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A Study of the Ocean Migrations of Sockeye Salmon and Estimation of the Carrying-Capacity of the North Pacific Ocean Using a Dynamical Salmon Ecosystem Model (NOPASA)

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A STUDY OF THE OCEAN MIGRATIONS OF SOCKEYE SALMON AND ESTIMATION OF THE CARRYING-CAPACITY OF THE NORTH PACIFIC OCEAN USING A DYNAMICAL NUMERICAL SALMON ECOSYSTEM MODEL (NOPASA)

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ABSTRACT

A transpacific, numerical, salmon ecosystem simulation model (NOPASA) is briefly outlined. Although still in a developmental stage, it permits simulations in space and time of previously descriptive models of oceanic migrations of sockeye salmon. Preliminary results indicate that the known offshore distribution of salmon can be reproduced numerically by prescribing summer and winter average migration speeds as derived from known seasonal distribution, or by permitting salmon to swim aginst the surface current with an average speed that is a function of salmon size and of the water temperature. Obviously in some areas salmon are carried downstream. In addition, optimum temperature limits for salmon are prescribed in the model and migrations toward optimum temperature are computed.

A separate ecosystem simulation model indicates that the survival rate of the smolt might be dependent on its growth rate and on the timing of the escapement from the coastal environment where the predation is high. Predation on salmon by mammals has been found to be of considerable magnitude and is greatly affected by the seasonal distribution of both predator and prey (i.e. encounter). It is suggested that the predation by mammals may affect the success of salmon enhancement projects.

The salmon food resources of the North Pacific (i.e. the carrying-capacity for salmon) could easily support a much higher standing stock of salmon than present if salmon were the most competitive consumer of zooplankton. However, food requirements may only be satisfied in areas of high concentrations of forage. Because such areas vary from year to year the annual growth of salmon could be affected.

1. Introduction

Distributions and migrations of Pacific salmon (Oncorhynchus spp.) have been the focus of extensive studies by Canada, Japan, and the United States for over 2 decades. Results are available in various documents, annual reports, and bulletins of the tripartite International North Pacific Fisheries Commission (INPFC); however, there has been no attempt to synthesize the extensive field data obtained into a dynamic, numerical model that provides insight into ecosystem interactions.

Because the seasonal distribution of salmon in the ocean is only generally known, reported migration routes and speeds are only approximations. It is not known what factors guide the migrations, although many hypotheses on this subject have been presented (Larkin 1975). Furthermore, some American and Asian stocks do not mix to any appreciable extent in the ocean despite the fact that the mean surface currents (the North Pacific Drift Current) could easily transport Asian stocks across the North Pacific more than once during their ocean life if they remained in the surface layer. Questions arise as to how the salmon counteract such transport by current and if the approximate distributional separations of Asian and American stocks varies from year to year due to changes in ocean currents?

An attempt has been made at NWAFC to synthesize all available pertinent information on the oceanic distribution of Pacific salmon into a numerical, ecosystem simulation model. This model and others will be used to study and where possible to determine the factors affecting the abundance and distribution of salmon and to ascertain the effects of environmental anomalies and the abundance of marine mammals on their distribution and abundance. This report presents some preliminary results from this ongoing project.

It has been stated (Paloheimo and Dickie 1973) that unfortunately variability in nature and vagaries of sampling procedures together give such high statistical variances of almost all parameters that numerical assessments of marine parameters seems to be more a display of brilliant intuitions and courageous speculations than a framework of scientific observation. We agree, but we also agree with McAllister (1973) who notes that knowing measurements and assumptions to be subject to wide errors from a wide variety of sources, one would be negligent in not seeking by whatever means possible to assess their implications for what one is trying to do—because in dealing with complex systems the consequence of errors, conflicting assumptions, alternate choices and decisions as to whether or not, or how to average data can rarely be divined by conventional inspections, whereas computer modeling would seem to be a rapid and useful way of doing so.

2. Objectives of the Study

The basic objectives of the initial simulation were to determine the average seasonal movements of salmon in the ocean as affected by currents and water temperature, and to determine whether the ocean food resources might be limiting salmon production. Specifically, answers to the following problems were sought.

(a) Development of numerical methods for reproducing the distribution of salmon as affected by environment (e.g. temperature and abundance of food).

(b) Determination of the average migration speeds along paths denoted by descriptive models and the effects of mean surface currents on their distribution and migration (the assumption being that if the effects of surface currents on salmon distribution are considerable, year to year differences in salmon distribution could be ascertained by knowing year to year anomalies in surface currents).

(c) Study of the possible mechanisms for separate offshore distributions of different age groups, species and stocks as a possible result of environmental interactions on migration patterns.

(d) Relatively large year to year variations in survival of salmon in the ocean, as well as timing of runs, have been observed; thus our intentions are to use the numerical model also for the study of the effects of the environmental anomalies on the survival and timing of runs of salmon and on smolt survival.

(e) Predation is an important process in controlling populations in the marine ecosystem; thus it was considered necessary to study the effects of size dependent feeding and predation on smolt and factors affecting smolt predation in general.

(f) Marine mammal populations have increased in recent years in the NE Pacific and as many marine mammals are known to prey upon salmon it was considered necessary to determine quantitatively the predation by marine mammals on salmon.

(g) Salmon enhancement and "ocean farming" of salmon are increasing in popularity in the North Pacific area; thus it seems necessary to determine the carrying capacity of the North Pacific in respect to salmon.

This report gives some preliminary results of some of the objectives of this project, together with some descriptions of the simulation techniques as applied to sockeye salmon (O. nerka).

3. Background

If one considers all species of Pacific salmon it is apparent that individuals return year-round to coastal waters and streams to spawn. However, sockeye stocks usually have a seasonal migration that peaks in late spring or early summer as smolts from lake systems enter the ocean, and nearly simultaneously maturing adults return to lake systems to spawn after completing the marine phase of their life cycle. Most sockeye reach maturation after either one or two years residence in lake systems followed by two to three years residence in the ocean, thus attaining ages of 3 to 5 years. Although marine survival estimates vary widely, 5% survival is a generally accepted figure.

The most recent and most complete description of the oceanic conditions and processes of the Pacific Subarctic Region where these salmon occur is by Favorite et al. (1976). During summer, salmon, particularly sockeye, are found in the upper layers of the ocean in areas where temperatures of approximately 4°C are found at depths less than 100m, thus generally northward of 45°N in the central part of the ocean. During winter, there is a general southward shift in population abundance and even indications of a retreat to deep layers (Favorite et al. 1977), but no evidence of any movement at the surface or at depth southward of the Subarctic Boundary near 40°N defined by an abrupt change in the vertical salinity distribution. Horizontal flow is dominated by 4 major current systems, which in spite of numerous branches form a relatively closed subarctic cyclonic circulation system that sweeps both Asian and North American coasts; and, by 4 major cyclonic gyres (Fig. 1) that serve not only to mix waters from various sources but provide a number of alternative pathways of transiting the region.

Although the above is undoubtedly an oversimplification of actual conditions, there are several interesting well established phenomena. Sockeye from the Vancouver Island and Gulf of Alaska area are rarely if ever found westward of the Alaskan Gyre; those from west or east Kamchatka are rarely if ever found eastward of the Western Subarctic Gyre or western portion of the Bering Sea Gyre; and, those from Bristol Bay are rarely if ever found outside of the influence of the Alaskan Gyre and eastern portion of the Bering Sea Gyre.

The annual mean commercial catch of sockeye (including high seas fisheries of Japan and coastal fisheries of Japan, Canada, U.S. and U.S.S.R.) for 1972-75 was 28.8×10^6 fish or 70.2×10^3 metric tons (Fredin et al. 1977), equivalent to an individual weight of 2.4 kg (5.4 lbs). In terms of overall numbers of sockeye salmon in the ocean, this does not include an overall escapement of roughly one-third, nor those immatures that have completed 1-2 (or more) years ocean residence.

In the present model sockeye are considered to originate from 5 areas: Washington-Oregon-British Columbia, Gulf of Alaska, Bristol Bay, East Kamchatka, and West Kamchatka and relative abundances based on commercial catch (Fredin et al. 1977) indicate ratios of 8:3:8:3:7, respectively; Oregon-Washington-British Columbia, Bristol Bay and West Kamchatka being the three important areas.

Other required input data and their derivation are described partly in the outline of the model and partly in the discussion of migration and predation.

4. General outline of North Pacific Salmon Simulation Model (NOPASA)

The North Pacific Salmon simulation model (NOPASA) is a numerical simulation, based on available quantitative data and knowledge of processes. The NOPASA I deals mainly with sockeye, although the carrying capacity of the North Pacific is computed using all species of Pacific salmon.

The simulation model grid for the region is given in Figure 2 (grid size is 190.25 km and 13 subregions are considered that enhance some geographical-dependent simulations). The following distributions have been digitized in this grid: sea-land and subregion table, monthly mean sea surface temperatures and surface currents, relative distribution of mammals which feed on salmon, relative distribution of birds and fish feeding on smolt, relative distribution of small pelagic fish which serves as food for salmon, and "geographic migration speeds" (u and v) of sockeye salmon, (smolt, winter, summer, and returning adult migration speeds). The zooplankton standing crop is simulated in monthly time steps in the program.

In addition, many rate coefficients must be given, such as for growth, food requirement, food composition, average salmon predation rates of predators (e.g. in the form of percentage of salmon in the food), mortalities from diseases (an unknown, but small component), etc. Furthermore, the annual mean distribution of five major species of Pacific salmon (pink, chum, sockeye, king, and coho) were digitized, using long-term mean run sizes as bases for abundance. In addition, the annual mean weight of all species, food requirements, and food compositions were introduced into the model.

Computations at each grid point in monthly time steps include migration, effects of the environment and availability of food, growth (as affected by the above factors), feeding, mortality, and grazing (e.g. by mammals), and return to rivers.

The essential computation formulas used in the model are the same as in DYNUMES and PROBUB models (for examples see in this Volume: Laevastu, Favorite, and Larkins, Appendix; or Laevastu and Favorite 1980 (in press - A.R. Longhurst, Analysis of Marine Ecosystems, Academic Press, Inc., London).

The present version of NOPASA program consists of eight main subroutines:

NOPASA - main program for input of parameters and required fields and initialization.

ZOOSTA - simulation of monthly mean zooplankton standing crop which is used initially among others as indicator of relative abundance of forage.

SOCKEYE - control program for sockeye salmon; input of smolt, calling of other computation subroutines and preparation of outputs; computation of consumption (predation) of salmon by mammals, (also by other fish and birds in first year); computation of offshore fishery.

ASVBIOM - computation of growth (as function of species, age, temperature, and food availability).

RANLOH - computation of migrations (active migrations as affected by currents and temperature).

TEMPTOI - computation of additional migrations as affected by temperature (temperature limits of distribution) and food abundance.

SPIMIG - simulation of sockeye migration speed and direction in response to surface currents.

SALCON - computes the average annual distribution of all five species of Pacific salmon and their food consumption (this subroutine has been run as a separate model for the determination of ocean carrying capacity in respect to salmon).

In addition, there are a number of auxiliary subroutines such as for printout, smoothing (diffusion), summarization, accounting for runs, etc.

The main computation procedure for sockeye is in general as follows: proper quantities of outmigrating smolt are prescribed in May, June, and July at selected grid points off the rivers from which the smolt originate. The smolt (and the oceanic sockeye biomass) are advected with prescribed "geographic migration speed" in weekly time steps. A smoother (diffuser) is applied in each time step to simulate random migration and dispersal.

The growth of the biomass is computed monthly with empirically derived monthly growth coefficients. Mortality is computed as predation mortality. Smolt in first calendar year are preyed upon by birds, other larger fish, and to a lesser extent by mammals. In the second year the predation on sockeye is mainly by mammals and to a small degree by other larger fish, and in the following years only mammal predation is operative.

Each month the prescribed sea surface temperature preference limits (3^o to 16^oC) are checked and if these are exceeded in given locations, the sockeye biomass is moved towards preferred temperatures. Furthermore, it is assumed that sockeye are in search for food and have a slight tendency to accumulate in areas of higher food concentrations. Therefore, a fraction of the biomass is moved each month towards higher food concentration, whereby the prescribed distribution of small pelagic fish is used as criterion of food abundance.

Each April a portion of the biomass of second year and older sockeye is separated and moved with predescribed homing migration speed towards the coasts from which the smolt originated. All third year ocean sockeye are moved with the homing migration speed towards the coasts.

5. Preliminary Results of Numerical Simulation

The general seasonal distribution of sockeye is approximately known from offshore exploratory fishing (e.g. French, Bilton, Osaka, and Hartt 1976; Hartt and Dell 1978). In order to simulate this offshore distribution and its seasonal changes, sockeye movement speeds must be computed and digitized. These speeds were derived by plotting the seasonal distributions, measuring the distances between the major distribution areas as these changed with seasons, and dividing the distances by the time required for change from one seasonal distribution to another. These migration speeds are not true migration speeds through water but rather geographic relocation speeds of salmon concentrations, the latter being determined by experimental fishing.

Although Kondo et al (1965) reported oceanic migration speeds for sockeye (in 1960) of 3.9 miles/day during June and July in the western Pacific, they also noted speeds of 15-18 miles/day in May and June during migrations from the Aleutian Islands to Bristol Bay; and, as high as 30 miles/day across the eastern Bering Sea shelf to Bristol Bay. Thus although speeds may increase as homing signals intensify, input speeds appear appropriate for modeling of oceanic migrations. Examples of these "geographic migration speeds" are given (Figures 3 to 5) for first-year salmon (smolts) and for winter and summer movements of immatures. The numerical values in the program are in km/day and vary from about 2 to 10 km/day (1-6 miles/day). These geographic migration speeds are applied in the simulation model in weekly time steps, which results in relatively smooth transition of biomass in space and time.

Three resulting computed distributions of sockeye are given as examples in Figures 6 to 8, which agree relatively well with known distributions.

The "geographic migration speeds" (see Figure 3) and resulting distribution of sockeye bear some resemblance to major surface circulation patterns in the North Pacific Ocean. French, Biltōn, Osako and Hartt (1976) suggest that some of the immature sockeye salmon in the summer recirculate in the Alaskan Gyre and remain in the northeastern Pacific until they leave for the natal streams, but they found that it could not be demonstrated that defined oceanographic features of the North Pacific Ocean had any direct influence on the north-south movements and distribution of sockeye. However, Godfrey, Henry, and Machidori (1975) found that the dispersal of juvenile, age .0, coho salmon of both Asian and North American origin, did not appear to be inconsistent with the directional pattern of surface circulation in the North Pacific. They suggested that the small juvenile coho may take advantage of the downstream flow of ocean currents in achieving the southerly and east-west dispersal that is observed the following spring.

If the offshore component of surface current enhances the offshore migration of smolt, then one can expect the smolt distribution in offshore waters (near and off the continental slope) in essentially a lower salinity, coastal belt. In fact Hartt and Dell (1978) found that although sockeye entered the ocean in June, they (and other salmon smolt) were still distributed in the coastal belt in September, but further north from the ocean entrance.

As will be shown later in this paper, the adult sockeye must head the surface currents (as many other fish are known to do) in order to maintain their known oceanic distributions; thus, the question rises when do the young salmon start to head the current? Hartt and Dell (1978) found that Frazer River sockeye traveled 7.6 to 14.4 (mean 11) miles/day during their early ocean life. The Skeena River sockeye smolt traveled 3.5 to 7.5 (mean 5.5) miles/day, and the Bristol Bay sockeye smolt traveled only 2.1 to 3.6 (mean 2.85) miles/day. It seems that the travel speed may be partly a function of temperature, as is known from tank tests, and it is also a function of surface current speeds.

Larson (1970) summarized the surface current speeds indicated in surface current atlases that has been derived largely from ship drifts. He found the surface currents off U.S. and Canadian Gulf of Alaska coast range from 0.25 to 0.75 knots (6 to 18 miles/day). Current speeds increased in the northern Gulf of Alaska, where off Kodiak and to the west it was 1.0 to 1.25 knots (24 to 30 miles/day). Thus, in the southern part of the Gulf of Alaska the surface current speed is about the same or slightly higher than the speed of travel of sockeye. However, in the northern part of the Gulf of Alaska the surface current speed is more than twice the speed of travel of smolt. Thus, it seems that the sockeye smolt must start to head current in September or October when they have been transported to northern and northwestern Gulf of Alaska in order to achieve the apparent spring distribution ascertained by Hartt and Dell (1978) and French et al. (1976).

Direct observations on the general behavior of fish in a current are few. Bishai's (1960) experiments showed that herring and lumpsucker larvae, when subjected to current in a glass tube are not carried passively, but they respond positively to the current, orientate themselves against it, and try to resist it by swimming upstream. Leggett (1977) has summarized the causes for fish migrations and for the guidance of migrations (guidance mechanisms); among these guidance mechanisms are polarized light, geoelectric fields, temperature, and currents. Electric fields generated by current moving through earth's magnetic field have been found to be detectable by salmon and eels and can also provide directional information. Barber (1979) concluded that salmon must be able to sense an aspect of their environment that continuously provides cues concerning their heading. Currents might also be used directly for this guidance of movement and migrations. Flock (1971) and others note that lateral line mechanoreceptor organs provide a sophisticated system for detection of water motion. For our present study it is immaterial whether salmon can sense the current directly or via geoelectric field created by currents.

In order to obtain the true movement of sockeye salmon through the water the surface current speed is subtracted from the "geographic migration speed" (see Figures 3 to 5), which is required to maintain the known geographic distribution of sockeye in the ocean. The five year average, monthly mean surface current speeds, as computed by Larson and Laevastu (1972) (see Figure 9), were used in the present numerical study.

An example of this subtraction is presented in Figure 10 and clearly indicates that if the sockeye are located in the surface layer above the thermocline, they must swim against the current in the surface layers in order to maintain the known ocean distribution. Although it has been speculated that in winter sockeye may retreat to depths of 500 m where they would be still within the Subarctic Water Mass (Favorite 1969) and would have access to forage performing 300-500 m diel migrations below the surface layer or overwintering at these depths, there is still no evidence for or against this view.

Numerical experiments were designed to simulate in NOPASA the movement of sockeye salmon in response to monthly mean surface currents. The following formulas were used to simulate migration speed components of sockeye:

$$U_{ma} = -U_w c_u \ell ts + 0.18 V_w k_u \tag{1}$$

if $U_{ma} < b_u$ then,

$$U_m = U_{ma} + \left[(U_w - b_u) k_o T_w\right] \tag{2}$$

$$V_{ma} = -V_w c_v ts - 0.18 ({}^{m}/U_w) \ell \tag{3}$$

if $V_{ma} < b_v$ then:

$$V_m = V_{ma} + \left[(V_w - b_v) k_o T_w\right] \tag{4}$$

where:

b_u, b_v - assumed maximum upcurrent random migration speed dependent on size of the fish (b_u = 16 to 20 cm/sec; b_v = 9.5 to 10.5 cm/sec)

c_u, c_v - "conversion coefficient" ($c_u = 1.21$; $c_v = 1.40$)

k_u, k_o - empirical tuning coefficients ($k_u = 0.182$; $k_o = 0.045$)

ℓ - "latitude effect" (migration speed decreasing with latitude)

m - empirical coefficient (3.7)

s - size factor (0.8 to 1.25) (migration speed increasing with the size (age) of the fish)

t, T_w - temperature effect on migration

U_m, U_{ma} - U migration speed component, km/day

U_w - U surface current speed component, cm/sec

V_m, V_{ma} - V migration speed component, km/day

V_w - V surface current speed component, cm/sec

The migration of salmon in the model is computed with the following "upcurrent interpolation" formula:

$$B_{(t,n,m)} = B_{(t-1,n,m)} - (t_d \, |U_{(t,n,m)}| \, UT_{(n,m)}) - (t_d \, |V_{(t,n,m)}| \, VT_{(n,m)})$$

UT and VT are the "upcurrent" biomass gradients:

U positive:

$$UT_{(n,m)} = (B_{(n,m)} - B_{(n,m-1)})/\ell$$

U negative:

$$UT_{(n,m)} = (B_{(n,m)} - B_{(n,m+1)})/\ell$$

The computation of VT is analogous to the computation of UT).

$B_{(t,n,m)}$ is biomass in time step t at the grid point n,m; t_d is time step length and $U_{(t,n,m)}$ and $V_{(t,n,m)}$ are migration speed components.

In addition to the effects of fish size and temperature on the migration speed, two other considerations are included in the migration speed simulation formulas above: The second term in formulas 2 and 4 presents the active downstream transport of salmon, if the current speed is above some predetermined value (16 to 20 cm/sec assumed here; size dependent), this downstream transport is made temperature dependent. The second term in formulas 1 and 3 (v contribution to u and vice versa) is a small additional term, in many ways similar to "Coriolis term" in hydrodynamical numerical computations.

The formulas 1 to 4 are preliminary and not yet properly tuned. The tuning is effected by reproduction of known sockeye distributions. Two examples of the distribution of sockeye salmon as computed using the above formulas and monthly mean surface currents, are given on Figures 11 and 12. Although general features of the sockeye distribution are reproduced, there are still some discrepancies which must be tuned. The discrepancy is apparent along the U.S. and Canadian Gulf of Alaska coast which is mainly caused by incomplete tuning of predation. The greatest discrepancy occurs in April (Figure 12) in the western Pacific where the sockeye concentration seems to be too far southwest. This discrepancy can be prevented by tuning the transport effect--i.e. decreasing the upcurrent movement. The same shortcoming is apparent in spring in the distribution of Bristol Bay sockeye, which seem to be too far west. Further, the grid size is too large to describe distributional details in the Alaskan Stream south of the Aleutian Islands.

Nevertheless, examples demonstrate the possible effects of surface currents on the general distributions of sockeye salmon. As the surface currents vary from year to year, salmon distributions in the open ocean are also expected to vary, and spatial variations in salmon distributions can be expected to cause changes in survival via predation by mammals, availability of food concentrations, etc.

6. Predation on Juvenile and Adult Salmon

According to Fiscus (1978) fifteen marine mammal species in the North Pacific prey on salmon; the greatest predators are fur seal, sea lion, beluga whale, and other toothed whale, and Pacific whiteside dolphin. Fur seal stomachs off Oregon and Washington coasts have been found to contain 20% of salmon, and stomachs of offshore fur seals have been found to contain 2.5% salmon.

The total predation of mammals on adult salmon is difficult to determine quantitatively. The spatial and temporal distribution of marine mammals in offshore areas is not well known, and the mean portion of salmon in the food of mammals is also uncertain. However, the predation by mammals on sockeye was simulated in the NOPASA model with conservative assumptions. The distribution of mammals, as well as salmon, is uneven in offshore waters and both the predator and prey are highly mobile, creating double density dependent predation effects. Thus the predation by mammals varies considerably in space and time. A detailed presentation of the results of model computations of mammal predation on salmon would require a lengthy discussion, as the various assumptions made must also be presented; however, a summary statement can be made. The consumption of adult salmon by marine mammals is apparently considerable—for example, the 1.4 million fur seal in the northeast Pacific and eastern Bering Sea could consume 15 x 10^3 tons of salmon annually if their diet contained one percent salmon. Furthermore, the model runs indicate that the total mammal consumption of salmon is of the order of half of the mean Bristol Bay sockeye run or ca 8 million fish (ca 16 x 10^3 tons). Straty (1974) reporting on seaward migrations of sockeye salmon in the Bristol Bay area indicated stomach contents of 101 beluga whales collected near the mouth of the Kvichak River contained 20,000 sockeye salmon smolts.

Considering the plausible high consumption of adult as well as juvenile salmon and that the mammals are known to aggregate for feeding on fish aggregations (e.g. returning salmon off estuaries), it becomes questionable whether the existing and planned salmon enhancement projects would be profitable until marine mammal herds are controlled and managed.

The mortality associated with the initial seaward migration of sockeye smolts in this area is not quantitatively well known, wherein predation by marine birds, fish, and mammals is not only evident but extensive as the smolts move slowly from river systems and become acclimated to the marine environment. Furthermore, coastal waters contain higher concentrations of larger fish which can prey on smolt; the idea that the main mortality of smolt in the sea occurs in coastal waters, has been generally accepted.

Because the grid size of NOPASA model is of necessity relatively coarse, a detail deterministic simulation of smolt in coastal waters is not possible. However, a simplified implicit auxiliary model can be used for this purpose. The theory of this model relates the survival of the smolt to its growth rate and to the time spent in the coastal regime: the rapidity with which the smolt (1) pass through their most vulnerable prey size (re. size dependent predation), (2) move into a more expansive environment with a reduced density of predators (i.e. to offshore waters), and (3) gain effective avoidance behavior (i.e. greater size and older age)--the lower the predation and the higher the survival.

An "escapement size" (i.e. the size of fish at which the mortality rate from grazing has reached a recognizable "leveling off" region) is graphically presented in Figure 13, which also shows the change of natural mortality with age. The effect of the growth rate of smolt on the time spent in the size range vulnerable to high predation mortality is shown on Figure 14. Finally, the relations between the predation (natural) mortality coefficient and the time spent in preferred prey size range is shown on Figure 15.

There are two essential elements in the presented theory and submodel: the growth rate of smolt, which can vary from year to year and the earliest possible timing of offshore migration (and/or transport mechanism), which also can vary from year to year. The theory is in agreement to Ricker's (1966) findings which state that one of the more important factors affecting sockeye survival rate after leaving the lake is the size of the smolt. Furthermore, the size-dependent predation mortality is a well-accepted (and proven) theory.

A number of investigations have ascertained that smolt moves or is carried downcurrent and that the currents might provide main mechanisms for moving smolt from coastal regime to offshore regime (see Chapter 5). Many earlier studies have also indicated passive seaward drifting of smolt by currents. It can be postulated that this passive seaward transport is enhanced by upwelling type of circulation if and where it is caused by temporal and local wind; and also by estuarine type circulation which is enhanced by increased runoff. Thus, it can be postulated that there might be considerable local and year-to-year variations in the offshore transport of smolt, as the upwelling type of circulation as well as the intensity of the runoff and estuarine type of circulation can vary from year to year and location to location. As there are more predators for smolt in coastal waters than in offshore waters, the timing and intensity of the offshore transport of smolt might affect considerably the smolt survival and the future run sizes of adults. In fact Wickett and Ballantyne (1979) observed that the sockeye returns decrease with increasing mean August and September sea level in the year the smolts go to sea. An increased sea level usually indicates anstau (the "piling up" of surface waters near the coast, i.e. opposite to upwelling).

The above is only a preliminary description of NOPASA and some initial results. The extension of this model continues but is dependent upon availability of funds and manpower.

7. Salmon Forage and the Carrying-Capacity of the North Pacific

A number of analyses of the contents of sockeye salmon stomach have been reported in the literature. Allen and Aron (1958) reported on food items (copepods, euphausiids, amphipods, pteropods, fish, squid, and crustacean larvae) from 227 stomachs collected in three areas of the western North Pacific Ocean--amphipods were dominant items off the southwest and southeast coasts of Kamchatka Peninsula, and copepods were dominant items in the area roughly 48 to 50°N, 165 to 172°E. Lebrasseur (1972) reported food items for sockeye salmon in the northeast Pacific as herbivores, primary and secondary carnivores 3, 30 and 67%, respectively--the dominant item in oceanic areas being squid (48% by weight)--and the dominant item in coastal areas being euphausiids (82%). Sanger (1972), however, derived markedly different ratios for herbivores, primary carnivores, and secondary carnivores--15, 80, and 5%, respectively. Further examples of the spatial and temporal variation of sockeye food are available: Leggett (1977) gives the composition of sockeye food as consisting of 35% zooplankton, 30% squids, 15% fish, and 20% other items; and Wing (1978) lists the food items of sockeye in southeastern Alaskan waters in the following order of importance: sand lance, herring, crustaceans, pollock, capelin, and squids.

Perhaps the most complete study in the oceanic area was conducted by Favorite (1970) in which 5,880 sockeye salmon stomachs were obtained from gillnet catches from May to August 1960 at 82 locations in the central North Pacific and Bering Sea (45°N to 57°N, 160°W to 170°E). Dominance at individual stations varied throughout the area among 5 taxonomic groups: amphipods 43%, fish 18%, squid 16%, euphausiids 12%, copepods 7%, pteropods 2%, and other 2%. Obviously the composition of food of sockeye and other salmon species varied with age (size) of the fish, season, and location, and mainly by the availability and relative abundance of food items. The food composition used in the preliminary model is given in Table 1.

Nishiyama (1970) found that salmon food requirement in the Bering Sea was 1.6 to 2.3% of body weight daily. These values are in general agreement with other food requirement data for fast-growing active fish. In our model a food requirement for salmon of 2.0 to 2.4% body weight daily was used, depending on the growth rate of the species.

Various opinions have been expressed as to the carrying-capacity of the North Pacific Ocean and its ability to provide an acceptable habitat for more salmon than at present. The determination of true carrying-capacity of an ocean area with respect to a given species must quantitatively account for

Table 1.--Average composition of food of five species of North Pacific salmon (used in NOPASA model) (in percent by weight).

	First year in the ocean			"Older" fish		
Species	Zooplankton (euphausiids, etc)	Squids	Fish	Zooplankton (euphausiids, etc)	Squids	Fish
Sockeye	80	10	10	60	20	20
King	80	10	10	10	20	70
Pink	80	10	10	-	-	-
Chum	80	10	10	60	20	20
Coho	60	20	20	-	-	-

Table 1.--Average composition of food of five species of North Pacific salmon (used in NOPASA model) (in percent by weight).

	First year in the ocean			"Older" fish		
Species	Zooplankton (euphausiids, etc)	Squids	Fish	Zooplankton (euphausiids, etc)	Squids	Fish
Sockeye	80	10	10	60	20	20
King	80	10	10	10	20	70
Pink	80	10	10	-	-	-
Chum	80	10	10	60	20	20
Coho	60	20	20	-	-	-

the predation on this species as well as its competitors for and availability of food. This determination can be done in a model which contains all species. An "apparent carrying capacity" can be estimated by computing the food requirements of various estimated standing stocks of this species, assuming that they are highly competitive for the food items considered, and comparing the computed food requirements with the plausible standing stocks and productions of the food items. This was computed by means of the NOPASA model. The annual mean distribution of the five major species of North Pacific salmon was digitized in the grid (see Figure 2). For determination of abundance (numbers), the long-term mean run sizes were used (Table 2) to obtain overall biomass using annual mean weights.

Figure 16 shows the annual consumption of larger zooplankters (larger copepods, euphausiids, pteropods, and amphipods) in kg/km^2. The distribution of the consumption of squids and small pelagic fish was similar, except quantities were ca 12% of the quantities of zooplankton consumed, reaching in a few areas up to 60 kg/km^2, but in most areas half this value.

Although the standing stocks of squids and small pelagic fish in offshore waters are not well known, the standing stocks of zooplankton have been investigated in the past. Using available knowledge on the distribution of zooplankton and its production (the latter was simulated in the NOPASA model), assuming that zooplankton reproduces its biomass twice a year and that half of the zooplankton biomass is suitable as salmon food, the percentage of its consumption by Pacific salmon was computed. The percentage consumption distribution is similar to the consumption distribution in Figure 16.

Table 2.--Mean run sizes of North Pacific salmon.

Species	Mean run in 10^6 fish	Mean run + 30% escapement in 10^6 fish	North American run	Asian run	North American/Asian
Pink	115	165	55	110	1:2
Chum	40	57	11	46	1:4
Sockeye	29	43	29	14	2:1
Coho	10	14	9	5	2:1
King	5	7	6	1	9:1
Total	199	286	110	176	

Only in a few limited areas was the percentage consumption slightly over one percent of available and suitable zooplankton production; in most of the North Pacific it was 0.5% and below. Thus one could conclude that the "apparent carrying-capacity" of the North Pacific is far from being reached by Pacific salmon and that they can be increased significantly above the present mean runs, if they are highly competitive for the available food. However, predation on salmon (e.g. by mammals) may seriously limit salmon production.

8. Summary

Using the North Pacific Salmon simulation model (NOPASA), which is briefly described in this paper, the following preliminary results were obtained from the initial application of the model, mainly on sockeye salmon:

—The offshore distribution of salmon can be reproduced with seasonal geographic migration speeds (for smolt, summer, winter, and return migrations).

—The adult salmon must swim against the mean surface current in order to remain in known seasonal distribution areas.

—Smolt are transported by surface currents and the juvenile sockeye salmon seems to start to head into the current in about October of the first year of ocean life.

—The known seasonal sockeye distributions can also be quantitatively simulated by making the salmon to swim into the current, whereas its swimming speed is a function of fish size and temperature (formulas given).

—Whether the salmon senses the current directly by mechanoreceptor organs at the lateral line or by sensing the geoelectric field created by surface currents, is immaterial to the fact that salmon movements are related to surface currents and can thus vary from year to year.

—The "apparent carrying capacity" (see definition in text) of the North Pacific in respect to salmon can easily sustain ten times higher standing stock of salmon than at present (provided that salmon is very competitive for food and predation on salmon is not a limiting factor).

—The predation by marine mammals on salmon is of considerable magnitude and might affect adversely any salmon enhancement and mariculture efforts.

—The survival of smolt in the sea is primarily a function of its growth rate and of the time spent in the coastal regime where predators are plentiful. The main mechanism which removes the smolt from coastal areas to offshore regime seems to be the transport by surface currents, especially in respect to the offshore component of current which is enhanced by upwelling and by increased runoff. This component has considerable spatial and temporal variations and can affect the smolt survival correspondingly.

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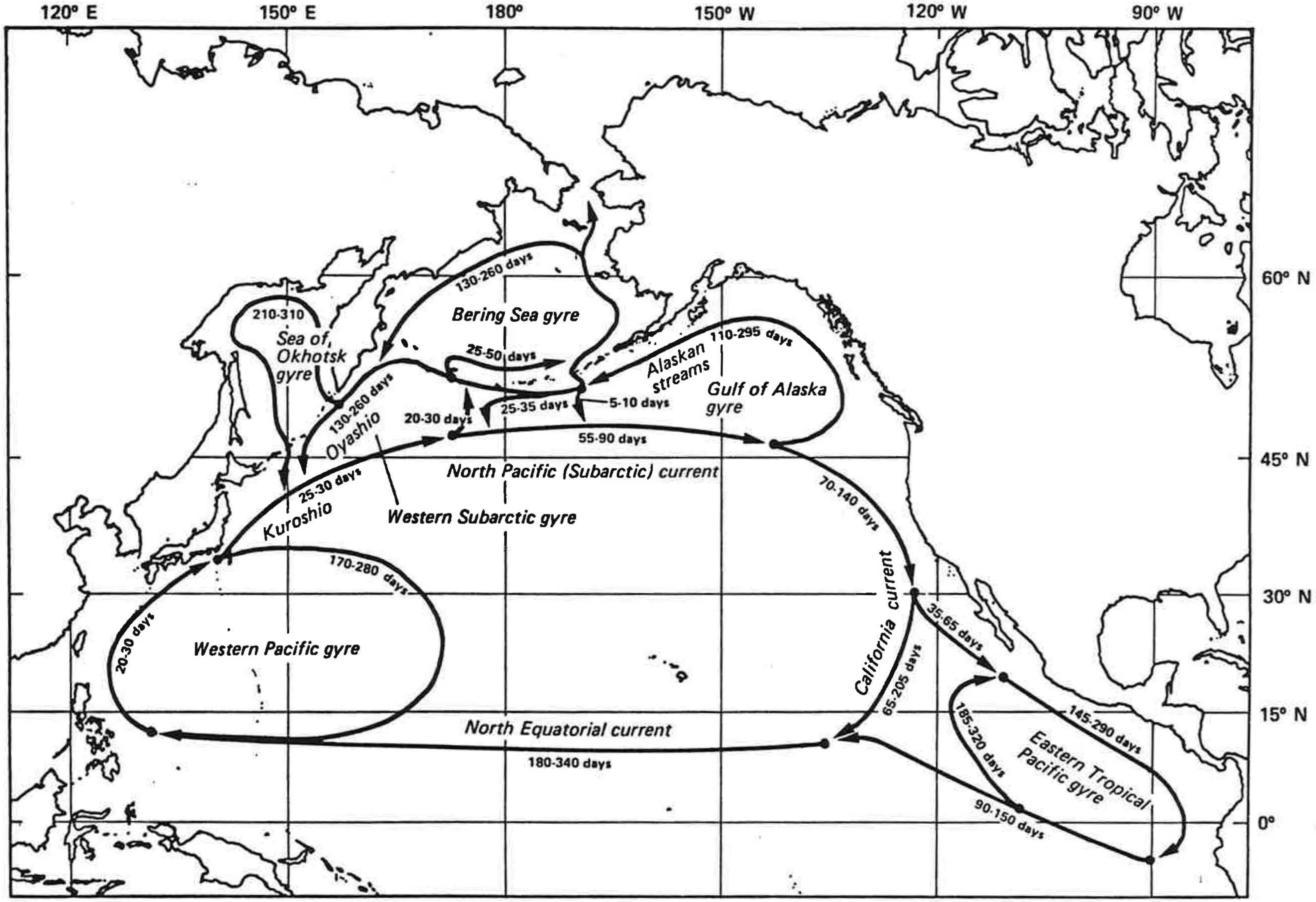


Figure 1.--Schematic presentation of major surface currents, gyrals, and minimum and maximum current travel time from point to point.

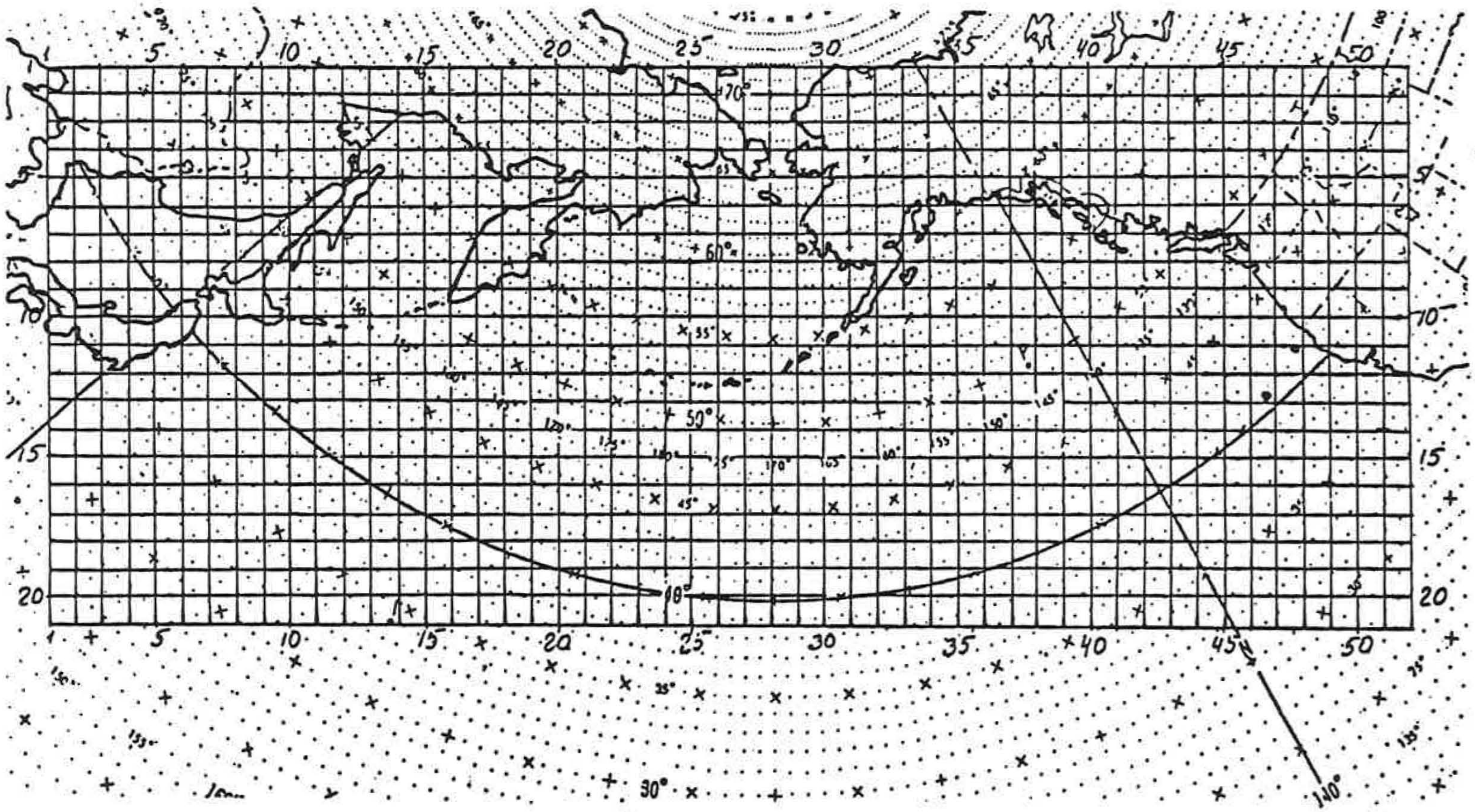


Figure 2.--Computation grid for North Pacific Salmon simulation model (NOPASA).

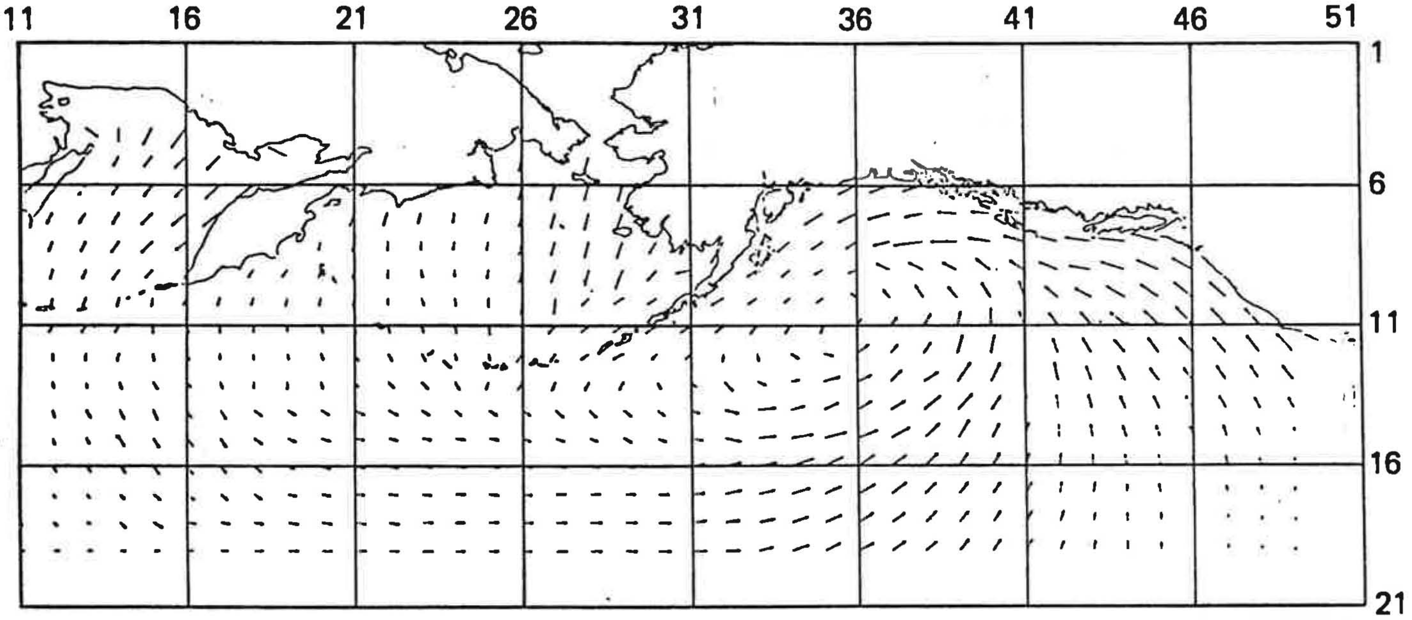


Figure 3.--Geographic migration speed for sockeye smolt for first autumn and winter. (The lines on the map are grid coordinates, see Figure 2.)

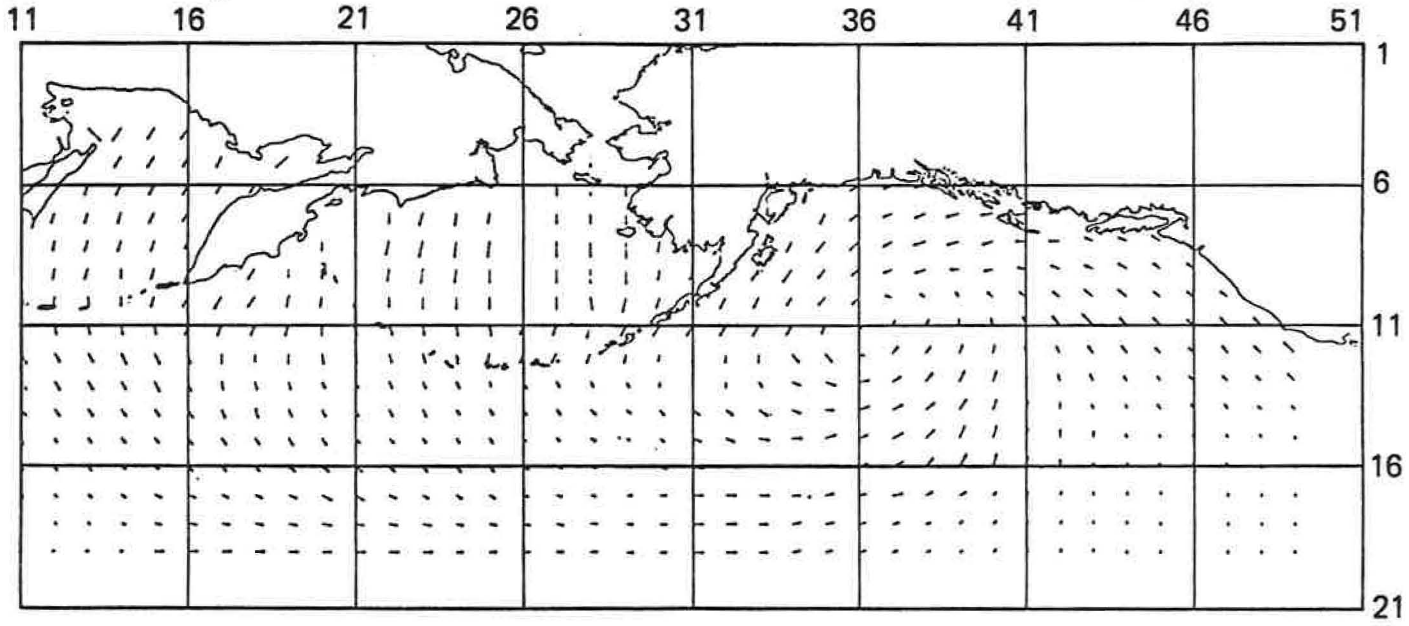


Figure 4.--Geographic migration speed of sockeye during winter. (The lines on the map are grid coordinates, see Figure 2.)

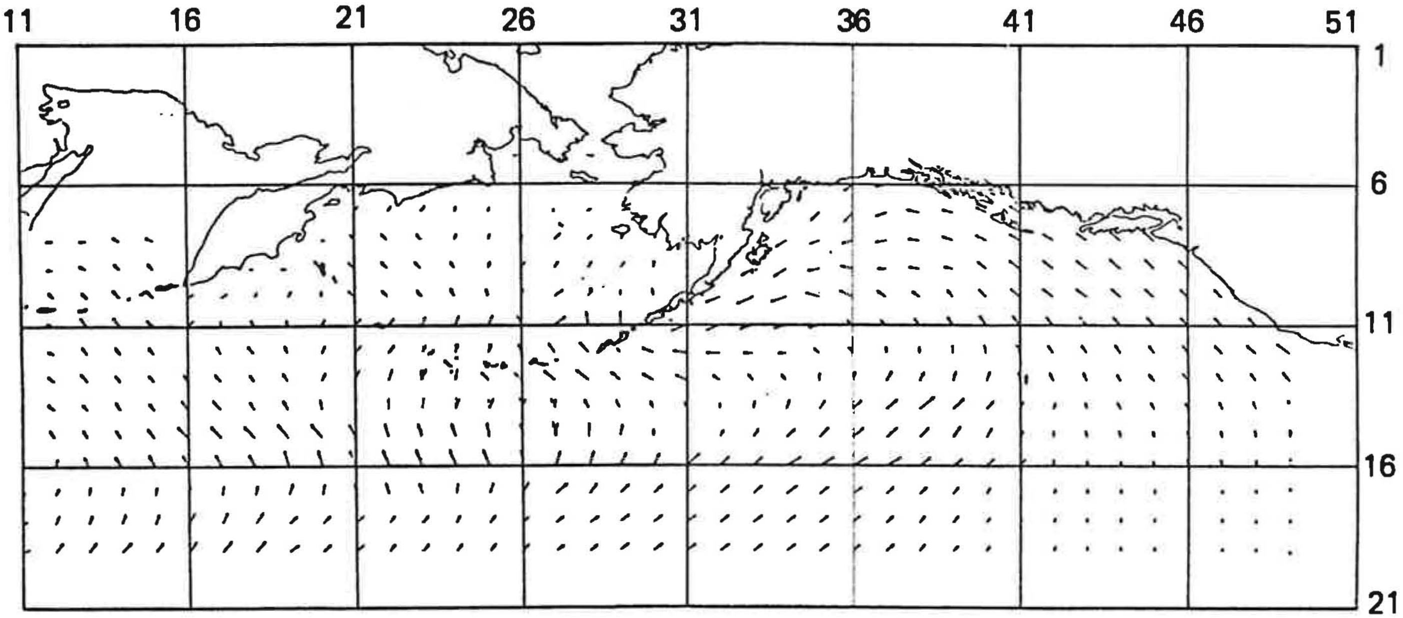


Figure 5.--Geographic migration speed of sockeye during summer. (The lines on the map are grid coordinates, see Figure 2.)

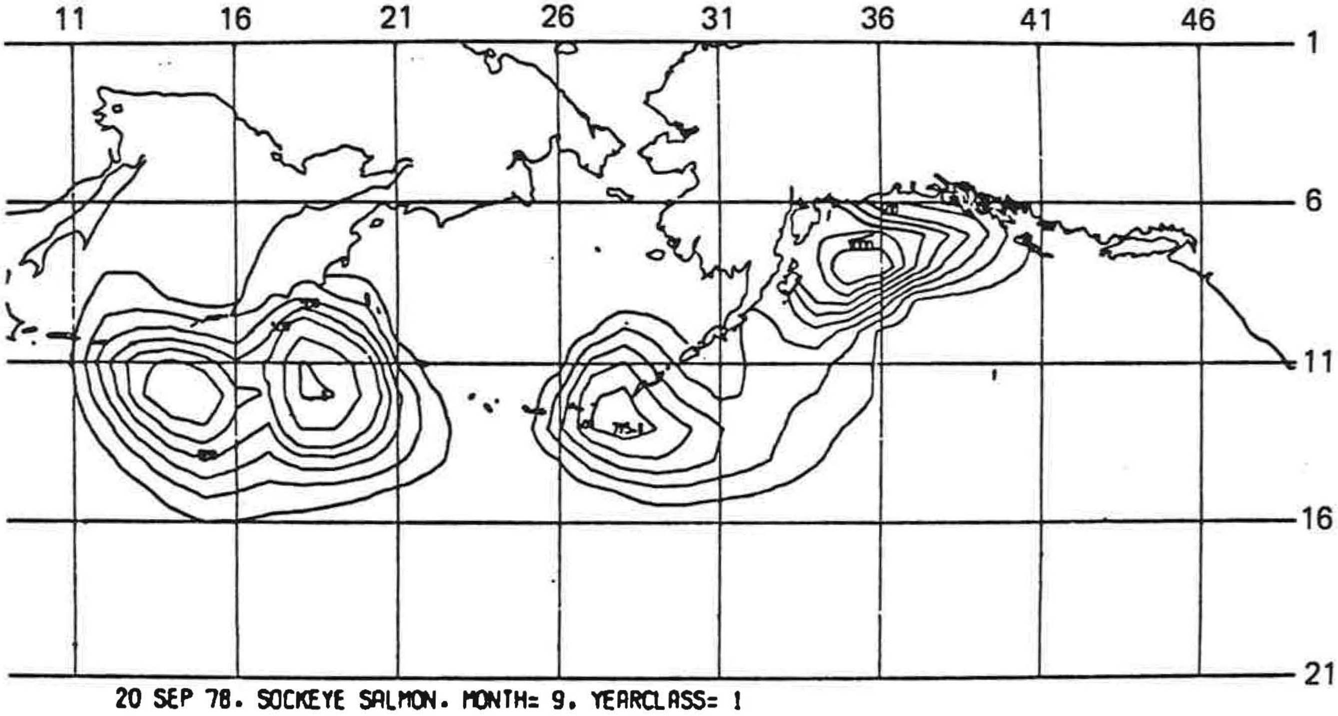
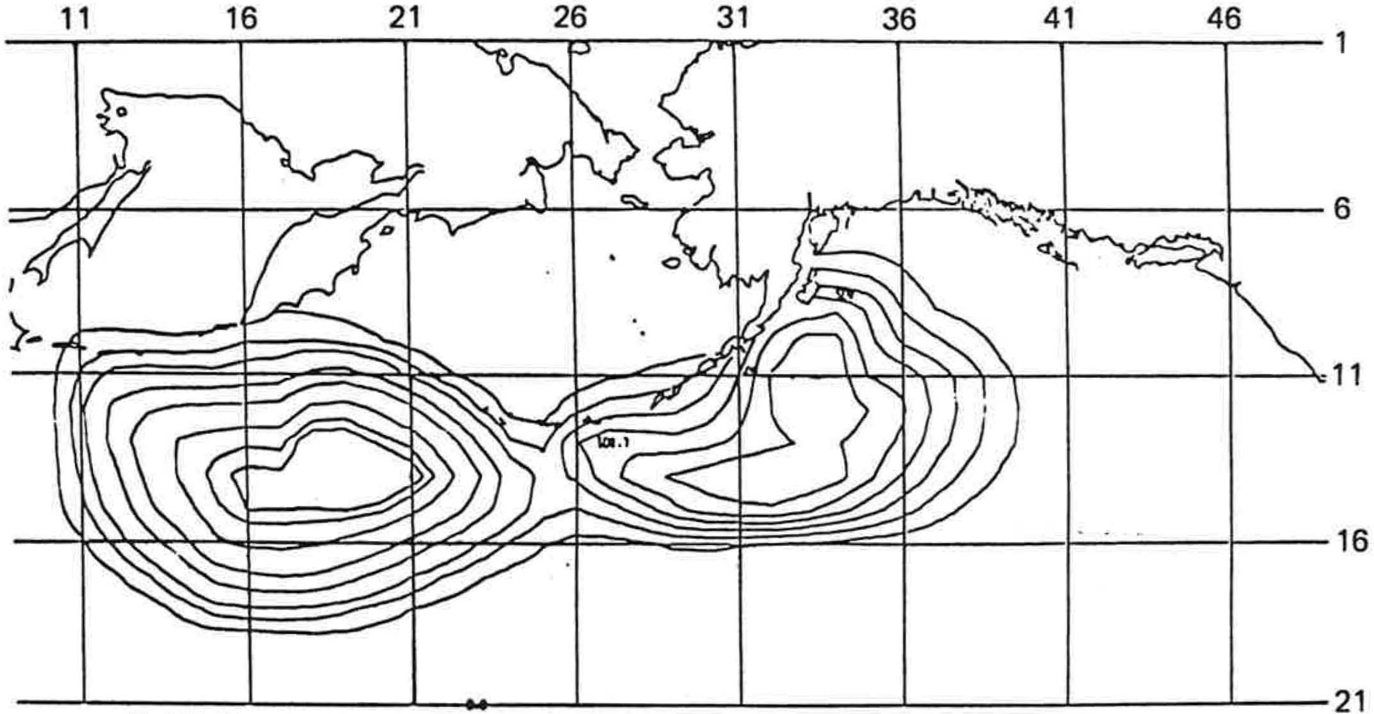
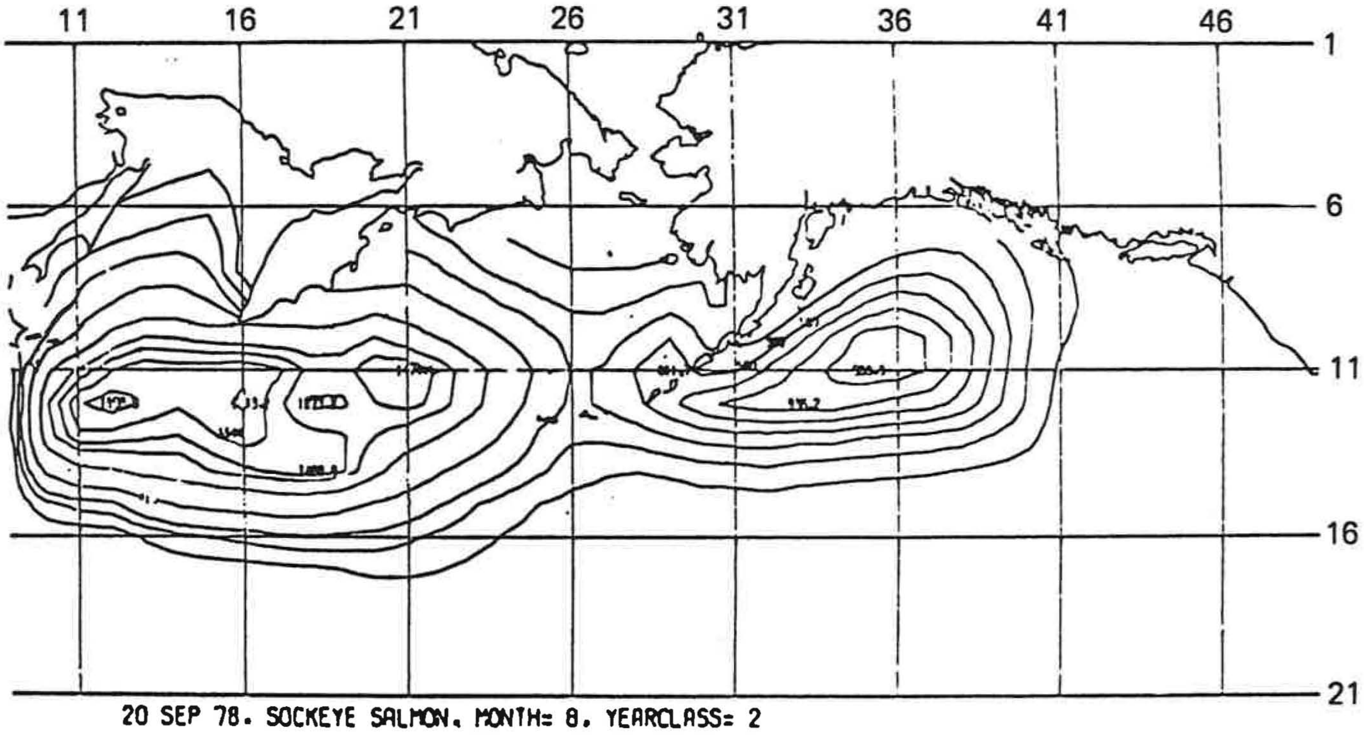


Figure 6.--Computed distribution of sockeye in September-October, first year in the ocean. (The lines on the map are grid coordinates, see Figure 2.)



20 SEP 78. SOCKEYE SALMON. MONTH=12. YEARCLASS: 1

Figure 7.--Computed distribution of sockeye in December-January, first year in the ocean. (The lines on the map are grid coordinates, see Figure 2.)



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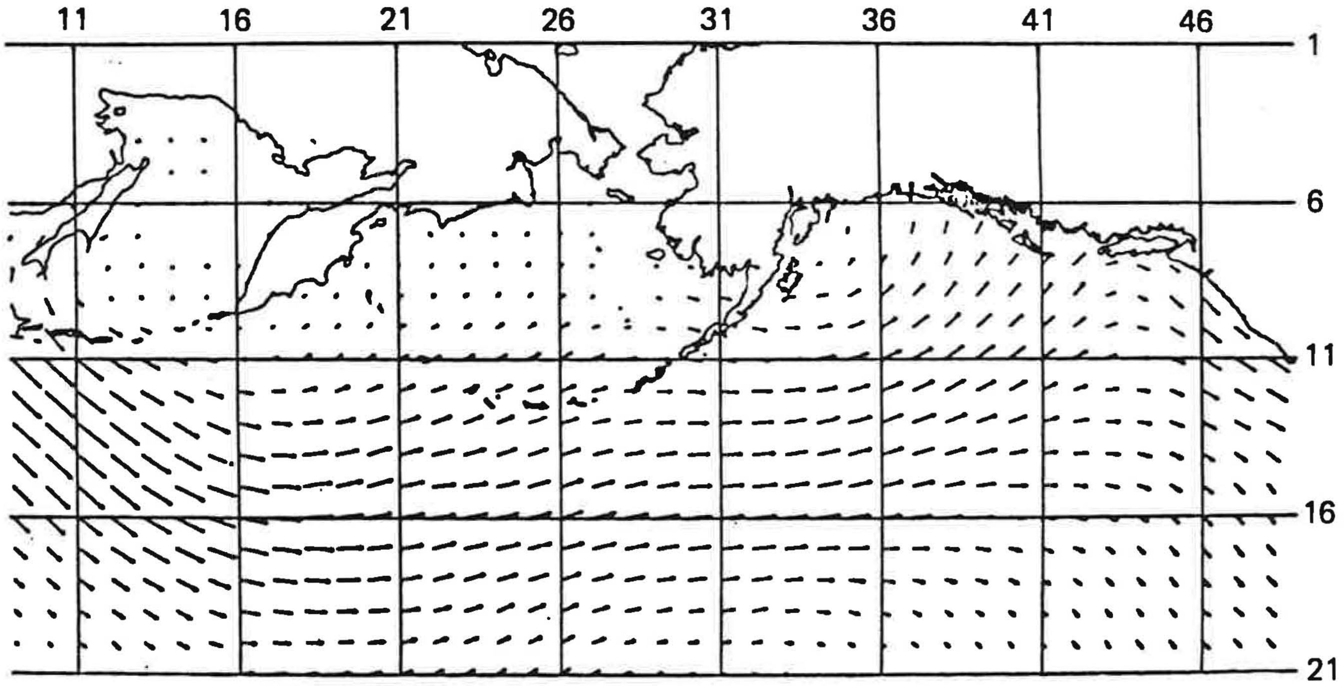

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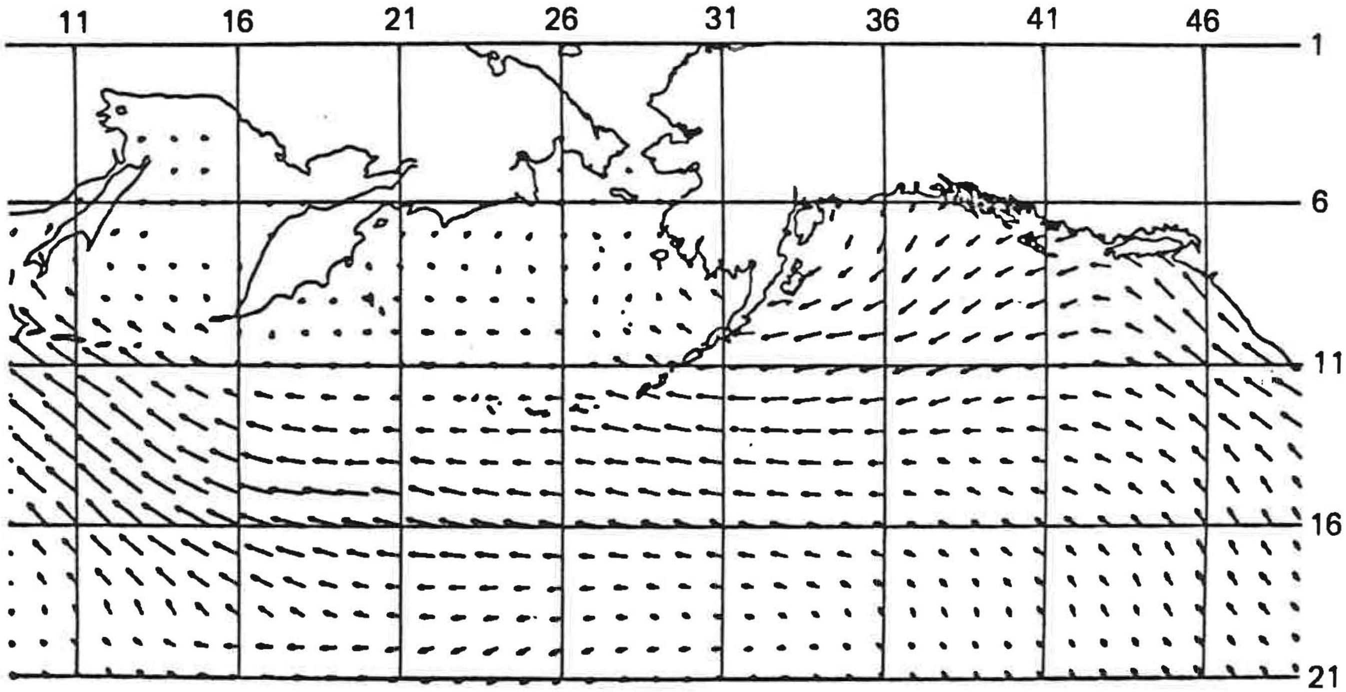

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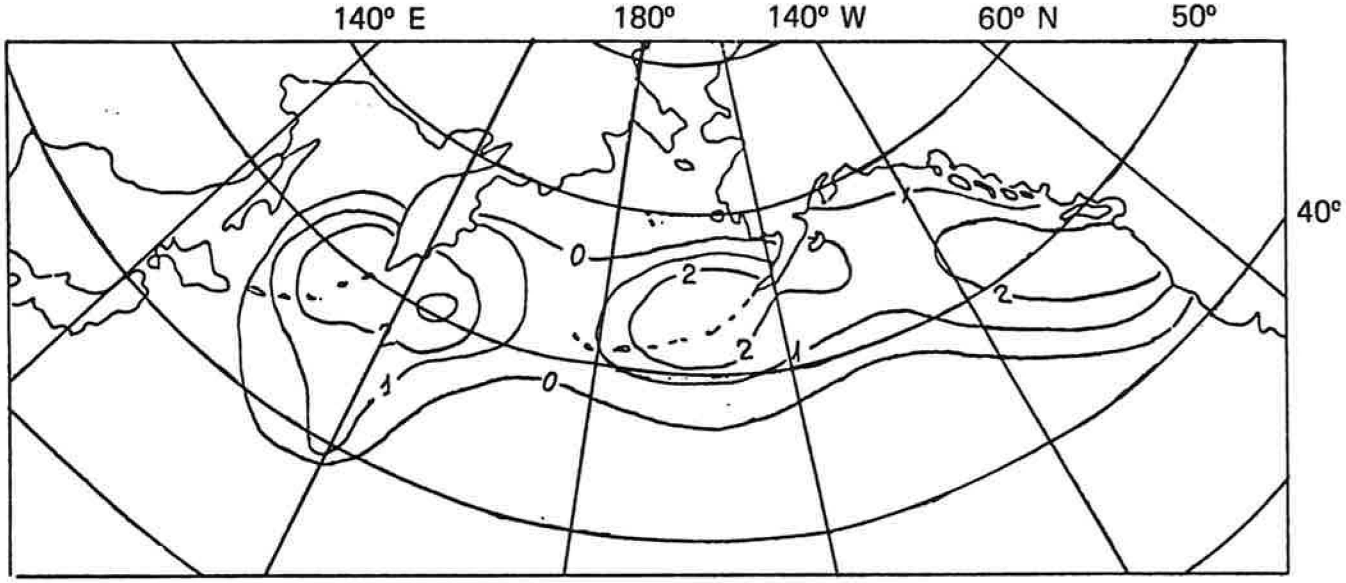

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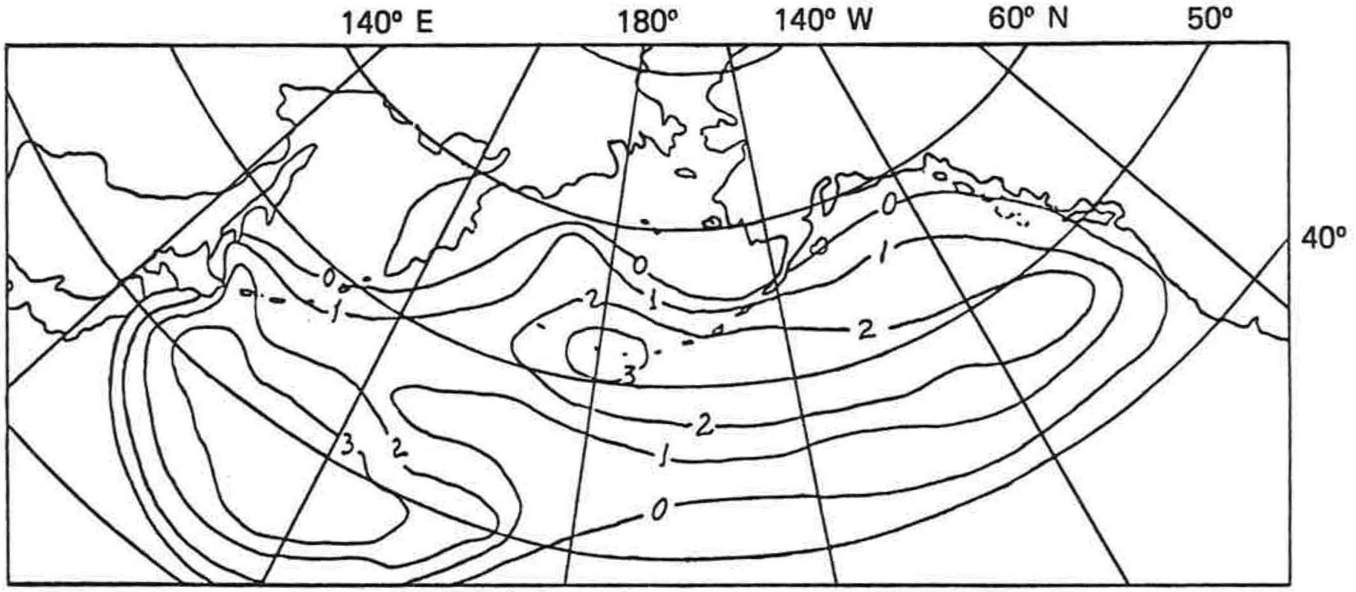

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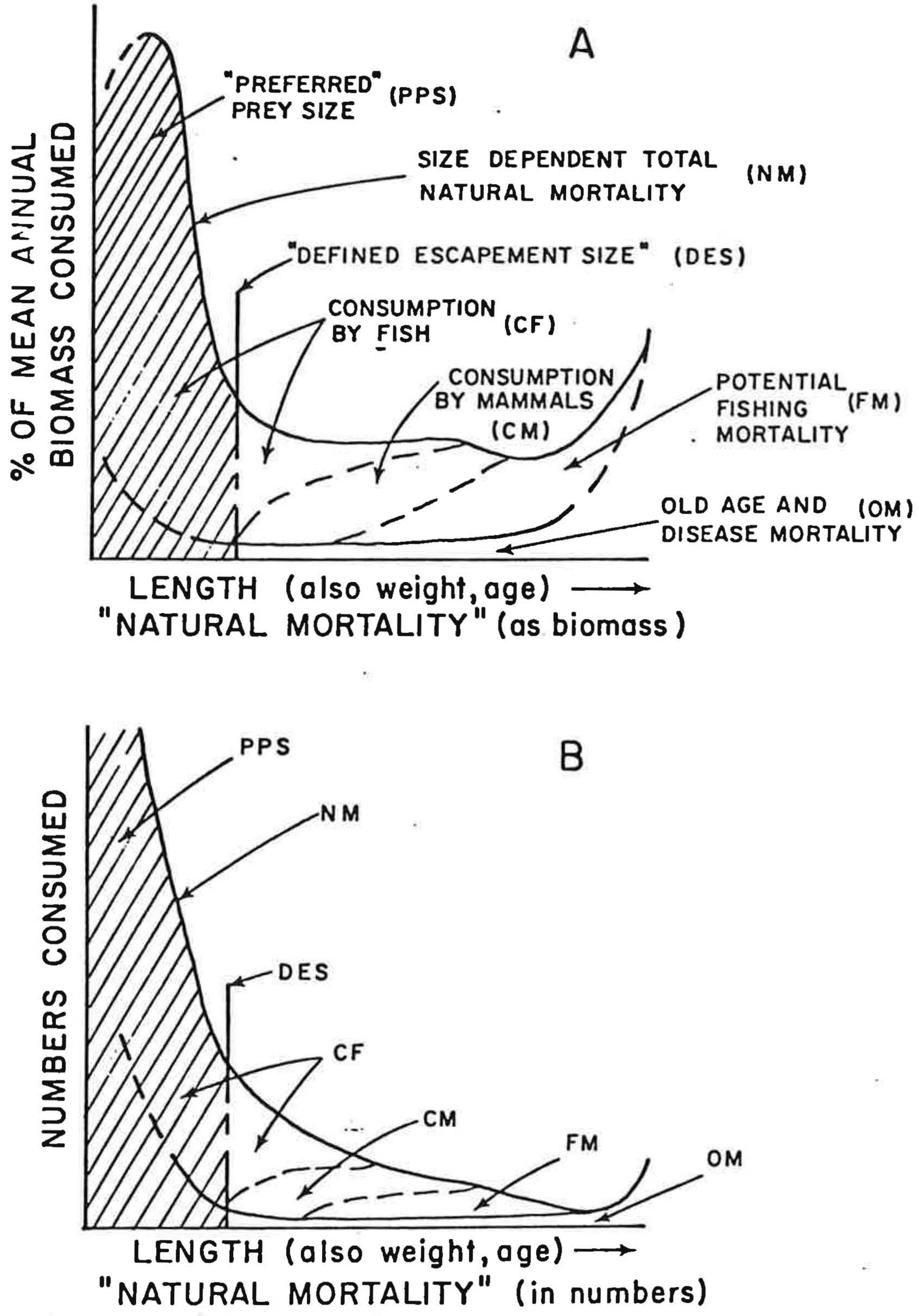

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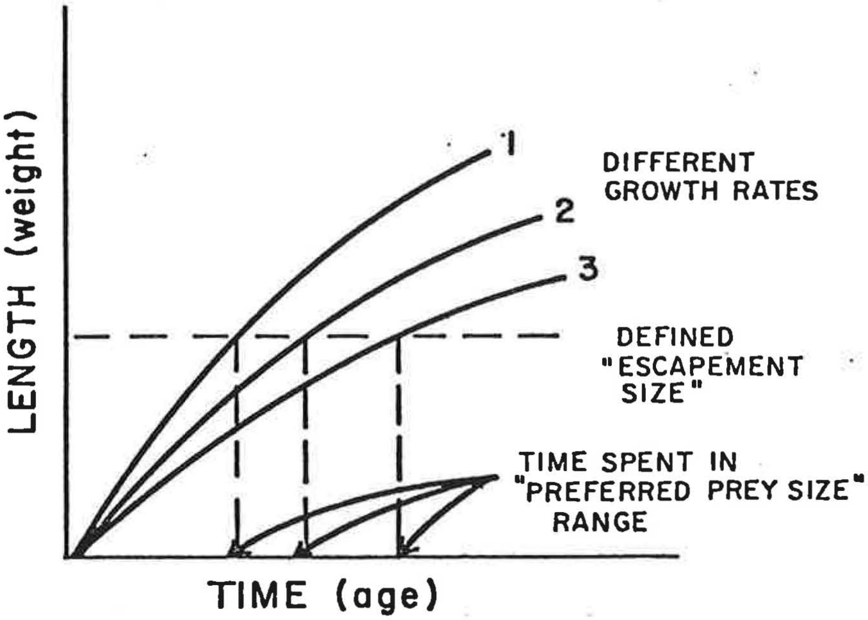

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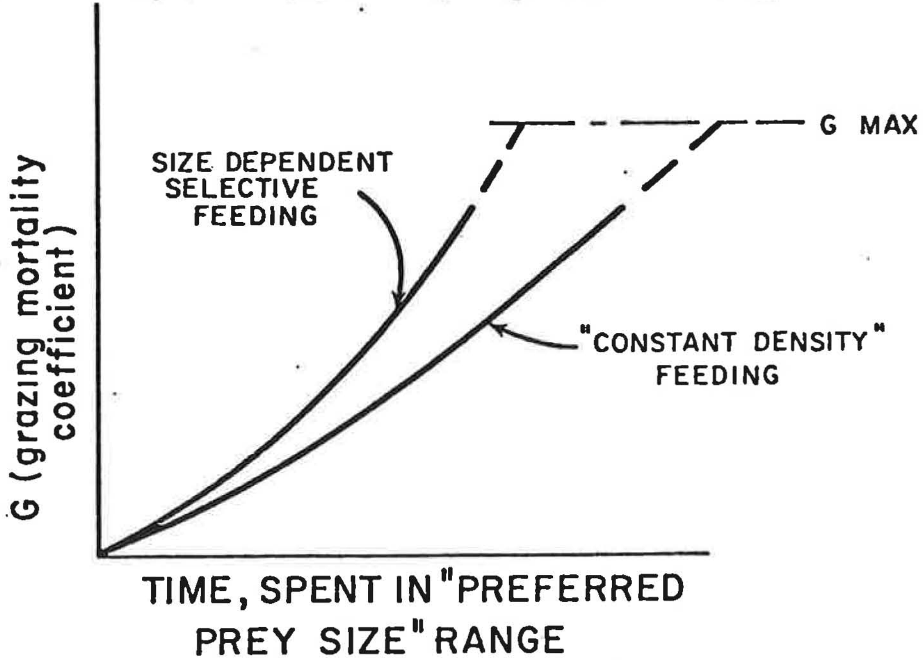
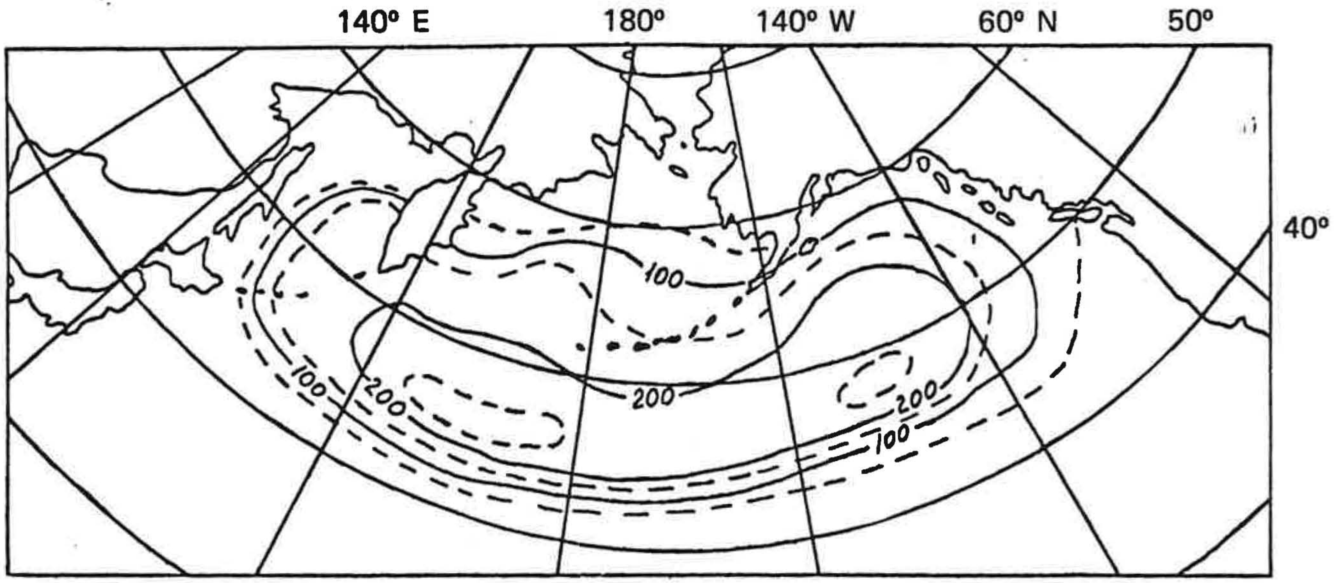


Figure 15.--Effects of time spent in "preferred prey size" on predation (natural) mortality.



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