (Higgs et al., 1992), leading to higher spawning returns (Burrows, 1969; Reimers, 1973). Faster growth and perhaps greater survival of juvenile chinook salmon, once in the ocean, may be a consequence of a typically favorable and stable thermal environment and the abundant food that results from the high biological productivity of this upwelling-dominated ecosystem (Ainley, 1990; McGowan et al., 1998). The abundant prey resources and lower metabolic costs associated with lower temperatures and ease of obtaining food may improve growth efficiency in the ocean compared with that in the San Francisco Estuary. Reliance on extended freshwater and estuarine residence prior to ocean entry could reduce Central Valley chinook salmon stocks, especially during prolonged periods of drought, which lower freshwater flows and raise temperatures. The ecological and evolutionary propensity of emigrating juveniles to conform to a strong ocean-type life history, with little estuarine dependency and a hastened ocean entry may be another unique attribute of Central Valley chinook salmon populations.

Acknowledgments

We thank Maxwell Eldridge and Brian Jarvis for their expert assistance in field collections and laboratory analy-

ses. We are grateful to David Woodbury, Keith Sakuma, and Dale Roberts for providing additional salmon and oceanographic data from their rockfish assessment cruise in the Gulf of the Farallones in May and June 1997. The officers and crew of the NOAA ship *David Starr Jordan* are also acknowledged for their highly professional conduct, skill, and expertise during our cruises in the Gulf of the Farallones. We thank the U.S. Fish and Wildlife Service and California Department of Fish and Game, Stockton, CA, for their assistance in collecting salmon at km 68 and for providing data from coded-wire-tagged fish. Anonymous reviewers provided insightful comments that improved the manuscript.

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