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**POTENTIAL FOOD SOURCES AND FEEDING ECOLOGY
OF JUVENILE FALL CHINOOK SALMON
IN CALIFORNIA'S MATTOLE RIVER LAGOON**

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Epibenthic and planktonic macrofauna were collected for two seasons from the Mattole River lagoon to determine potential food sources for juvenile chinook salmon, *Oncorhynchus tshawytscha*. Juvenile chinook salmon (64-103 mm fork length) were captured by beach seine and their stomachs removed to determine food habits in relation to food sources; feeding preferences were determined based on use versus availability. Zooplankton species composition and abundance varied by month, year, and by day and night. In 1986, juvenile amphipods were abundant in zooplankton samples from late July through mid-September, whereas in 1987 amphipods were nearly absent until September. Copepods and ostracods, hardly taken in 1986, were important zooplankters in 1987. Dipterans, copepods, and amphipods were more numerous in the water column at night. Epibenthic samples were usually dominated by the amphipod *Corophium spinicorne*; isopods commonly ranked second in abundance. Juvenile chinook consumed primarily allochthonous food items from riverine and wind-borne sources. Dipterans, terrestrial insects, and hemipterans were important in their diet. Adult amphipods were seldom found in chinook stomachs. There was no evidence of epibenthic feeding or nighttime feeding in either year.

INTRODUCTION

The estuaries of several northern California streams are transformed into coastal lagoons during the summer by a combination of sediment deposition from onshore ocean currents and riverine sources, constructive wave action, and decreasing stream flow (Pritchard 1967; Bames, R.S.K. 1980). These lagoons become traps for nutrients and detritus from allochthonous and autochthonous

sources (Tenore 1977; Reimers¹ 1978; Odum et al. 1979; Barnes, R.S.K. 1980; Simenstad 1983). Much of this organic material is eventually utilized by the benthic and planktonic communities, forming the base of a food web that supports populations of anadromous salmonids (Sibert et al. 1977, Reimers¹ 1978, Healey 1979, Naiman and Sibert 1979, Sibert 1979).

Chinook salmon, *Oncorhynchus tshawytscha*, typically reside in estuaries longer than do other species of anadromous salmonids (Reimers 1973, Reimers¹ 1978, Simenstad et al. 1982, Healey 1982). In the Sixes River, Oregon, a small coastal stream, the most successful life history pattern of subyearling fall chinook salmon was emigration from freshwater in early summer and residence in the estuary for about 3 months before entering the ocean in the fall (Reimers 1973). In the Mattole River, located in northern California, emigrating juvenile fall chinook salmon are trapped in a coastal lagoon when the estuary closes in late spring or early summer; thus, they are forced to rear in the lagoon until the fall wet season opens the lagoon (Young² 1987).

Growth and survival of juvenile salmon in estuaries and lagoons are influenced and perhaps limited by the abundance of epibenthic and planktonic prey items such as amphipods, copepods, dipteran larvae and pupae, and mysid shrimp (Sibert et al. 1977; Healey 1979, 1982; Naiman and Sibert 1979; Simenstad and Wissmar 1984; Alien and Hassler 1986; Grosse and Pauley 1986; Rondorf et al. 1990). Our study describes the species composition of the planktonic and epibenthic macrofaunal communities and estimates the abundance of potential food items available to juvenile chinook salmon in the Mattole River lagoon during the summer and early fall of 1986 and 1987. We compare these data to the occurrences of prey items found in the stomachs of juvenile chinook salmon rearing in the lagoon to determine food preferences.

STUDY SITE

The Mattole River basin is a 785-km² coastal drainage in Mendocino and Humboldt counties, California. The river flows in a northwesterly direction and enters the Pacific Ocean 60 km south of Eureka, California (Fig. 1). Mattole River flow, measured by a United States Geological Survey gauging station approximately 15 km upstream from the mouth, is variable through the year (Fig. 2). In 1986 the minimum, maximum, and mean flows were 10.1, 990.5, and 40.5 m³/s. In 1987 the minimum, maximum and mean flows were 0.1, 356.6, and 25.3 mVs.

When the river mouth is closed by the built-up sand bar, river water floods approximately 3 ha and forms a freshwater lagoon. When full, approximately one-half of the lagoon is <0.5 m deep. Depths in the remainder of the lagoon ranged

¹ Reimers, P.E. 1978. The need for research on the estuarine ecology of juvenile chinook salmon. Oregon Department of Fish and Wildlife, Research Section. Information Report Series, Fisheries 78(4).

² Young, D. A. 1987. Juvenile chinook salmon abundance, growth, production and food habits in the Mattole River lagoon, California. M.S. Thesis, Humboldt State University, Arcata, California, USA.

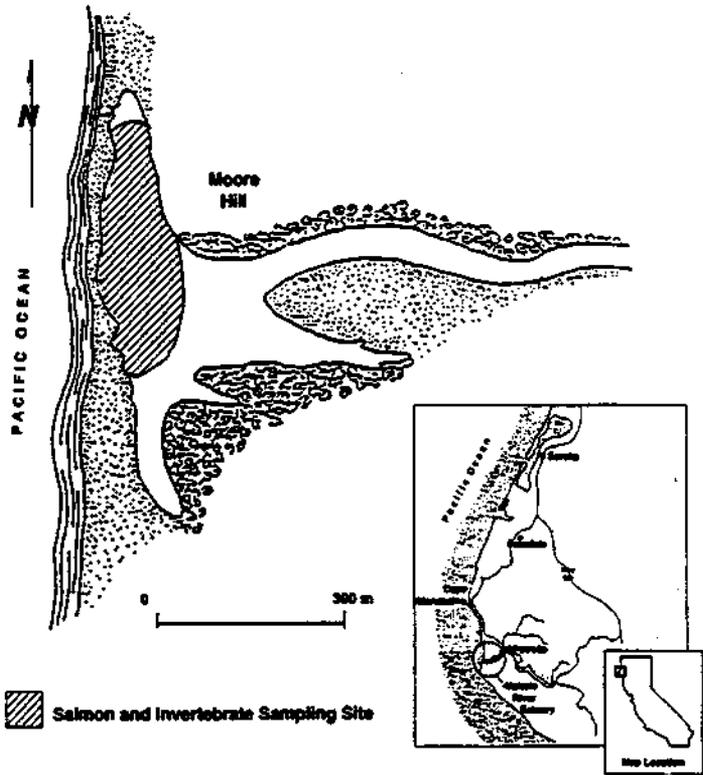


Figure 1. Location of the Mattole River estuary and lagoon, Humboldt County, California.

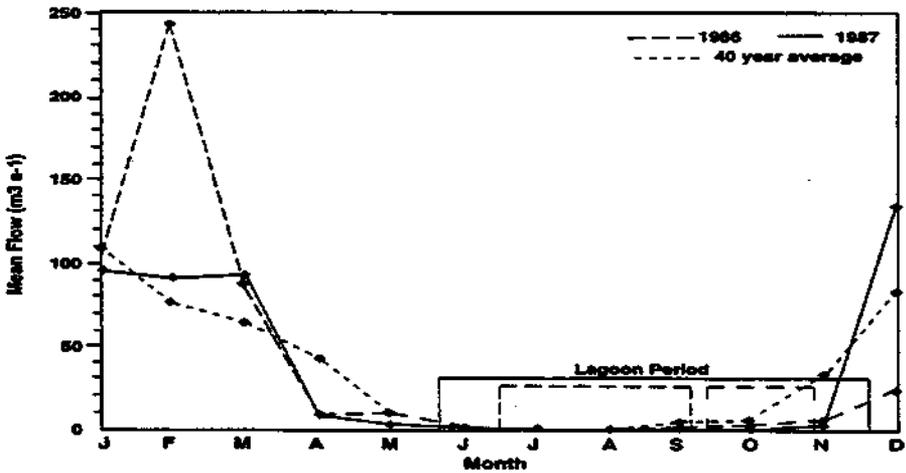


Figure 2. Mattole River, California, mean monthly flows and periods of lagoon formation, 1986-1987.

from 0.5 to 4.0 m (Busby et al.³ 1988). Depth and surface area of the lagoon gradually decrease in late summer as a result of diminishing river flow, increased evaporation, and seepage through the sand berm. The lagoon is exposed to strong onshore winds from the northwest during the summer and seawater occasionally washes over the sand berm at high tide. Schools of threespine stickleback, *Gasterosteus aculeatus*, inhabit the shallow areas of the lagoon. Juvenile steelhead, *Oncorhynchus mykiss*, and chinook salmon use the deeper areas. The substrate of the lower lagoon, where juvenile chinook salmon reside, is mostly sand with larger rocks and boulders along the eastern shore. A mat of organic material covers the bottom by midsummer and filamentous algae grow abundantly. Numerous aquatic invertebrates inhabit this algal covering. For this phase of Mattole River estuarine investigations, the study site was confined to the portion of the lower lagoon utilized by juvenile chinook salmon (Fig. 1).

METHODS

The field study was done in June-October 1986 and late May-November 1987. Water temperature, salinity, conductivity, dissolved oxygen profiles, and pH were determined biweekly in 1986 and monthly in 1987 (Busby et al.³ 1988).

Zooplankton

We towed a 0.5-m diameter plankton net with 0.333-mm mesh at mid-depth along a 300-m transect for 5 min biweekly to collect zooplankton during daylight hours in 1986 and for 5 min monthly in 1987. We considered zooplankters <0.3 mm to be too small to be significant in the diet of juvenile chinook salmon. In 1987, monthly tows were also conducted near midnight to detect diel changes in the plankton community, to document diel vertical migrations of crustaceans, and to determine if the quantity of drift organisms increased at night. A flow meter suspended in the center of the net opening allowed us to determine the volume of water sampled.

Epibenthic Macrofauna

All organisms retained on a 0.5-mm mesh screen after thorough washing were referred to as macrofauna. We considered all benthos <0.5 mm too small to be significant in the diet of juvenile chinook salmon. In 1986, an Ekman sampler was used to collect epibenthic organisms three times each month in the lower lagoon. Three grabs were collected and combined on each sampling date. In July 1987, in the lower lagoon, we used SCUBA gear to bury 16 plastic containers (21.5 x 16.5 x 8.0 cm) filled with representative bottom material level with the substrate at 3.1 m

³ Busby, M.S., R.A. Bamhart, and P.P. Petros. 1988. Natural resources of the Mattole River estuary, California. Natural Resources and Habitat Inventory Summary Report. United States Department of the Interior, Bureau of Land Management, Arcata, California, USA.

depth in a 4 x 4 grid with a distance of 50 cm separating each container. These samplers were an adaptation of basket-type substrate samplers (Mason et al. 1967, Bull 1968, Slack et al. 1973). After 30 d, four containers were randomly selected, sealed, and removed. At each 30-d period thereafter, four more containers were removed. The containers were processed separately to provide four replicate samples for each sample date. Sampler contents were sieved, sorted, and preserved in 70% ethanol or 5% buffered formalin.

Food Habit Analysis

Salmon stomachs were collected biweekly in June, July, and August 1986 and monthly in June, July, August, and September 1987. We used a 54.7-m x 4.8-m beach seine of 6.4-mm square mesh in the lower lagoon to capture juvenile chinook salmon for food habit analysis. From preliminary seining, direct observation, and electrofishing, we found that juvenile chinook salmon used only the small portion of the estuary with greatest depth adjacent to the sand berm (Fig. 1). When available, 10 juvenile chinook salmon from each seine haul were sacrificed, measured to the nearest millimeter fork length (FL), weighed to the nearest 0.1 g, slit ventrally, and preserved in 10% buffered formalin. Smith and Carlton (1975), Horror et al. (1981), Barnes, R.D. (1980), and Merritt and Cummins (1985) were used to identify organisms to species when possible. A complete list of all identified taxa can be found in Busby⁴ (1991). Empty stomachs were not included in any calculations.

Statistical Methods

Descriptions of analytical procedures can be found in Johnson (1980), Zar (1984), and Rondorf et al. (1990). The Mann-Whitney U statistic, and one-, two-, or three-way analysis of variance (ANOVA) were used to test for differences in means of samples over time and within samples (Zar 1984). The Mann-Whitney U test was used only with the day-night copepod abundance data that were not normally distributed. All other data sets (benthos, zooplankton, and stomach contents) were normally distributed either untransformed or after square-root transformation. Residuals from ANOVA were plotted to visually inspect for homogeneity of variance. Bartlett's test was used to confirm that variances were similar between samples. Tukey's multiple comparison test for unequal sample sizes was used to determine where specific differences existed. Simple linear regressions were performed to determine relationships between numbers of various organisms collected and water quality data. Food preferences of juvenile chinook salmon were determined using the analysis of Johnson (1980) that incorporates the multiple

⁴ Busby, M.S. 1991. The abundance of epibenthic and planktonic macro fauna and feeding habits of juvenile fall chinook salmon (*Oncorhynchus tshawytscha*) in the Mattole River estuary/lagoon, Humboldt County, California. M.S. Thesis, Humboldt State University, Arcata, California, USA.

comparison tests described by Waller and Duncan (1969). Johnson's nonparametric analysis determines preference based on the differences between the ranked abundances of prey types in the environment and their occurrence in the salmon stomachs. Based on chinook salmon diet analysis, we did not use data on benthos in food preference calculations. Statistical analyses were made at the order level of taxonomy.

RESULTS

In 1986, the estuary closed to form a lagoon on 18 June. The lagoon persisted until 17 September when a rain storm caused the sand berm to be breached, draining the lagoon (Fig. 2). A week later the berm closed and the lagoon refilled, remaining until the week of 30 October.

In 1987, the estuary was closed from 25 May until mid-November (Fig. 2). A combination of high tides and rough seas resulted in saltwater washing over the berm into the lagoon from 3 to 8 October. During this period, saltwater was usually visible as plumes of lighter-colored water pushed southeast by the prevailing wind. Denser saltwater sank and formed a layer 0.5-2.0 m thick in isolated, deeper pockets of the lagoon. These saltwater layers rarely persisted more than 24 h because they were mixed with freshwater by both wind action and inflow from the Mattole River.

Zooplankton

Zooplankton abundance varied by year, month, and day and night (Figs. 3 and 4). In June and early July 1986, Hydracrina (aquatic mites) were the primary zooplankters in the lagoon. Juvenile amphipods dominated plankton samples on 25 July, 26 August, and 13 September. Amphipods were also collected in greater numbers than

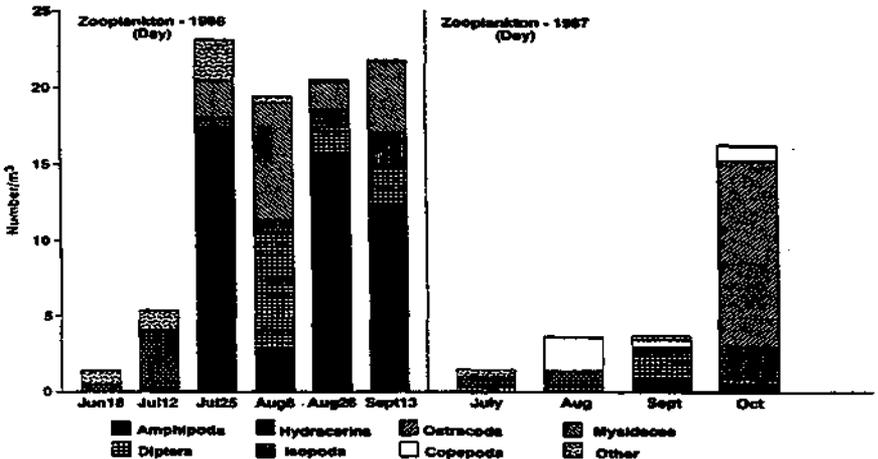


Figure 3. Numbers of plankton per m^3 in daytime tows in the lower lagoon of the Mattole River, California, 1986 and 1987.

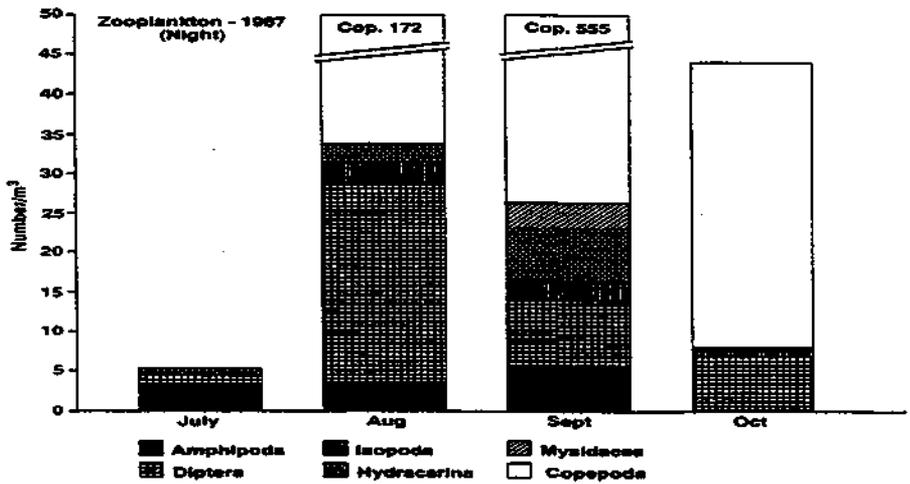


Figure 4. Numbers of plankton per m^3 in nighttime tows in the lower lagoon of the Mattole River, California, 1987.

all other taxa over the entire season; they made up 60% of organisms captured ($F = 5.01$; $df = 11, 60$; $P < 0.0005$).

Overall zooplankton abundance in 1987 was lower than in 1986. In addition, copepods and ostracods, practically absent in 1986, were numerous in 1987. Amphipod abundance was low throughout the year. Copepods were present in September and October and were abundant in August. Ostracods were numerous in October.

In 1987, abundance and composition of zooplankton differed markedly between day and night (Figs. 3 and 4). The most striking difference was the number of copepods collected in August, September, and October. Numbers of copepods taken were 225 times higher at night than during the day (Mann-Whitney $U = 51$, $P < 0.05$) and 10 times higher than all other taxa combined over the entire study period ($F = 2.27$; $df = 11, 37$; $P < 0.05$). Dipteran catches also were higher (20 times) at night than during the day. Amphipods were numerous in night samples, but were absent in day samples in July 1987. Ostracods were numerous in October day samples, but only a few were collected at night.

In 1987, day catches of zooplankton in the lagoon were significantly and positively correlated with salinity ($r = 0.987$, $P < 0.05$). These increases corresponded with seawater washing over the sandbar during high tides. Concentrations of zooplankton were also greater when vigorous wind mixing suspended bottom sediments in late summer and early fall.

Epibenthic Macrofauna

Epibenthic samples in the lower lagoon were dominated numerically by amphipods in both years (Fig. 5). *Corophium spinicorne* was collected most frequently. In 1986, *C. spinicorne* constituted 100% of the June amphipods collected, 96% in the

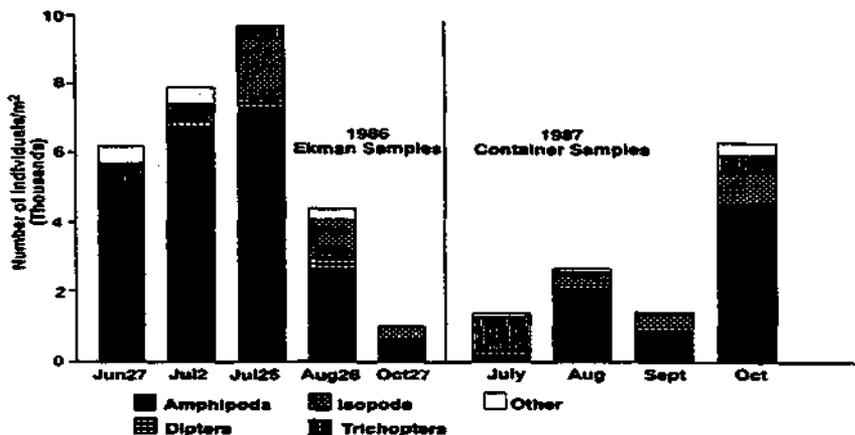


Figure 5. Number of epibenthic organisms per m² in Ekman grab samples in 1986 and in container substrate samples in 1987 in the lower lagoon of the Mattole River, California.

2 July sample, 99% in the 25 July sample, 88% in the August sample, and 62% in the October sample. In 1987, *C. spinicornis* made up 100% of the July, August, and September amphipods collected and 85% of the October sample. *Eogctmmams confervicolus* was the only other amphipod collected and it increased in abundance in the fall. Isopods, especially *Gnorimosphaeroma oregonensis*, usually ranked second in abundance. Numbers of epibenthic organisms declined from late July through October 1986.

Densities of benthic organisms sampled in 1987 were lower than in 1986, and trends and patterns of abundance were also notably different (Fig. 5). Numbers increased moderately from July through August 1987. The trichopteran *Gumaga griseus* dominated epibenthic samples in July. *Corophium spinicornis* did not become a dominant component of the community until August. In both years, overall densities of amphipods were 50-75% greater than all other taxa combined (several ANOVAs, $P < 0.001-0.025$).

Salmon Food Habits

We collected 63 juvenile chinook salmon stomachs in five sampling sessions in 1986 and 46 stomachs in four sampling sessions in 1987; 10 of the 63 stomachs from 1986 and nine of the 46 stomachs from 1987 were empty (Table 1). Variation in numbers of food items per individual fish was high, ranging from 0 to 106 in 1986 and 0 to 132 in 1987. The mean number of organisms per stomach for the five sample dates in 1986 ranged from 5.3 on 29 August to 30.7 on 9 July; the mean number of organisms per stomach sample for the four sample dates in 1987 ranged from 9.9 on 22 July to 34.7 on 19 September (Fig. 6).

Dipteran food items dominated the diet of young chinook salmon in both years. Overall, dipterans were consumed in significantly greater numbers than the remaining taxa (1986: $F = 3.80; df = 13, 56; P < 0.0005$; 1987: $F = 7.35; df = 10, 33; P < 0.0005$)

Table 1. Preference ranks (1 = most preferred, 5 = least preferred) of food items¹ of juvenile chinook salmon in the Mattole River lagoon, 1986-87. Within each row, food items with the same letter in parentheses (w, x, y, or z) were not significantly different ($P > 0.05$) in rank of preference as determined by Waller-Duncan multiple comparison tests.

Date	N	Mean FL of fish (mm)	Rank of preference				
			1	2	3	4	5
6/27/86	14 (0) ^b	80 (77-86) ^c	Dipt(w) 13 ^d	Terr(wx) 10	Cole(xy) 7	Hemi(yz) 4	Orth(z) 1
7/9/86	15 (1)	86 (81-90)	Terr(y) 9	Hemi(z) 5	Dipt(z) 12	Ephe(z) 2	Mysi(z) 1
7/24/86	11 (2)	88 (84-90)	Ephe(z) 1	Hemi(z) 1	Dipt(z) 8	Terr(z) 1	Lepi(z) 1
8/12/86	8 (1)	94 (91-100)	Dipt(y) 5	Amph(y) 5	Mysi(z) 2		
8/29/86	15 (6)	99 (94-103)	Cole(x) 3	Ephe(x) 1	Terr(y) 2	Oste(y) 1	Iaop(z) 1
1986 Overall	63 (10)	89 (77-103)	Terr(y) 24	Hemi(y) 11	Ephe(yz) 7	Isop(z) 2	Dipt(z) 44
6/22/87	15 (3)	72 (64-82)	Hemi(y) 3	Ephe(y) 2	Odon(y) 1	Terr(z) 4	Amph(z) 4
7/21/87	15 (4)	76 (69-82)	Amph(x) 9	Terr(y) 2	Isop(y) 1	Dipt(y) 11	Cole(z) 1
8/23/87	8 (0)	79 (72-87)	Isop(x) 1	Ephe(x) 4	Dipt(y) 7	Amph(y) 4	Hydr(z) 1
9/19/87	8 (1)	82 (75-87)	Terr(y) 4	Amph(z) 3	Dipt(z) 6	Isop(z) 4	
1987 Overall	46 (9)	77 (64-87)	Ephe(y) 7	Terr(y) 14	Hydr(z) 3	Odon(z) 1	Dipt(z) 36

¹ Abbreviations: Amph=Amphipoda, Cole=Coleoptera, Dipt=Diptera, Ephe=Ephemeroptera, Hemi = Hemiptera, Hydr = Hydracarina, Isop = Isopoda, Lepi = Lepidoptera, Mysi = Mysidacea, Odon = Odenata, Orth = Orthoptera, Oste = Osteichthyes, Terr = Terrestrials.

^bNumber of empty stomachs.

^cRange of fish lengths in millimeters.

^dNumber of stomachs in which the organism occurred.

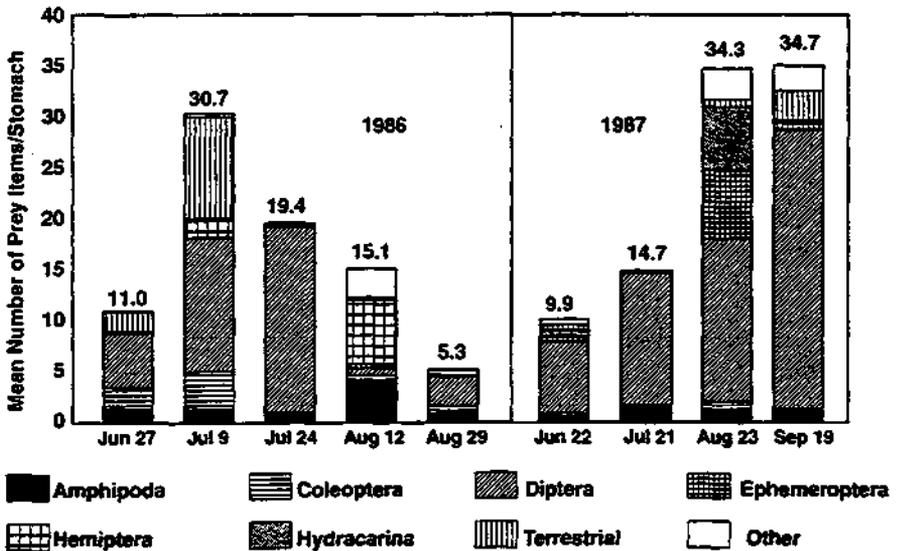


Figure 6. Mean numbers of prey organisms per juvenile chinook salmon stomach in the Mattole River estuary and lagoon, California, 1986 and 1987.

(Fig. 6). In 1986, hemipterans and terrestrial food items, predominantly ants (Hymenoptera) and spiders (Arachnida), also occurred frequently in the diet. In 1987, ephemeropterans and Hydracarina were important diet components of young chinook salmon sampled on 23 August. Proportions of food items used by young salmon did not closely correspond to abundance of prey items (Figs. 3,4,5, and 6). Although amphipods and isopods dominated epibenthos, and juvenile amphipods and dipterans were common in zooplankton samples, juvenile chinook preferred terrestrial insects and hemipterans in 1986 (Table 1). Both items were scarce in the environment. However, the diet shifted by early August to autochthonous sources (hemipterans, juvenile *Corophium* <5.0 mm without antennae, and mysids). There was little evidence of epibenthic feeding by juvenile chinook salmon in 1986 (Fig. 6). Because of this, we adjusted our calculations of preference ranks to omit benthic samples (Table 1). Terrestrial food items were less numerous and dipteran larvae were more numerous in the diet in 1987 than in 1986 (Fig. 6). Also, significantly more dipterans were consumed in 1987 than in 1986 ($F = 5.73$; $df=2, 72$; $P < 0.025$). Ephemeropterans and terrestrials were the overall preferred food items in 1987 (Table 1). As in 1986, there was little evidence of epibenthic feeding in 1987 (Fig. 6). Other items in stomachs included small gravel, feathers, green algae, leaves, and wood.

DISCUSSION

We did not realize before beginning the study that terrestrial and near-surface drift organisms would be important in the diet of juvenile chinook salmon. Sampling

with a neuston net would have provided better information on the abundance of such organisms. The plankton net we used sampled at mid-depth except at the start and finish of towing. Since terrestrial and drift organisms were probably undersampled, their preference rank as prey items by juvenile chinook salmon might have been artificially elevated.

Data on occurrence and abundance of benthic organisms would have been improved had we not incorporated the experimental benthos colonization containers into the sampling regime for 1987 and had we continued to use standard Ekman grabs. Additional grab samples for each sampling period also would have strengthened the validity of results. However, chinook salmon used a relatively small portion of the available habitat and we reported only benthic data from that area of the lagoon. Additional samples from that limited area would probably have revealed little more variation in species composition and abundance.

Juvenile chinook salmon consumed primarily allochthonous food (terrestrial and aquatic insects) from wind-borne and riverine drift sources in early 1986, a period of peak juvenile chinook salmon abundance and low zooplankton numbers (Busby⁴ 1991). Our results indicate that juvenile chinook salmon feeding was mostly neustonic, feeding in the surface film at or just below the surface; sometimes they fed at mid-depths (also reported by Rondorf et al. 1990).

Amphipods, especially *C. spinicorne*, although usually abundant in the lagoon, were infrequently found in the diet of juvenile chinook salmon. This was probably due to lack of availability and possible avoidance by juvenile salmon. Reimers et al.⁵ (1979) found that only 0.1 - 2.5% of adult *Corophium* spp. are out of their tubes and visible to fish at any given time. Moreover, vertical migrations of *Corophium* spp. occur primarily at night during periods of reduced or no moonlight (Nicholas et al.⁶ 1984). Salmonids are primarily sight feeders and generally do not feed at night unless there is sufficient light (Chapman and Bjornn 1969, Fausch 1991). Although copepods were taken in large numbers in night plankton samples in 1987 (Fig. 4), they were never important in the diet of juvenile chinook, indicating that chinook salmon were not feeding at night.

In 1986, although we collected numerous juvenile *C. spinicorne* in daytime plankton tows (Fig. 3), they were not a preferred food item and may have actually been avoided by juvenile chinook salmon. Young salmon (64-103 mm FL) may have difficulty ingesting *Corophium* spp. as these amphipods have the ability to extend their spiny antennae in opposite directions when mouthed by a fish (Reimers et al.⁵ 1979). *Corophium* spp. were, however, an important component in the diet of juvenile chinook salmon in the Sixes River estuary, Oregon (Reimers et al.⁵ 1979). Studies, simultaneous with our investigation, on Redwood

⁵ Reimers, P.E., J.W. Nicholas, D.L. Bottom, T. W. Downey, K.M. Maciolek, J.D. Rodgers, and B.A. Miller. 1979. Coastal salmon ecology project, fish research project, annual progress report, AFC-76-3. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

⁶ Nicholas, J.W., T.W. Downey, D. Bottom, and A. McGie. 1984. Pages 15-21 in: Fish research project, annual progress report, 82-ABD-ORIE. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Creek estuary and lagoon - a system with physical characteristics similar to those of the Mattole River lagoon - revealed that juvenile chinook fed mostly on drift organisms, especially in spring and early summer (Larson⁷ 1987, Salamunovich⁸ 1987).

Juvenile chinook salmon were smaller in 1987 than in 1986 (Table 1). Mark-recapture experiments (Busby et al.³ 1988) estimated much higher densities (10 times) of chinook salmon in 1987 than in 1986. The reduction in growth rate and apparent mortality of chinook salmon suggested a density-dependent mechanism was operating and that the fish carrying capacity of the lagoon was probably exceeded in 1987.

We found that juvenile chinook salmon resided mostly in the lower lagoon near the sand berm and that juvenile steelhead used primarily the upper lagoon where there was some overhanging riparian habitat and a slight current. We found that young chinook salmon ate terrestrial, planktonic, and drift organisms, whereas Zedonis⁹ (1992) reported that juvenile steelhead in the lagoon consumed mostly epibenthic macrofauna, particularly *C. spinicorne*. Similar partitioning of habitat and food resources between juvenile chinook salmon and steelhead was reported by Salamunovich⁸ (1987) in Redwood Creek estuary and lagoon. MacDonald et al. (1988) observed that smaller juvenile chinook salmon in the Campbell River estuary, British Columbia, Canada used different habitat and ate different organisms than did larger chinook salmon and larger coho salmon, *Oncorhynchus kisutch*, residing in the same estuary.

Juvenile chinook salmon use a wide variety of feeding strategies (Craddock et al. 1976, Kjelson et al. 1982, Rondorf et al. 1990). Our analysis of food use and its potential availability showed that juvenile chinook salmon preferred some food items, but they shifted to other, presumably less-preferred organisms when those organisms were abundant. Differences in feeding strategies of juvenile chinook salmon from different areas and in different seasons suggest that physical characteristics of the environment influence the feeding strategy used. Healey (1980, 1982) found temporal and spatial differences in the diet of juvenile chinook salmon in the Nanaimo River estuary, British Columbia, Canada. McCabe et al. (1986) found that subyearling chinook of varying sizes differentially used habitat types and food resources of the Columbia River estuary. Rondorf et al. (1990) showed that juvenile chinook salmon consistently preferred terrestrial insects in all months in the littoral riverine habitat of the Columbia River. The importance of terrestrial insects in the diet of juvenile chinook salmon suggests to us that enhancement projects that increase the amount and diversity of riparian vegetation surrounding the Mattole estuary would indirectly benefit juvenile chinook salmon.

⁷ Larson, J.P. 1987. Utilization of the Redwood Creek estuary, Humboldt County, California by juvenile salmonids. M.S. Thesis, Humboldt State University, Arcata, California, USA.

⁸ Salamunovich, T. J. 1987. Fish food habits and their interrelationships in lower Redwood Creek, Humboldt County, California. M.S. Thesis, Humboldt State University, Arcata, California, USA.

⁹ Zedonis, P. A. 1992. The biology of the juvenile steelhead (*Oncorhynchus mykiss*) in the Mattole River estuary/lagoon, California. M.S. Thesis, Humboldt State University, Arcata, California, USA.

LITERATURE CITED

- Allen, M.A. and T.J. Hassler. 1986. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific southwest), chinook salmon. United States Department of the Interior, Fish and Wildlife Service, Biological Report 82(11.49).
- Barnes, R.D. 1980. Invertebrate zoology. 4th edition. Saunders/Holt Rinehart and Winston, Philadelphia, Pennsylvania, USA.
- Barnes, R.S.K. 1980. Coastal lagoons. Cambridge University Press, Cambridge, UK.
- Borror, D. J., D.M. DeLong, and C. A. Triplehorn. 1981. An introduction to the study of insects. 5th edition. Saunders College Publishing, New York, New York, USA.
- Bull, C.J. 1968. A bottom fauna sampler for use in stony streams. *Progressive Fish Culturist* 30:119-120.
- Chapman, D.W. and T.C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 *in*: T.G. Northcote, editor. Symposium on salmon and trout in streams. H.R. McMillan lectures in fisheries. University of British Columbia, Vancouver, British Columbia, Canada.
- Craddock, D.R., T.H. Blahm, and W.D. Parente. 1976. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. *Transactions of the American Fisheries Society* 1:72-76.
- Fausch, K.D. 1991. Trout as predator. Pages 65-80 *in*: J. Stolz and J. Schnell, editors. Trout. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Grosse, D.J. and G.B. Pauley. 1986. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific northwest). Amphipods. United States Department of the Interior, Fish and Wildlife Service, Biological Report 82(11.69).
- Healey, M.C. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: I. Production and feeding rates of juvenile chum salmon, *Oncorhynchus keta*. *Journal of the Fisheries Research Board of Canada* 36:488-496.
- Healey, M.C. 1980. Utilization of the Nanaimo Estuary by juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Fishery Bulletin* 77:653-668.
- Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: The life support system. Pages 315-341 *in*: V. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Kjelson, M.A., P.F. Raquel, and F. W. Fisher. 1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin Estuary, California. Pages 393-411 *in*: V. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.
- MacDonald, J.S., C.D. Levings, C.D. McAllister, U.H.M. Fagerlund, and J.R. McBride. 1988. A field experiment to test the importance of estuaries for chinook salmon survival: Short term results. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1366-1377.
- Mason, W.T., J.B. Anderson, and G.E. Morrison. 1967. A limestone-filled artificial substrate sampler-float unit for collecting macroinvertebrates in large streams. *Progressive Fish Culturist* 29:74.
- McCabe, G.T. Jr., R.L. Emmet, W.D. Muir, and T.H. Blahm. 1986. Utilization of the Columbia River estuary by subyearling chinook salmon. *Northwest Science* 60:113-124.
- Merritt, R. W. and K.W. Cummins, editors. 1985. An introduction to the aquatic insects of North America. 2nd edition. Kendall-Hunt Publishing Company, Dubuque, Iowa, USA.

- Naiman, R.J. and J.R. Sibert. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: III. Importance of detrital carbon to the estuarine ecosystems. *Journal of the Fisheries Research Board of Canada* 36:504-520.
- Odum, W.E., J.S. Fisher, and J.C. Pickral. 1979. Factors controlling the flux of particulate organic carbon from estuarine wetlands. Pages 69-80 *in*: R. J. Livingston, editor. *Ecological processes in coastal and marine systems*. Plenum Press, New York, New York, USA.
- Pritchard, D.W. 1967. What is an estuary?: Physical viewpoint. Pages 3-5 *in*: G.R. Lauff, editor. *Estuaries*. American Association for the Advancement of Science, Publication 83, Washington, D.C., USA.
- Reimers, P.E. 1973. The length of residence of juvenile fall chinook salmon in the Sixes River, Oregon. *Research Reports of the Fish Commission of Oregon* 4(2).
- Rondorf, D. W., G.A. Gray, and R.B. Fairley. 1990. Feeding ecology of subyearling chinook salmon in riverine and reservoir habitats of the Columbia River. *Transactions of the American Fisheries Society* 119:16-24.
- Sibert, J. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: II. Meiofauna available as food to juvenile chum salmon, *Oncorhynchus keta*. *Journal of the Fisheries Research Board of Canada* 36:497-503.
- Sibert, J., T.J. Brown, M.C. Healey, B.A. Kask, and R.J. Naiman. 1977. Detritus-based food webs: Exploitation by juvenile chum salmon (*Oncorhynchus keta*). *Science* 196:649-650.
- Simenstad, C.A. 1983. The ecology of estuarine channels of the Pacific Northwest coast: A community profile. United States Department of the Interior, Fish and Wildlife Service, FWS/OBS-83/05.
- Simenstad, C.A. and R.C. Wissmar. 1984. Variability of estuarine food webs and production may limit our ability to enhance Pacific salmon (*Oncorhynchus spp.*). Pages 273-286 *in*: W.G. Percy, editor. *The influence of oceanic conditions of the production of salmonids in the North Pacific - a workshop*. Sea Grant College Program, ORESU-W-83-001, Oregon State University, Corvallis, Oregon, USA.
- Simenstad, C.A., K.L. Fresh, and E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: An unappreciated function. Pages 343-364 *in*: V. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York, New York, USA.
- Slack, K.V., R.C. Averett, P.E. Greeson, and R.G. Lipscomb. 1973. Methods for collection and analysis of aquatic biological and microbiological samples. Chapter A4, Book 5 *in*: *Techniques of water-resources investigations of the United States Geological Survey*. Washington, D.C., USA.
- Smith, R.I. and J.T. Carlton, editors. 1975. *Lights manual, intertidal invertebrates of the central California coast*. 3rd edition. University of California Press, Berkeley, California, USA.
- Tenore, K.R. 1977. Food chain pathways in detrital feeding communities: A review, with new observations on sediment resuspension and detrital recycling. Pages 37-52 *in*: B.C. Coull, editor. *Ecology of marine benthos*. University of South Carolina Press, Columbia, South Carolina, USA.
- Waller, R. A. and D.B. Duncan. 1969. A Bayes rule for the symmetric multiple comparisons problem. *Journal of the American Statistical Association* 64:1484-1503.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd edition. Prentice-Hall, Inc. Englewood Cliffs, New Jersey, USA.