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Estimation  
of the  
Salmon Carrying Capacity  
of the  
North Pacific Ocean

December 1984

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ESTIMATION OF THE SALMON CARRYING CAPACITY  
OF THE NORTH PACIFIC OCEAN

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## INTRODUCTION

During the past several years, the REFM group at the Northwest and Alaska Fisheries Center has been investigating the fisheries oceanography of northeast Pacific and Bering Sea salmon populations. As part of this effort it has developed the NOPASA model which simulates the oceanic migration of sockeye salmon biomass (Favorite and Laevastu, 1979; Honkalehto and Rabe, in prep.; Rabe and Honkalehto, in prep.). There has been much discussion in the scientific literature of whether the food resources in the North Pacific Ocean are adequate to support an increase in salmon aquiculture (Sanger, 1972; Bailey et. al., 1977; Walters et. al., 1978; Favorite and Laevastu, 1979). This report details an investigation of potential salmon carrying capacity using a biomass-based simulation model.

The determination of true carrying capacity of an ocean area with respect to a given species must quantitatively account for the species' predators, competitors and food availability (Favorite and Laevastu, 1979). Using a simple carrying capacity simulation model and assuming salmon out-compete other potential predators for their prey, an estimate was made of the food resources available to pink, coho, chum, king and sockeye salmon. Yearly food requirements of each species were computed. These were then compared with the best available prey biomass estimates and the results interpreted in light of the ocean's potential to sustain salmon enhancement.

## METHODS

### Salmon diets

An extensive literature survey was conducted in order to identify the major prey of five species of north Pacific salmon (*Oncorhynchus spp.*) during the marine portion of their life cycle. Pacific salmon feeding habit data obtained during the past several decades (Allen and Aron, 1958; Andrievskaya, 1958, 1966; Bailey et al., 1977; Favorite, 1970; Kanno and Hamai, 1971; LeBrasseur, 1966, 1972; Livingston and Goiney, 1983; Manzer, 1968; Nishiyama, 1970; Pritchard and Tester, 1944; Reid, 1961) were divided for analysis into offshore and nearshore data sets to coincide with the different zooplankton and nekton productions caused by differing depths and nutrient regimes. The sources and sample sizes for each salmon species are given in Appendix Table I. More data were available for sockeye salmon than for any other species.

For each data set, the mean percent by weight of total stomach contents from each food category was calculated. Simple offshore means were entered into carrying capacity simulation for sockeye, chum, and king salmon. As coho data included samples with fewer than ten stomachs, weighted means were used. Figure 1 shows the compositions of sockeye salmon (*O. nerka*) diets from several

sources. Figures 2, 3, and 4 present data used to estimate an average diet composition for pink (*O. gorbuscha*), chum (*O. keta*), and coho (*O. kisutch*) salmon.

#### Prey standing stock estimation

Recent zooplankton, larval fish and squid literature were surveyed to check the validity of the standing stock simulations. Biomass estimates were made treating zooplankton as one category rather than as separate taxa for several reasons. Euphausiids have been routinely under-sampled by net surveys, especially day trawls, due to their net-avoidance ability and their diurnal vertical migration. Although Brinton (1962) showed that the major concentrations of *Euphausia pacifica* in the north Pacific lay in a narrow band near the Aleutians along the 45th parallel, there is no information describing *Thysanoessa spp.*, the most common euphausiid found in salmon stomachs (Motoda and Minoda, 1974). Although quantitative data existed for north Pacific copepods, very little data are available for amphipods or for the less abundant zooplankton.

Larval fish biomass in the upper three hundred meters of the northeast Pacific has been estimated from Bongo net hauls taken across much of the north Pacific during successive years (Bates and Clark, 1983; Clark, 1984; Kendall and Clark, 1982, 1982b; Kendall et. al., 1980; Walline, 1980). From the average of these

estimates it was determined that larval fish biomass could be simulated in the carrying capacity model as one-tenth of the zooplankton standing crop.

The function of squid in marine food webs has often been overlooked, however, their rapid growth rates and piscivorous habits make them important marine predators. They are also important as prey of salmon, albacore, sablefish, cod, sperm whale, seal, and birds (Barracough, 1967; Mercer, 1981). Fisheries biologists are just now expanding the scope of Pacific cephalopod research (S. Maupin, personal communication) and thus available data are sparse. Squid species known to be predators and prey of Pacific salmon are *Berryteuthis magister*, *Loligo opalescens*, and *Ommastrephes sp.* (Barracough, 1967; Roper and Young, 1975; Bernard, 1980). However, insufficient data on squid stocks have been reported to estimate their biomasses for the carrying capacity model (Laevastu, personal communication; Favorite and Laevastu, 1979).

#### Carrying capacity simulation

Figure 5 is a flow chart outlining the Pacific salmon carrying capacity simulation model for thirteen physiographic regions using zooplankton biomass estimations from the month of July. A description of this model has been presented by Favorite and Laevastu, 1979. Ensuing paragraphs highlight the assumptions and

principal equations used in the model. Model input parameters are summarized in Appendix Table II.

The sea-land table from the salmon migration simulation model, NOPASA (Honkalehto and Rabe, in prep.), with a grid size of 190.5 km was superimposed with salmon abundance data (Figure 6). The biomass at each grid point and the total biomass were computed for each species from the following equation:

$$SL(N,M) = (SK(N,M) * PT * WA(2,LY)) / AR \quad (1)$$

where SL(N,M) - salmon species biomass in grams/km<sup>2</sup>  
SK(N,M) - species abundance at each grid point  
PT - proportion of each year class in the run  
WA(2,LY) - weight of individual fish in each year class (grams)  
AR - area (km<sup>2</sup>) of individual squares  
N - grid rows 1-21, latitude (north to south)  
M - grid columns 1-52, longitude (west to east)  
LY - year

The assumptions were that zooplankton, larval and juvenile fish, and squid made up 100% of the diet, and that diets differed between species and between year classes. For each salmon species and year class, the amounts of food required during one or more years of their oceanic migration were calculated with the following equation:

$$\text{FOOD} = \text{SL}(\text{N},\text{M}) * \text{R} * \text{DAYS} \quad (2)$$

FOOD - food requirement (grams/km<sup>2</sup>). Computed total weight of food necessary to maintain the weight sockeye salmon at given NOPASA grid point.

R - individual ration required in proportion of body weight per day

DAYS - number of days year class individual is in ocean

In order to compute the total required food biomass at each grid point, the food needed by each salmon species was multiplied by the percentages of zooplankton, fish and squid estimated to compose that species' diet. The following equation illustrates the computation of the sockeye salmon zooplankton requirement:

$$\text{FE}(\text{N},\text{M}) = \text{FE}(\text{N},\text{M}) + (\text{FOOD} * \text{EP}) \quad (3)$$

FE(N,M) - weight of zooplankton consumed at grid point (N,M) by sockeye salmon

EP - proportion of zooplankton in sockeye diet (varies with year class)

Pelagic north Pacific zooplankton biomass was simulated with the assumptions that zooplankton reproduce their biomass twice each year and that half of the zooplankton biomass is utilizable by salmon (Favorite and Laevastu, 1979). Monthly variations in zooplankton biomass were simulated with a cosine function as follows:

$$ZOP(N,M) = H1(I) + H2(I) * \cos(PKAP * ALP * TK) + H3(I) * \cos(ZKAPP * ALPP * TK) \quad (4)$$

where ZOP(N,M) - zooplankton biomass (mg/m<sup>3</sup>)

H1(I) - mean annual zooplankton biomass (mg/m<sup>3</sup>)

H2(I) - 1/2 amplitude of mean annual biomass peak

H3(I) - amplitude of tertiary biomass peak

I - index for 1-13 physiographic regions of the NOPASA grid.

PKAP - latitude effect in radians

ALP - 30-day periodicity in radians

ALPP - 60-day periodicity in radians

TK - month

ZKAPP - 160-day periodicity

Examples of the resulting biomass curves are given in Figures 7 and 8.

Finally, the percentage consumptions of zooplankton, larval and juvenile fish by Pacific salmon were computed from the following equations:

$$FO(N,M) = FE(N,M) / ZOP(N,M) * 100 \quad (5)$$

$$FI(N,M) = FF(N,M) / FIS(N,M) * 100 \quad (6)$$

FE - total accumulated consumption of zooplankton

FO - percent of zooplankton stock consumed

FF - total accumulated consumption of fish

FIS - total fish standing stock (mg/m<sup>3</sup>)

FI - percentage of fish standing stock consumed.

The distribution of squid biomass was not simulated due to lack of reliable species abundance data. Thus the total computed carrying capacity in this simulation refers to salmon consumption of zooplankton and fish only. As young squid are an important food source for sockeye, their biomass will be added when data become available.

## RESULTS

### Salmon diets

The food regime encountered by Pacific salmon during their marine life stage varies according to time of year, location (Andrievskaya, 1966), proximity to a coastline, latitude, presence of other predators and natural variability in the prey populations. Figures 1-4 illustrate the relative dietary proportions of squid, fish and zooplankton as determined from stomach content analysis for sockeye, pink, chum and coho salmon, respectively. Coho salmon eat mainly fish while chum salmon eat a wide variety of zooplankton taxa and few fish or squid. Pink and sockeye salmon diets are similar, although pink salmon consume more fish. The data presented here show that zooplankton, larval and juvenile fish represent about 65% of the total salmonid diet, with squid making up the rest.

## The Carrying Capacity Simulation Model

Initial runs of the carrying capacity model were made using July zooplankton and larval fish biomasses only. The zooplankton biomass generated in the subroutine Z00CRO (Figure 5) was consistent with the overall biomasses reported by Motoda and Minoda (1974) and Reid (1962). Results indicate that Pacific salmon consume less than 0.5% of the available zooplankton biomass and less than 5.0% of the larval fish biomass. Varying latitude, month and area suggest the following: (1) prey biomass decreases with increasing latitude within any given NOPASA grid area, (2) the Aleutians, Bristol Bay and the Japan Sea are regions of high prey density (areas 2, 10, 11, and 12, respectively, in Figure 6) and (3) the percent of zooplankton biomass consumed does not vary greatly between months of the year.

## DISCUSSION

Most *Oncorhynchus spp.* stomachs contain a wide variety of food items suggesting that salmon in general are very opportunistic; they make use of available food as long as it falls in the appropriate size range. Okada and Taniguchi (1971) found that while juvenile chum and pink salmon are 60 mm or less they eat

relatively small prey (primarily microcopepods, amphipods and insects). At around 60mm (fork length) the salmon suddenly switch to include much larger prey such as euphausiids, squid, adult amphipods and fish larvae as well as the smaller prey in their diets.

Food quality influences salmon diets, as different food taxa provide quite different caloric values to salmon. Nishiyama (1970) estimated that adult sockeye salmon consume approximately 2% of their body weight per day. Sockeye salmon prefer high-calorie food items like squid, fish larvae and euphausiids over relatively lower calorie prey such as pteropods and decapod larvae. The availability of these preferred food items varies depending on where they are in the ocean. Bristol Bay, for example, provides a richer food environment than the open waters of the Bering Sea (Motoda and Minoda, 1974).

The presence of large runs of one salmon species may upset normal feeding patterns of a less aggressive species where ranges overlap during migration. Andrievskaya (1966) reported such an interaction between pink, chum and sockeye salmon in the western Pacific. Pink and sockeye salmon are more selective feeders than chum salmon (Andrievskaya, 1966; Barraclough, 1966, 1967) and their diets, which are similar, differ from the average chum salmon diet. During a large pink salmon run year, pink and sockeye salmon may out-compete chum for euphausiids, forcing the chum to rely on less desirable zooplankton such as pteropods.

Based on the above discussion it may be concluded that individual salmon species often display between-year diet differences that compare in size to between-species diet differences within a given year. In this simulation no allowance for these sources of variability has been made. This limits the simulation as it now stands, but does so in a manner consistent with the data available. As more relevant diet data becomes available expansion of the simulation will be possible.

The carrying capacity simulation suggests that the standing crop of salmon is not limited by the food supply during the ocean portion of their life cycle. Two further adjustments would allow a more realistic representation of pelagic salmon feeding dynamics. First, to answer the question of what happens when prey biomass fluctuates between seasons (and years) as Frost (1984) and Motoda and Minoda (1974) have documented, the zooplankton biomass simulation must be modified. Assuming steady consumption rates for salmon during the year, the combination of very low winter zooplankton crops and high salmon numbers may locally strain zooplankton food supplies. This work is in progress. Second, new data on squid abundances must be incorporated, because only with the entire salmon diet available can a successful determination of oceanic carrying potential for salmon be made. This is more difficult as it may be years before enough data exist to successfully model squid biomass distributions and simulate their interactions with salmon.

#### ACKNOWLEDGEMENTS

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- Figure 3. Chum salmon diet compositions in percent by weight of fish, squid and zooplankton. Numbers along x-axis refer to references listed in Appendix Table I.
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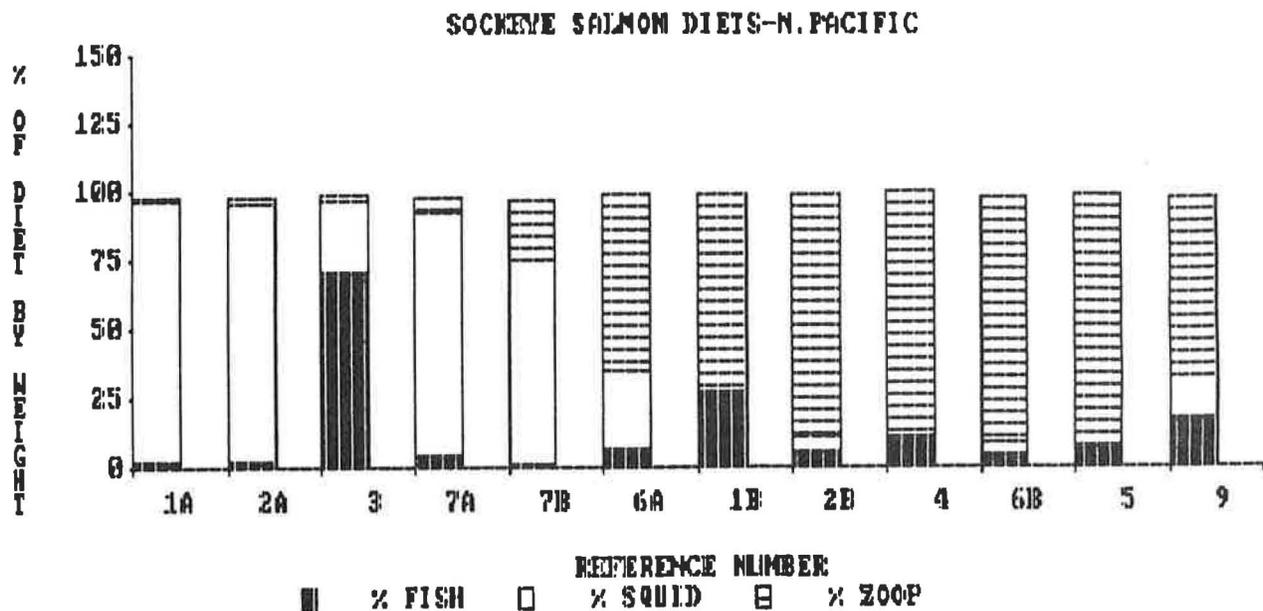


Figure 1. Sockeye salmon diet compositions in percent by weight of fish, squid and zooplankton. Numbers along x-axis refer to references listed in Appendix Table I.

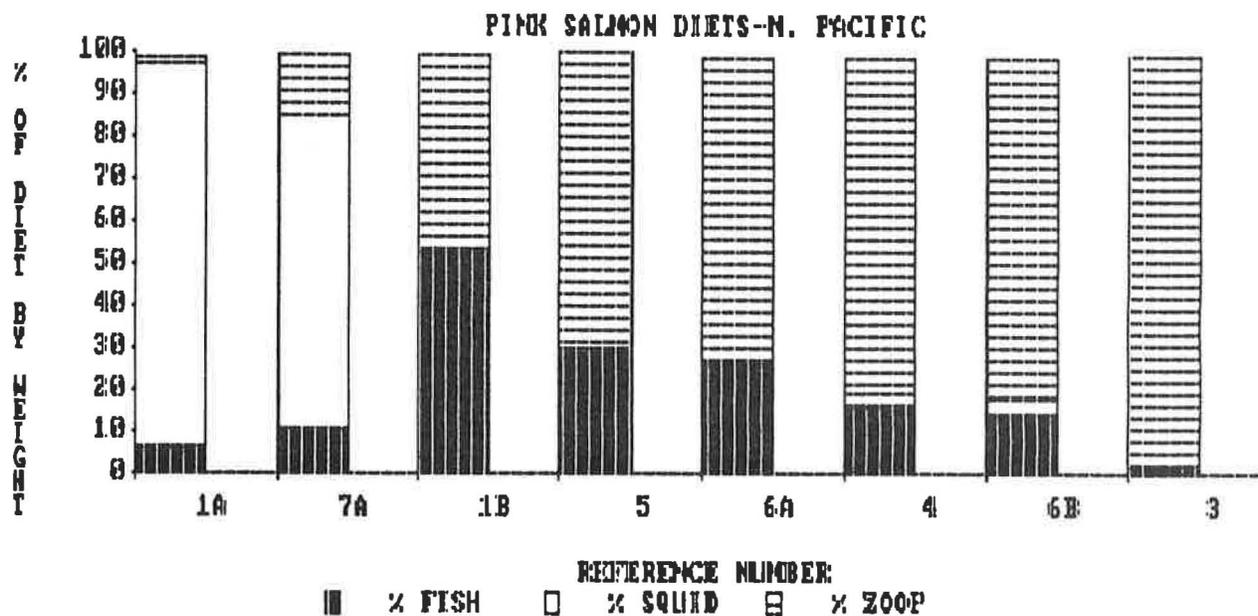


Figure 2. Pink salmon diet compositions in percent by weight of fish, squid and zooplankton. Numbers along x-axis refer to references listed in Appendix Table I.

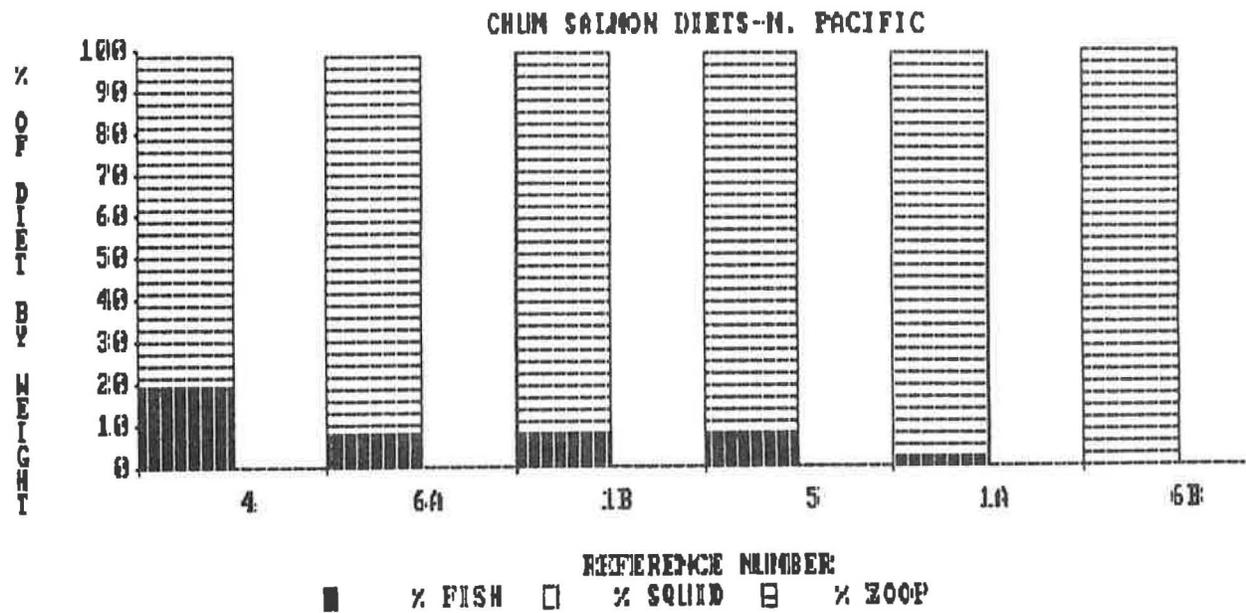


Figure 3. Chum salmon diet compositions in percent by weight of fish, squid and zooplankton. Numbers along x-axis refer to references listed in Appendix Table I.

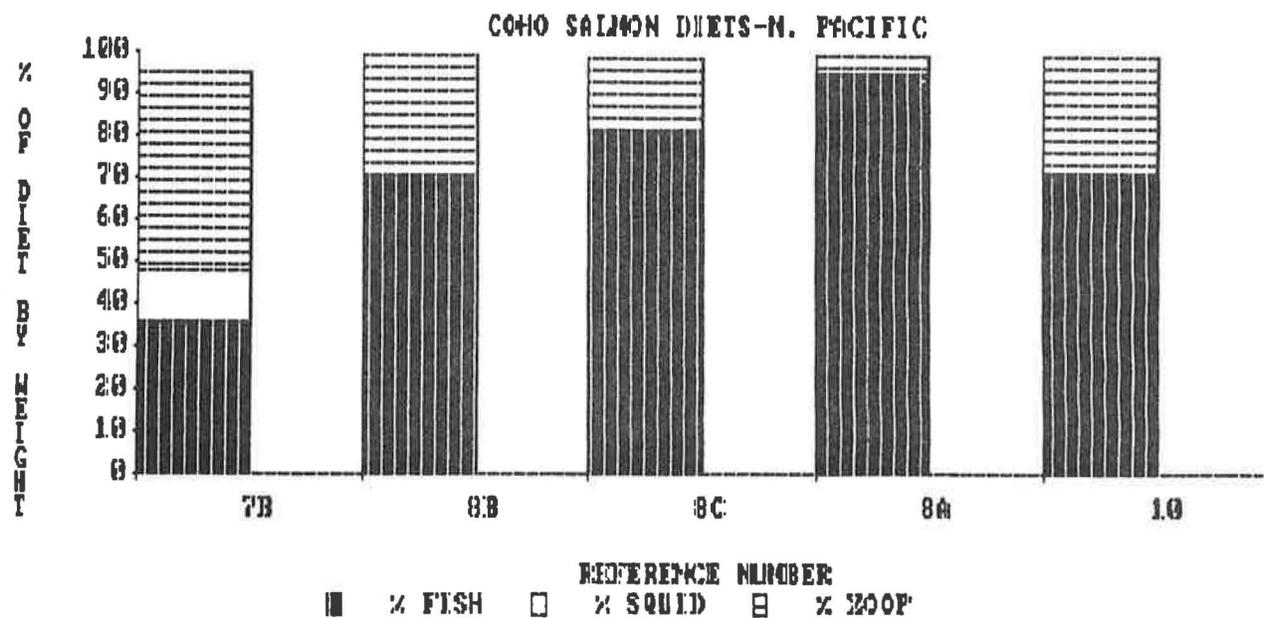


Figure 4. Coho salmon diet compositions in percent by weight of fish, squid and zooplankton. Numbers along x-axis refer to references listed in Appendix Table I.

SALMON CARRYING CAPACITY SIMULATION MODEL

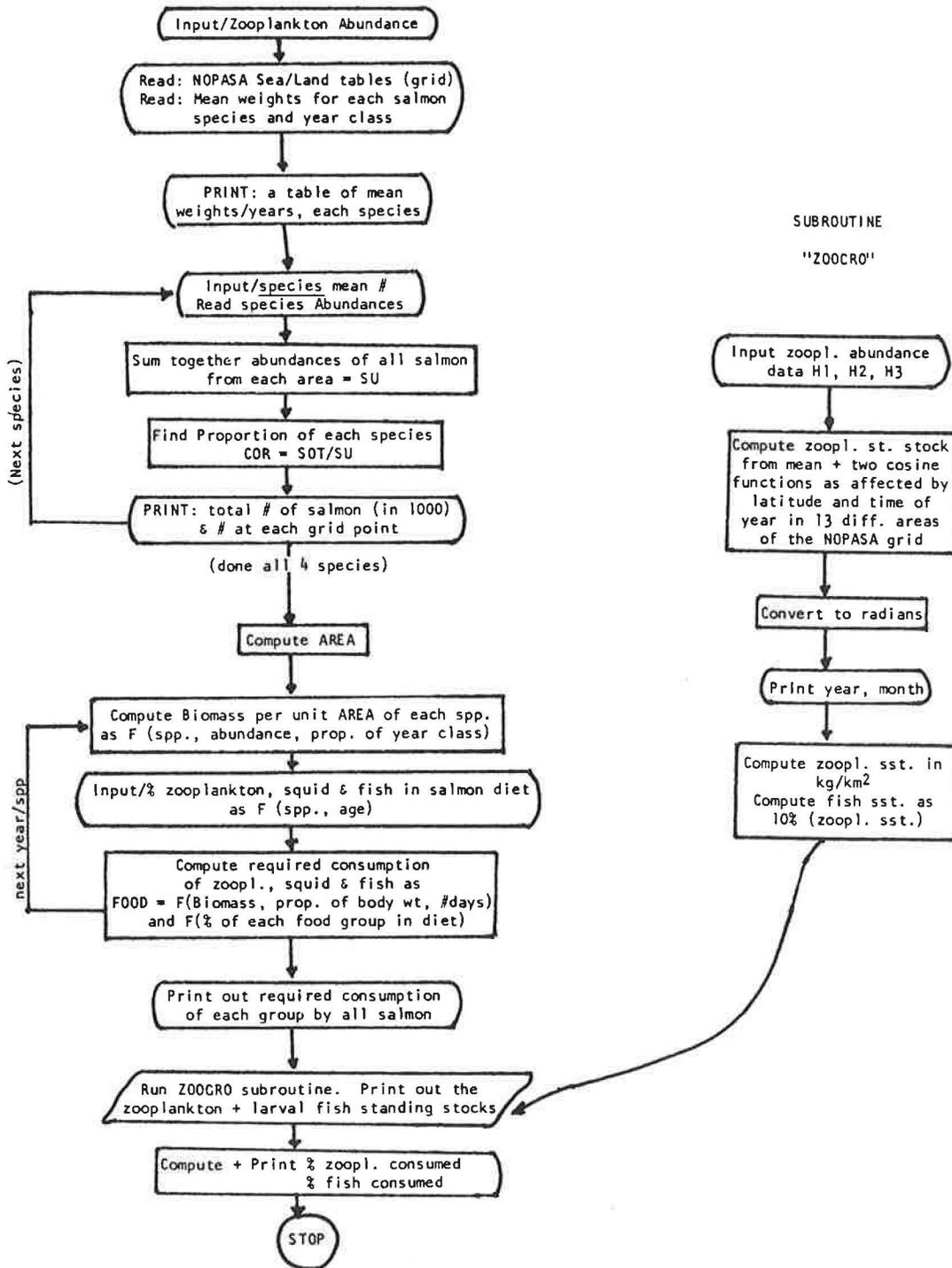
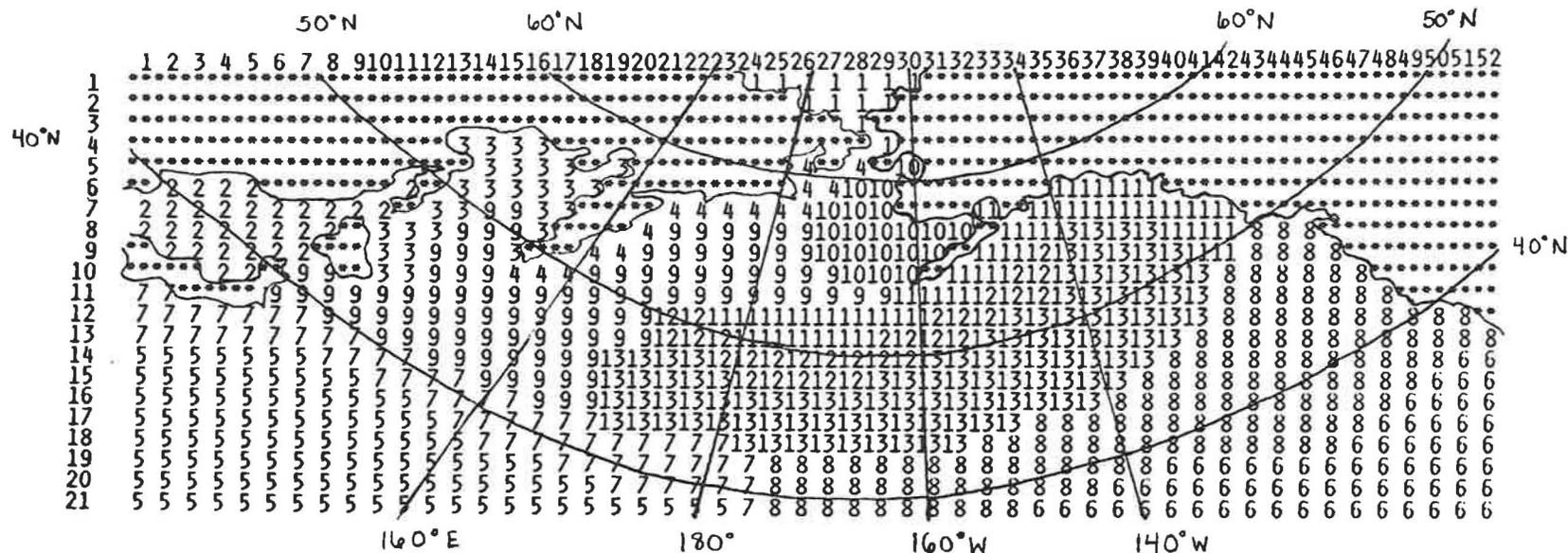


Figure 5. Flow diagram for the salmon carrying capacity simulation model.



AREA #	ZOOPLANKTON BIOMASS (MG/M3)	AREA #	ZOOPLANKTON BIOMASS (MG/M3)
1	(334)	8	(381)
2	(436)	9	(401)
3	(379)	10	(483)
4	(383)	11	(496)
5	(301)	12	(442)
6	(321)	13	(419)
7	(361)		

Figure 6. Sea-Land diagram used in zooplankton biomass simulation (ZOO-CRO). Divides the north Pacific Ocean into 13 different physiographic areas. # indicates land. Numbers in parentheses represent July zooplankton biomass (mg/m<sup>3</sup>). From NOPASA (Favorite and Laevastu, 1979).

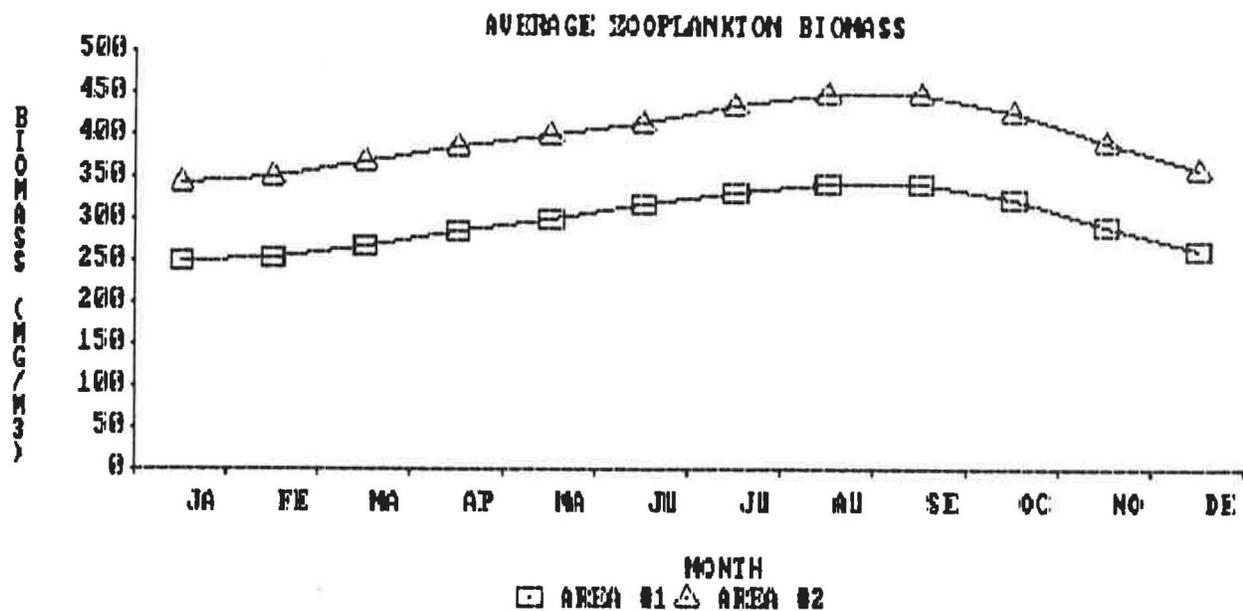


Figure 7. Simulation of average monthly zooplankton biomass (mg/m<sup>3</sup>) in Areas I and II of Figure 6.

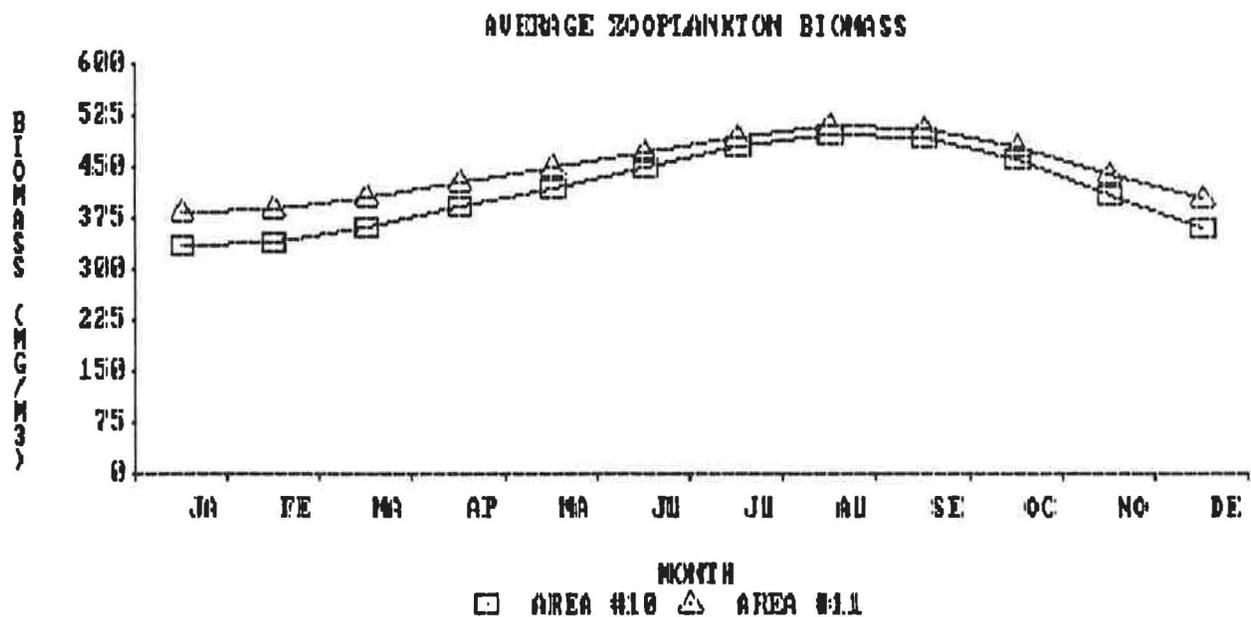


Figure 8. Simulation of average monthly zooplankton biomass (mg/m<sup>3</sup>) in Areas X and XI of Figure 6.

APPENDIX TABLE 1. Salmon Diets Reference List and Sample Sizes

SOURCE	NO. FISH SAMPLED				LOCATION	SAMPLE DATE
	Sockeye	Pink	Chum	Coho		
1. Kanno & Hamai (1971)	a. 103	107	105	--	C,W Bering Sea	Summer 1966
	b. 142	79	123	--	NE Bering Sea	Summer 1966
2. Nishyama (1970)	a. 115	--	--	--	W Bering Sea	Summer 1966
	b. 58	--	--	--	"	Summer 1965
3. Manzer (1968)	87	24	--	4	G of Alaska	Winter 1964
4. Allen & Aron (1958)	104	111	88	--	W Pacific	Summer 1955
5. Andrievskaya (1958)	150	250	250	--	W Pacific	August 1955
6. Andrievskaya (1966)	2200	1700	3200	--	W Pacific	1962
						a. Summer b. Spring
7. LeBrasseur (1966)	a. 71	47	--	7	G of Alaska	Summer 1958 adults
	b. 116	--	--	28	G of Alaska	Summer 1958 immature
8. Pritchard & Tester (1944)	a. --	--	--	45	Vancouver BC	1939
	b. --	--	--	126	"	1940
	c. --	--	--	86	"	1941
9. Favorite (1970)	5880	--	--	--	Subarctic Pacific	Summer 1960
10. Reid (1961)	a. --	--	--	200	SE Alaska	Summer 1957
	b. --	--	--	222	"	Summer 1958

Appendix Table II. Input values for carrying capacity simulation.

Species	North Pacific salmon mean run size +30% escapement; Asian and N. American runs	Percent of body weight required for consumption to maintain salmon biomass					Salmon diet composition from stomach content analyses (% by weight)					No. of days salmon feed in ocean	Salmon individual weights (kg)					
		Age					Age						Age					
		1	2	3	4	5	1	2	3	4	5		1	2	3	4	5	
Sockeye	43,000,000	0.029	0.022	0.022	0.22	0.022	Zoopl	80	50	50	50	50	365 each of 5 years	0.3	0.9	1.9	2.5	3.0
							Squid	10	35	35	35	35						
							Fish	10	15	15	15	15						
King Chum King & Chum	7,000,000 57,000,000 64,000,000	0.028	0.021	0.021	0.021	0.021	Zoopl	80	91	91	91	91	365 each year	0.4	1.0	2.0	3.2	4.0
							Squid	10	1	1	1	1						
							Fish	10	8	8	8	8						
Pink	165,000,000	0.03	0.03	-	-	-	Zoopl	60	60	-	-	-	550	0.8	1.5	-	-	-
							Squid	20	20	-	-	-						
							Fish	20	20	-	-	-						
Coho	14,000,000	0.03	0.03	-	-	-	Zoopl	25	25	-	-	-	480	1.8	3.0	-	-	-
							Squid	4	4	-	-	-						
							Fish	71	71	-	-	-						
Total	286,000,000																	