

AN ABSTRACT OF THE THESIS OF

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Title: FACTORS INFLUENCING THE LIFE HISTORY OF SPRING

CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA)

SPAWNING IN THE COLUMBIA RIVER WATERSHED

FROM 1960 to 1977

Abstract approved: \_\_\_\_\_

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U John D. McIntyre /

A statistical analysis of factors influencing the survival rate of both upper Columbia River and Lemhi River spring chinook salmon was performed using correlation and multiple regression techniques. The results of the statistical analyses suggested that ocean upwelling and Columbia River flow regimes during outmigration influence the survival rates of the studied fish. The interpretation of the statistically significant relationship between the return per spawner for upriver spring chinook salmon and the Canadian troll fishing effort was unclear.

A theoretical model characterizing a Columbia River spring chinook salmon population was developed to: (1) suggest the types of data to be collected in future studies; and, (2) suggest the nature of functional relationships influencing selected life history events. The

major components of the theoretical model were designated according to the age of fish in the fall of each year. The driving variables included environmental factors, food availability, natural mortality and fishing mortality. The functional relationships describing life history events in the model were partially based upon the results of the statistical analyses and published literature.

An outline for a management model was developed within the framework of the theoretical biological model to illustrate a potentially useful application of the modelling effort. The management model also suggested specific areas for future research. The results of the modelling effort indicated that the following types of data need to be collected to enhance the current understanding of upriver spring chinook salmon: (1) in-depth stream studies, (2) the growth rates at age for ocean fish, (3) the ocean locations of upriver spring chinook salmon, (4) the juvenile mortality rate during outmigration, (5) in-depth estuarine studies; and, (6) the food habits of ocean fish.

Factors Influencing the Life History of Spring  
Chinook Salmon (Oncorhynchus tshawytscha)  
Spawning in the Columbia River Watershed  
From 1960 to 1977

by

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FACTORS INFLUENCING THE LIFE HISTORY OF SPRING  
CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA)  
SPAWNING IN THE COLUMBIA RIVER  
WATERSHED FROM 1960 TO 1977

INTRODUCTION

The Columbia River (Fig. 1) is a major spawning area for Pacific salmon (Oncorhynchus sp.). In the past twenty years, activities influenced or controlled by man, such as logging, irrigation, and dam construction, have reduced the availability of spawning habitat and altered the physical characteristics of the watershed (Fulton, 1968). Prior to 1957, three major dams had been constructed on the Columbia and Snake rivers. Since 1957, this number has increased to 18 with eight of these dams encountered by salmon spawning in Snake River tributaries. To compensate for the loss in spawning habitat related to increased dam construction in the past 20 years, hatcheries have been constructed. Extensive changes in the physical characteristics of the river also have resulted from dam construction. For example, the Columbia and Snake rivers, at one time free-flowing systems, are now predominantly flow-regulated. Junge and Oakley (1966) attributed decreased turbidity in the Columbia River at Bonneville Dam from 1953 to 1964 to newly constructed dams. Gas supersaturated water, first described (cf. Ebel et al.,

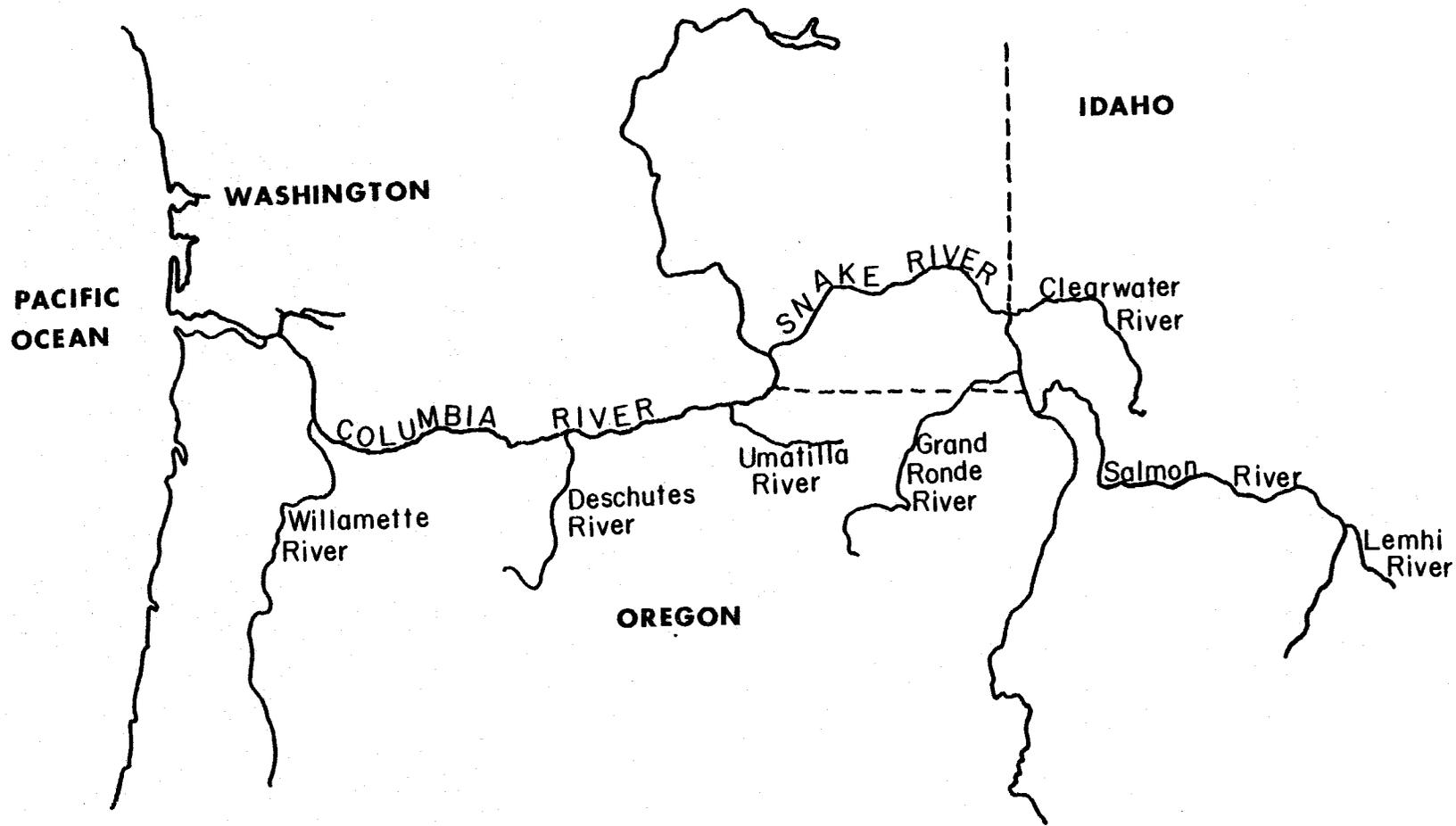


Figure 1. A map of the Columbia River watershed (from Galbreath, 1966).

1975) for the Columbia River system in the 1960's, has resulted from the "spill" of water over dams.

Environmental changes resulting from dam construction have affected all species of Pacific salmon spawning above Bonneville Dam, known as upriver runs (Fulton, 1968). One of the most severely impacted runs is the race of chinook salmon (Oncorhynchus tshawytscha) that enters the river in the spring enroute to hatcheries and natural spawning areas. Although these fish do not spawn until fall, they commonly are called "spring chinook salmon." They migrate to upriver areas and spend the summer in cool, deep pools. Spawning in either the hatchery or in the wild occurs in the early fall. On the spawning grounds, mature females excavate gravel depressions, known as redds, for egg deposition in the stream bed. Mature males may fertilize eggs in several redds. Soon after the eggs are fertilized, all spawners die. Wild fish (i. e. offspring from parents spawning in the wild) reside in tributary streams until their second spring. Downstream migration of these age 1+ juveniles peaks in April and May (Mains and Smith, 1964; Bjornn, 1978). Age 1+ juveniles produced in hatcheries also are released in the spring. Raymond (1968, 1969) estimated the mean rate of downstream migration in the Columbia River for yearling chinook salmon to be 11 km/day. Based on this downstream migration rate, the peak in abundance of yearling upriver spring chinook salmon in the Pacific Ocean occurs during June and July.

The distribution of Columbia River spring chinook salmon in the ocean is inadequately described (French et al., 1975; Manzer et al., 1965); however, tag recoveries that have been made indicate that migration is northward toward the coast of Alaska. Spring chinook salmon remain in the ocean one to four years and return to freshwater as three-, four-, five-, and six-year-old fish. Mature three-year-old fish, primarily precocious males, are known as jack salmon. The abundance of six-year-old spring chinook salmon spawning in the Columbia River watershed is very low ( $\ll 5\%$ ). The age structure of returning adults varies annually. Within a single year, the age composition of fish examined in the gill net fishery (Table 1) differs markedly from that of Snake River spring chinook salmon (Table 2).

The general relationship between the numbers of parent spawners and progeny has been graphically described for numerous species of fish (cf. Ricker, 1975; Beverton and Holt, 1957; Cushing, 1973). These types of relationships, known as general reproduction curves, describe the average offspring abundance given the number of parent spawners. For example, the Ricker-type reproduction curve, descriptive of salmonid populations, indicates that maximum progeny abundance will most often occur with an intermediate number of parent spawners. The Ricker reproduction curve accounts for the influence

Table 1. The percentage age composition of the upriver spring chinook salmon as determined from the landings in the Columbia River gill net fishery. The age compositions are adjusted for bias in the sampling method.

Run Year	Age Composition (%)		
	3-year-olds	4-year-olds	5-year-olds
1960	7	75	18
1961	16	41	43
1962	9	78	13
1963	12	46	42
1964	10	61	29
1965	9	68	23
1966	9	70	21
1967	9	62	29
1968	10	63	27
1969	7	59	34
1970	7	59	34
1971	10	62	28
1972	7	68	25
1973	7	52	41
1974	7	51	41
1975	8	57	35
1976	8	62	30
1977	13	75	12

Table 2. The percentage age composition of the spawning escapement of spring chinook salmon spawning in the Lemhi River, Idaho.

Run Year	Age Composition (%)		
	3-year-olds	4-year-olds	5-year-olds
1965	0	51	49
1966	4	65	31
1967	4	49	47
1968	2	38	60
1969	5	68	27
1970	2	56	43
1971	4	77	19
1972	3	44	53
1973	2	32	67
1974	4	57	39
1975	3	22	75
1976	3	49	48

of density dependent factors (i. e. events resulting in a mortality rate dependent upon parent population density) on the progeny survival. Deviations from the expected Ricker reproduction curve are attributed to density independent factors (i. e. events resulting in a mortality rate independent of parent population density).

Previous studies have illustrated the importance of environmental (i. e. density independent) factors in influencing the abundance of anadromous fish populations. Lantz (1971) reviewed the important effects of water temperature on salmonid survival, growth, and behavior in the freshwater environment. The positive relationship between stream flow during brood year outmigration and the number of coho salmon (Oncorhynchus kisutch) returning to spawn in Washington streams (Smoker, 1953) currently forms the basis for the management of this species by the Washington Department of Fisheries. Silliman (1950) suggested that stream flow was twice as important as winter temperature in affecting fluctuations in the abundance of chinook salmon returning to the Columbia River.

The types of freshwater environmental factors affecting salmon survival in the Columbia River may be partially controlled by man. For example, changes in temperature, flow, and turbidity, resulting from increased dam construction, may influence salmonid survival. Junge and Carnegie (1976) noted a strong positive correlation ( $r = .97$ ,

$P < .001$ ) between river flow and percentage loss of adult spring chinook between Bonneville and Ice Harbor dams. Junge and Oakley (1966) suggested that the decrease in turbidity associated with increased dam construction may result in increased predation on juvenile salmon. Raymond (1968, 1969) suggested that Columbia River dams slowed the migration rate of downstream migrants.

Density independent events, such as ocean environmental factors, not directly influenced by man, also may influence the survival of Pacific salmon. Vernon (1958) calculated a positive relationship between summer salinity in Georgia Strait and pink (O. gorbuscha) and chum (O. keta) salmon abundances. In addition, Vernon also showed a negative correlation between summer water temperatures in Georgia Strait and the abundance of adult pink salmon returning to the Fraser River the following year. Van Hyning (1973) also calculated a negative correlation between ocean water temperatures and the survival of Columbia River fall chinook salmon.

In northeast Pacific coastal waters, annual fluctuations in the strength of the upwelling event may contribute to fluctuations in biological populations. The upwelling event, prevalent in the summer months, is characterized (Smith, 1968) by the transport of cold, high salinity waters below the pycnocline to the surface along the coastal boundary. Indirect effects of this event may include an increase in

the nutrient level. Although the upwelling event is not directly measured, indices have been theoretically derived (Bakun, 1973) from atmospheric pressure data. Upwelling indices were positively correlated with both zooplankton abundance (Peterson and Miller, 1975) and dungeness crab (Cancer magister) survival (Peterson, 1973).

Gunsolus (1978) described a positive relationship between the upwelling index and a production index for coho salmon. In addition, the negative correlations between ocean water temperatures and salmonid survival (Van Hyning, 1973; Vernon, 1958) may actually reflect effects related to the upwelling event.

Ocean fishing pressures, which can be either density independent or density dependent events, also influence the abundance of Pacific salmon. Van Hyning (1973) attributed the decline of Columbia River fall chinook salmon from 1938 to 1959 to ocean fishing mortality. Although a selected group of fish may not contribute heavily to a fishery, the fishing pressure may be strong enough to contribute to fluctuations in abundance of the fish group. Based upon the very limited returns from a small number of tagging studies with Columbia River spring chinook salmon, Wright (1976) concluded that these fish do not contribute heavily to the catch (5% of each total) in the Washington and Oregon troll fisheries. No studies have been performed to determine the contribution of these fish to the Canadian or Alaskan troll fisheries.

Fisheries agencies in the Pacific Northwest currently recognize the necessity of understanding the relative importance of environmental factors and fishing pressures in limiting or controlling the distribution and abundance of economically important species, such as Pacific salmon. The availability of carefully controlled experimental data provide little insight into these problems because of the complex interplay of biological and physical factors among and within years. Therefore, the specific and relative importance of such variables is not understood. Many data with some potential for increasing our understanding of salmon population dynamics have been systematically accumulated. The types of environmental data available include freshwater temperature, flow, discharge, turbidity, and gas supersaturation, and ocean upwelling indices. In this study, flow refers to the velocity of water passing through a power turbine and discharge is the velocity of water flowing out of the Columbia River into the Pacific Ocean. Many of these data are available for periods in excess of 15 years.

The understanding of the potential influence of these types of factors on salmon is inadequate for all species in the Columbia River drainage and is particularly acute for spring chinook salmon. Since the mid-1950's, the number of upriver spring chinook salmon returning to the Columbia River has fluctuated greatly (Fig. 2). Record low

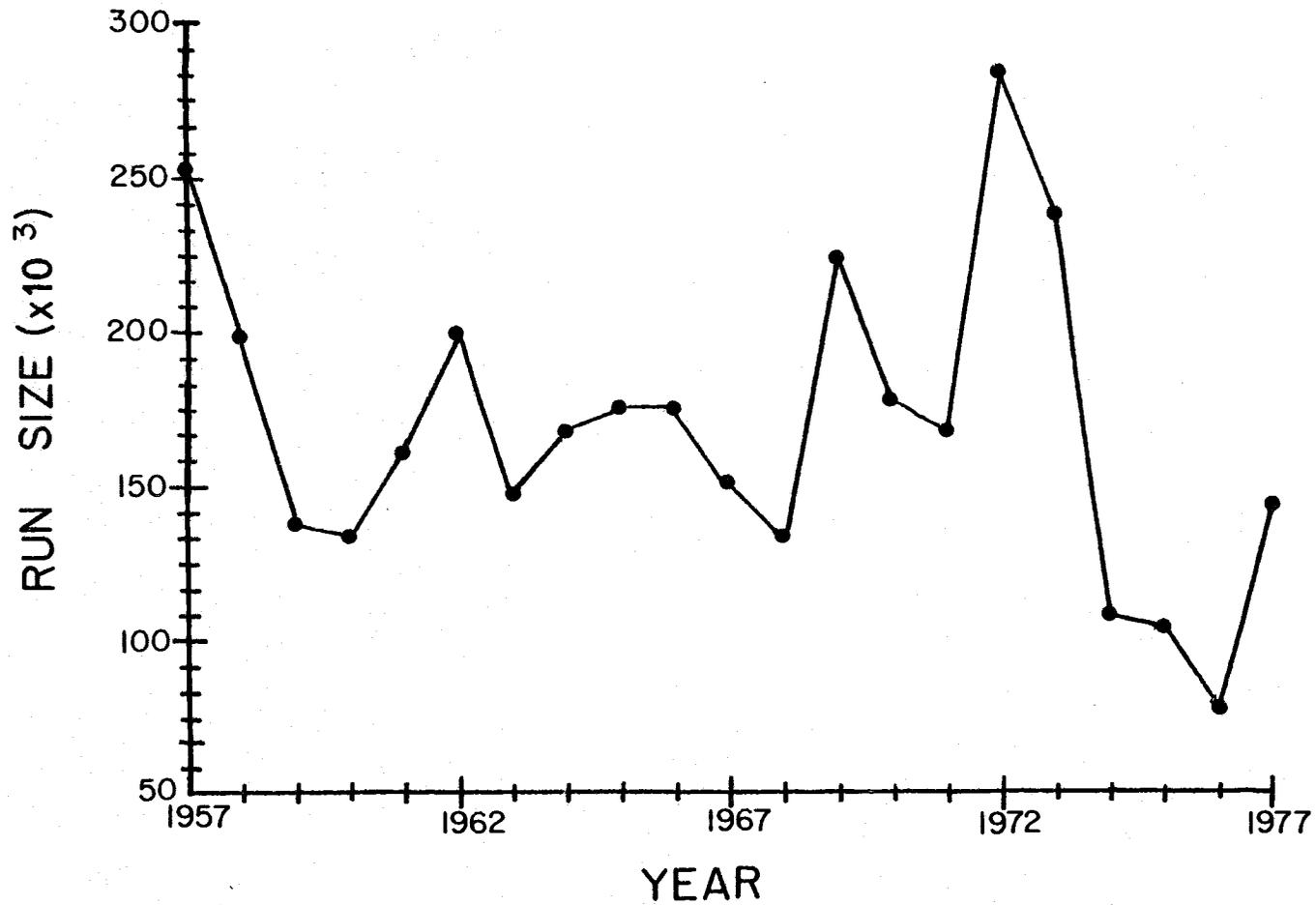


Figure 2. Fluctuations in the run size of upriver spring chinook salmon returning to the Columbia River from 1957 to 1977.

numbers of returning fish have been noted since 1973. In addition, the catch of spring chinook salmon in the Columbia River gill net fishery has declined over the past 20 years (Fig. 3). In view of the recent trends in spring chinook salmon abundance, this study was initiated to isolate factors influencing the fluctuations in the abundance of upriver spring chinook salmon since 1957. Specifically, the objectives of this study were: 1) to determine the relationships, using a simple correlation analysis approach, between selected density independent factors and designated abundance indices for Columbia River spring chinook salmon spawning above Bonneville Dam, 2) to assess the relative contribution, using a multiple regression analysis approach, of these selected factors acting in concert in controlling the fluctuations in abundance of upriver spring chinook salmon, and 3) to develop a conceptual model to suggest the types of functional relationships influencing the life history of upriver spring chinook salmon.

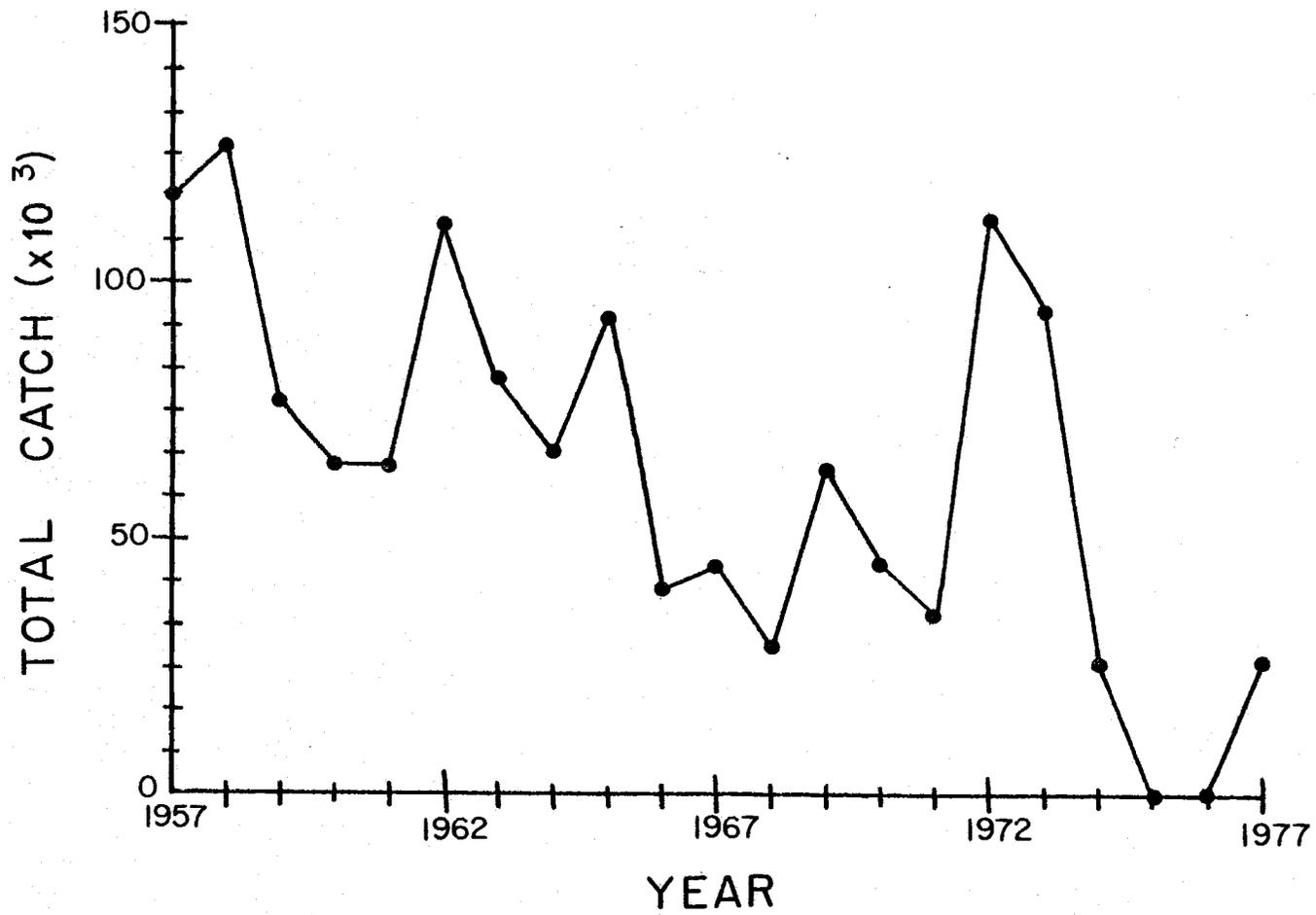


Figure 3. Fluctuations in the numbers of spring chinook salmon landed in the Columbia River gill net fishery from 1957 to 1977.

## MATERIALS AND METHODS

### Correlation Analysis

An index of spring chinook salmon survival rate was developed from Ricker's (1975) general reproduction curve for salmonids as a variable in the correlation analysis. The shape of this type of reproduction curve is determined from the linear regression between  $\ln(R/S)$  and  $S$ , where  $R$  is a measure of progeny abundance,  $S$  is a measure of parent spawner abundance, and  $\ln$  is the natural logarithm. Deviation from the linear relationship between this survival rate,  $\ln(R/S)$ , and the number of parent spawners,  $S$ , is attributed to density independent factors.

The spawning escapement of spring chinook salmon above Bonneville Dam from 1957 to 1972 (Oregon Department of Fish and Wildlife (ODFW) and Washington Department of Fisheries (WDF), 1977) provided a measure of parent spawner abundance. This escapement had been adjusted for mortality associated with the commercial gill net fishery above Bonneville Dam. A measure of progeny abundance was derived from the total return, or run size, of upriver spring chinook salmon to the mouth of the Columbia River from 1960 to 1977. ODFW and WDF (1977) provided an estimate of this run size by adjusting the count of spring chinook salmon over

Bonneville Dam for the loss of upriver fish to both commercial and sport fishery mortality below the dam.

Based on age-composition data (Table 1) obtained from the capture of upriver spring chinook salmon in the Columbia River gill net harvest, the returning numbers of upriver spring chinook salmon for each of three age classes were calculated. For the two years when the gill net season was closed (1975, 1976), ODFW (W. L. Robinson, pers. comm.) provided age composition data based on test fishing surveys. Since all age composition data were obtained from fishing data, adjustments were made to correct for the size-related bias due to net selectivity. Based upon test studies (ODFW, W. L. Robinson, pers. comm.), the observed percentages of three-year-old fish were increased by five percent and the observed percentages of five-year-old fish were decreased by five percent. No adjustment was made on the observed percentage of four-year-old fish (Table 1). From the age composition data, the total number of fish returning for each age group was calculated. The total number of upriver spring chinook salmon returning from each brood year (1957-1972) was calculated by summing the number of three-, four-, and five-year-old returns from three consecutive years. The spawning escapement and brood year returns were plotted and a Ricker reproduction curve was fitted (Ricker, 1975) to these data.

The spring chinook salmon spawning in the Snake River drainage comprise on the average 31 percent of the entire upriver run (Table 3). The annual variability in the relative contribution of Snake River fish to the upriver spring chinook salmon run suggested that conditions in the Snake River drainage may significantly influence the abundance of these fish. Although all Snake River fish were included in the upriver fish, additional data (Bjornn, 1978) existed for spring chinook salmon spawning in the Lemhi River (Fig. 1). Spawning escapement was recorded at a weir at the mouth of the Lemhi River from 1962 to 1971 (Bjornn, 1978). Age composition data of returning fish was determined from scale samples and length data taken at the weir. The return of fish from 1965 to 1976 from each brood year (1962-1971) was calculated using the method previously described for the upriver fish. Total returns from brood years beyond 1971 could not be determined.

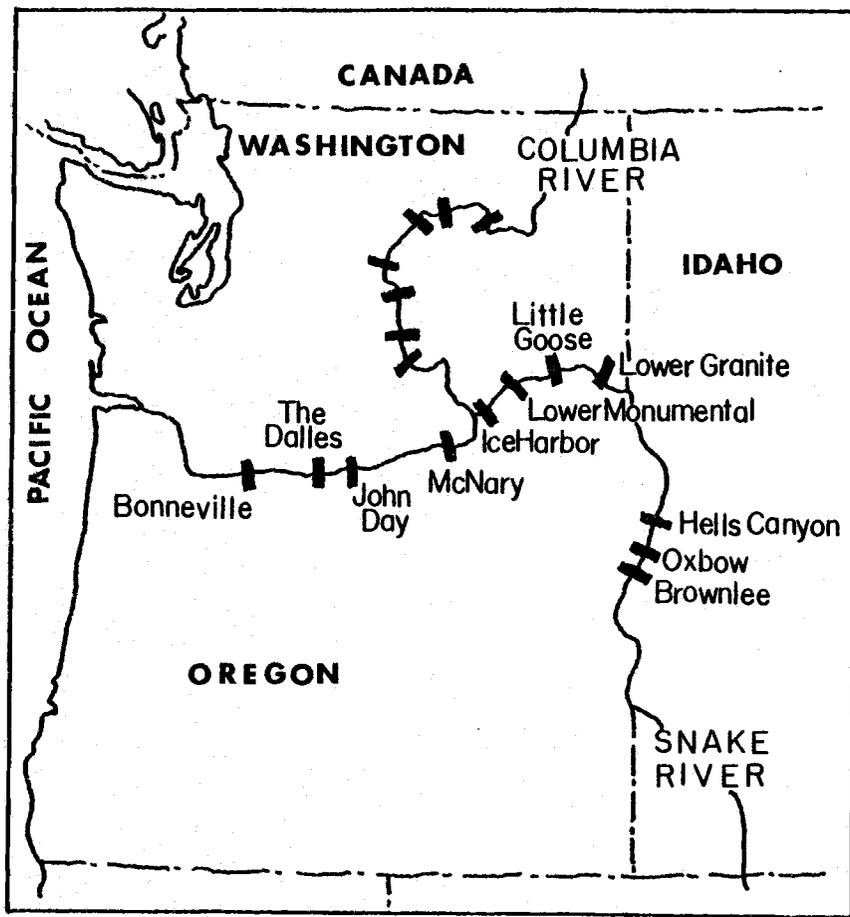
A Ricker reproduction curve was determined from the linear relationship between the return per spawner rate,  $\ln(R/S)$ , and spawning escapement,  $S$ . The deviation from this linear regression was assumed to be attributed to density independent factors. To assess the importance of selected factors on this relationship, an extensive correlation analysis was conducted. Correlation coefficients were calculated between selected density independent factors and the calculated indices

Table 3. The number of spring chinook salmon counted at both Ice Harbor Dam and the Lemhi River weir expressed as a percentage of the total upriver spring chinook salmon count at Bonneville Dam from 1962 to 1976.

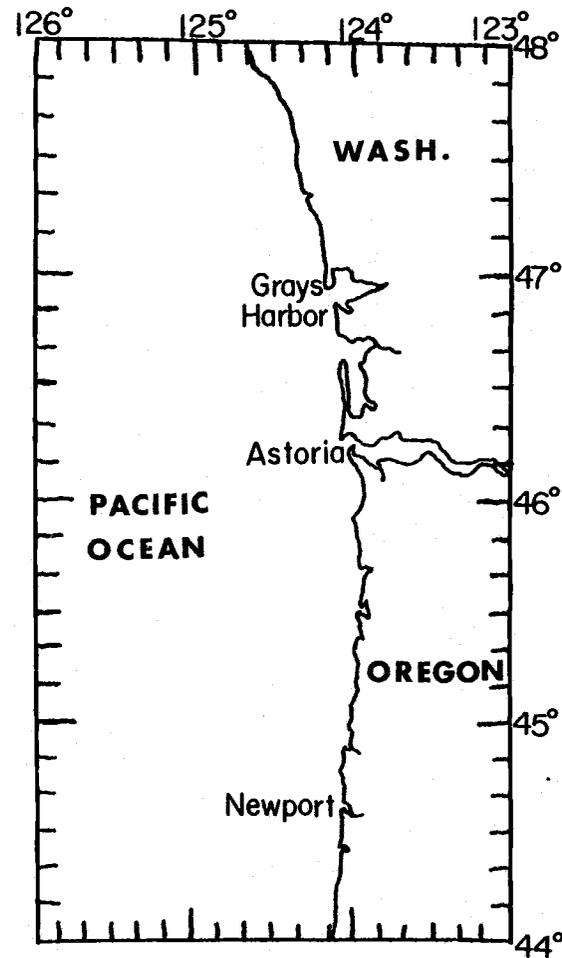
Year	$\frac{\text{Ice Harbor Dam Count}}{\text{Bonneville Dam Count}} \times 100$	$\frac{\text{Lemhi River weir count}}{\text{Bonneville Dam count}} \times 100$
1962	36.9	--
1963	35.5	--
1964	26.6	1.2
1965	14.4	.91
1966	38.9	1.3
1967	41.9	2.2
1968	45.1	2.0
1969	30.0	.43
1970	43.2	1.1
1971	26.0	.66
1972	27.3	.64
1973	42.7	.73
1974	14.4	.32
1975	20.6	.86
1976	22.1	.56

of spring chinook abundance for each set of data. The statistical significance of these correlations was determined with a test described by Snedecor and Cochran (1967; Table A-11).

The environmental data used in the correlation analyses were obtained primarily from federal and state agencies. The types of data included in the analyses were restricted by their availability and the length of the time series. Consideration was primarily given to those factors which conceivably influenced the run-strength of spring chinook salmon. Daily freshwater environmental data recorded from 1959 to 1974 at Bonneville Dam (Fig. 4) were used in analyses with the upriver return per spawner index; the same data recorded from 1966 to 1973 at Ice Harbor Dam (Fig. 4) were used with the Lemhi River data. The data from each of these sites were considered representative of environmental conditions prevalent in the Columbia and Snake rivers, respectively. Freshwater temperature, flow, and turbidity were obtained from records maintained at each freshwater site (U.S. Army Corps of Engineers, 1959-1974). Gas supersaturation data, available from 1967 to 1974 at Bonneville Dam, were obtained from the Water Quality Division of the U.S. Army Corps of Engineers. Since supersaturation data recorded at Ice Harbor Dam was only available from 1970, this variable was not considered in the Lemhi River correlation analysis. Columbia River discharge, recorded at Astoria, Oregon, was obtained as



A



B

Figure 4. Locations of the data collection sites: A) location of dams along the Columbia and Snake rivers (from Collins *et al.*, 1975); and, B) location of ocean data collection sites.

monthly mean data from the U. S. Geological Survey from 1959 to 1974. Monthly mean upwelling indices from 1959 to 1974 were provided by the National Marine Fisheries Service (Pacific Environmental Group, Monterey, California). These indices were calculated (Bakun, 1973) from geostrophic wind data at  $45^{\circ}\text{N } 125^{\circ}\text{W}$  and  $48^{\circ}\text{N } 125^{\circ}\text{W}$  (Fig. 4). For the Lemhi River correlation analysis only data from 1966 to 1973 were considered.

Hypotheses were developed to propose functional relationships linking the return per spawner indices with each density independent variable included in the statistical analyses. For example, given the assumption that differential mortality rates were experienced by fish passing through turbines rather than over dams, the relative magnitude of the flow measured at dam sites during brood year outmigration should be related to the survival rate of the brood year. A positive relationship was also proposed between turbidity and survival. That is, high turbidity during outmigration of the brood year could lead to reduced predation on the juvenile salmon with an overall increase in survival. The proposed relationship between the return per spawner ratio and temperature during outmigration was indirectly associated with nitrogen supersaturation. That is, temperature could indirectly influence survival by controlling the absolute level of supersaturated water prevalent at dam sites. The direct negative effect of nitrogen supersaturation on juvenile survival was based on an increased mortality attributed to gas bubble "disease" during years of high nitrogen supersaturation.

Although direct measures of ocean conditions during the year of outmigration were unavailable, hypothetical relationships were proposed between brood year survival and indirect measures of environmental events. A direct relationship was proposed between the magnitude of the Columbia River discharge measured at Astoria, Oregon, and the prevalence of the Columbia River plume. Since outmigrating juvenile salmon are required to make significant physiological adjustments prior to their ocean life, the Columbia River plume may act as a refuge during the first months at sea. Based on these assumptions, a relationship was anticipated between the brood year survival and the strength of the Columbia River discharge recorded during the year of brood year outmigration. Given the assumption that productivity is related to the magnitude of the upwelling index, a functional relationship was proposed between brood year survival and the strength of the upwelling index when the outmigrants first entered the ocean as post smolt fish. It was hypothesized that upwelling could indirectly impact survival by influencing the ocean post smolt growth rate during the first months at sea.

Simple correlation coefficients were calculated between all environmental data and both the Columbia and Lemhi River return per spawner indices. To study the effects of environmental conditions during the months of juvenile outmigration on subsequent brood year

returns, the return per spawner index for the brood produced in one year was correlated with the environmental data accumulated two years later. Since peak outmigration of spring chinook salmon occurs over the months of April and May (Mains and Smith, 1964; Bjornn, 1978), the daily freshwater environmental parameters considered in the correlation analyses were averaged over these months. Correlation indices were also calculated between each summer monthly mean Columbia River discharge value recorded from June through October and the return per spawner index. Average monthly upwelling indices at each site for each selected month (March through September) were correlated with each return per spawner index. In addition, average upwelling indices for all sets of consecutive months were correlated with the survival rate. Cross correlations also were calculated between all variables. Independent variables significantly correlated with the return per spawner index were incorporated in the multiple regression analysis.

Insufficient data exist to determine the contribution of upriver spring chinook salmon to the coastal troll fisheries. If these fish contribute to the troll fisheries, they must be caught no later than the year prior to spawning escapement since the peak upstream migration past Bonneville Dam coincides with the opening of the troll season. In addition, spring chinook jack salmon, returning

as three-year-old fish, escape the fishery because of size limitations. Spring chinook salmon returning as five-year-old fish presumably are available to the fishery for two consecutive years as three- and four-year-old fish; adults returning as four-year-old fish contribute to the fishery as three-year-old chinook salmon. Therefore, the offspring returning from a single brood year are subjected to zero, one, or two years of ocean fishing pressure.

To determine if the coastal chinook salmon troll fisheries contributed to fluctuations in upriver spring chinook salmon abundance, the total numbers of adult (i. e. four- and five-year-old) fish crossing Bonneville Dam in one year were correlated with annual landings in the Oregon, Washington, British Columbian, and S. E. Alaskan troll fisheries the previous year. The adult counts over Bonneville Dam represented actual counts of four- and five-year-old fish based on the size differences between jack salmon and adult fish (U. S. Army Corps Engineers, unpublished data). Total numbers of fish landed from 1960 to 1974 in each American chinook salmon troll fishery were provided by ODFW (P. Reed, pers. comm.). Annual poundages of salmon landed and annual effort recorded as boat days in the Canadian chinook salmon troll fishery were obtained from 1963 to 1977 (Environment Canada, 1977). The annual percent capture of the spring and fall races of chinook salmon and the age composition of

the landed fish were not available for any of the troll fisheries.

Based upon the results of the initial correlations, the effects of the Canadian troll fishery on one age class were isolated. A return per spawner index was generated using the return of four-year-old fish from the 1960-1972 brood years to Bonneville Dam as the index of progeny abundance. This return per spawner index was correlated, using the previously described methods, with selected variables. Spawning escapement was obtained for the 1960-1972 brood years. Freshwater environmental variables, measured from 1962 to 1974, included April-May mean temperature, flow, and turbidity recorded at Bonneville Dam. Columbia River discharge for the same years was measured for the months of June through October. Of the selected upwelling indices, only the mean June-July upwelling index for 48°N 125°W was considered in this analysis. Canadian effort measured in thousands of days and annual landings in thousands of pounds were obtained (Environment Canada, 1977) from 1963 to 1975. All data used in the statistical analyses are presented in Appendix I.

### Regression Analyses

All data used in the regression procedure were analyzed using the forward stepwise multiple regression analysis (Neter and Wasserman, 1974) available with the Statistical Interactive Programming System

(SIPS) on the Oregon State University Cyber computer. Basic to the use of this procedure is an assumption that there is a "best" model linking the dependent variable to a selected number of independent variables and that a linear relationship exists between the dependent variable and any independent variable.

The dependent variables used in this analysis were the calculated return per spawner indices for Columbia and Lemhi River spring chinook salmon and the four-year-old return per spawner index for the upriver fish. Independent variables were partially determined from the correlation study. Those factors correlated ( $\alpha \leq .05$ ) with the return per spawner index were considered for inclusion in the regression analysis.

The variable added at each "step" in the regression analysis was that variable associated with the greatest reduction in the total variability of the dependent variable adjusted for the independent variable(s) in the model. Since the main objective of this part of the study was to assess the impact of density independent factors acting in concert on the fluctuations in spring chinook salmon abundance, the parent spawners, S, were always introduced as the first variable in the analysis. The "best" model was chosen based on the significance of the F-statistic, the t-statistic, and the value of the coefficient of variation,  $R^2$ . Since the F-statistic provided a test of the model as a whole whereas

the t-statistic tested each independent variable, the former was most useful in determining the "best" model. When the addition of a new variable resulted in very little improvement in  $R^2$ , it was concluded that this variable did not contribute significantly to the model. Due to the relatively small numbers of data points (16 years for the upriver data; eight years for the Lemhi River data), a maximum of three independent variables were included in any regression model.

The residuals from the "best" model with the four-year-old survival rate as the dependent variable were plotted against time to determine if a non-random relationship existed among the error terms over time.

## RESULTS

The age composition for returning spring chinook salmon is more variable for the Lemhi River fish than for the total escapement above Bonneville Dam (Tables 1 and 2). From these data, it is possible to assess the relative success of a single brood year by determining the total number of returning three-, four-, and five-year-old fish for three consecutive years. The relative success of a single brood year, commonly called the year-class strength, is a measure of the mean number of returning fish from each brood year.

The year-class strength for the Lemhi River spring chinook salmon (Fig. 5) is more variable than the year-class strength for the upriver fish (Fig. 6). For the upriver fish, the 1957 brood year was characterized by a weak year class. The poorest returns for the upriver fish were produced by the 1970 to 1972 brood years. The relative contribution of returning three-, four-, and five-year-old fish produced by the weak brood years of 1957, 1971, and 1972 was below average (Fig. 7). Both the 1958 and the 1968 broods produced strong year classes (Fig. 6). These strong year classes were also characterized by above average returns from each of the three age groups (Fig. 7). The brood year returns for the Lemhi River spring chinook salmon have declined since the 1963 brood year (Fig. 5). The 1963

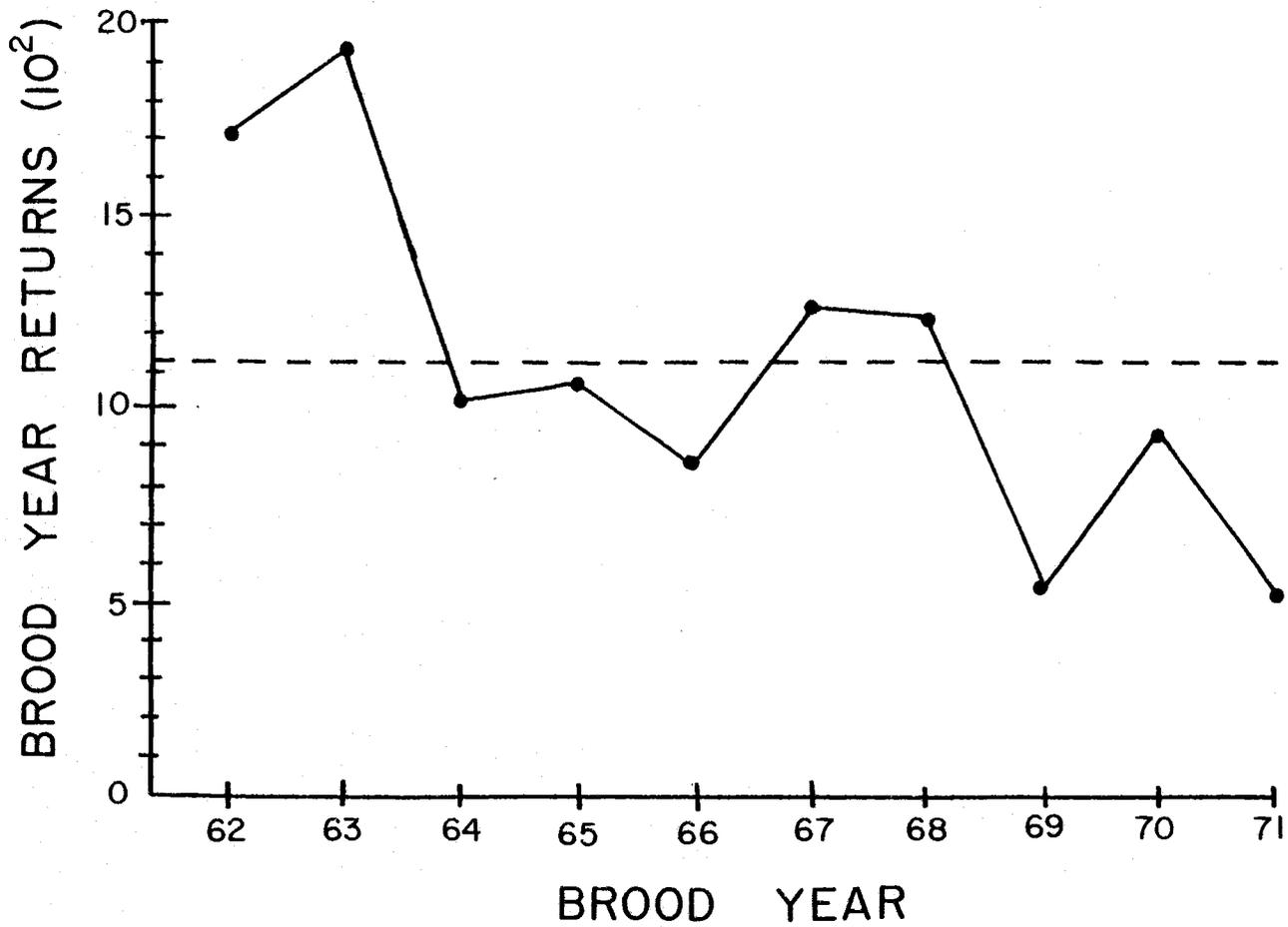


Figure 5. Total numbers of spawning progeny produced by parents spawning in the Lemhi River from 1962 to 1971. The dashed line represents the mean progeny returns of 1,112 fish for the designated time period.

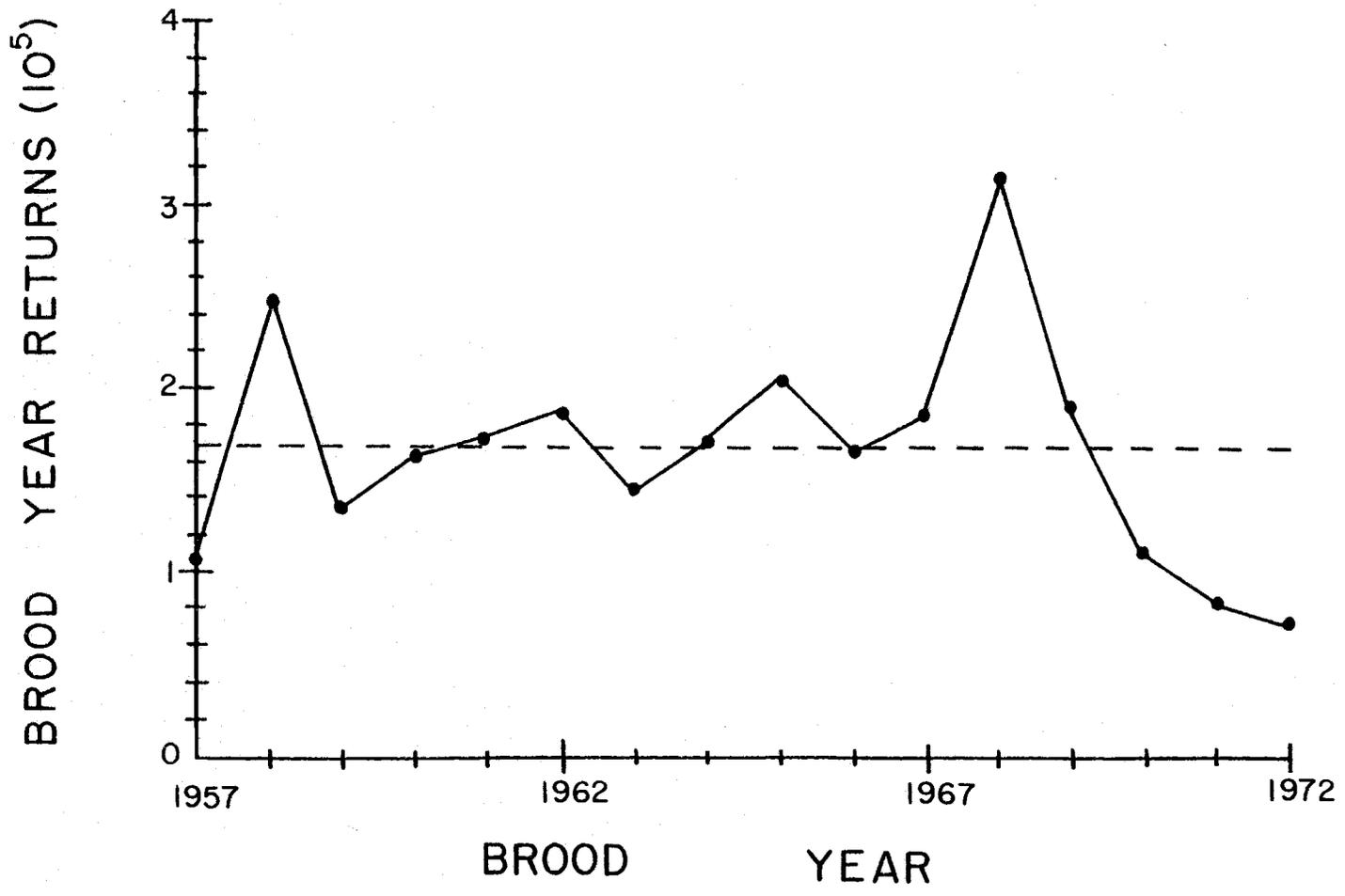


Figure 6. Total numbers of spawning progeny produced by parents spawning above Bonneville Dam from 1957 to 1972. The dashed line represents the mean progeny returns of 166,000 fish for the designated time period.

Figure 7. The number of spawning progeny of each of three age classes produced by parents spawning above Bonneville Dam from 1957 to 1972. The dashed lines represent mean progeny abundances of 15,261 three (••), 102,138 four (••••), and 47,985 five (•••••) year old fish.

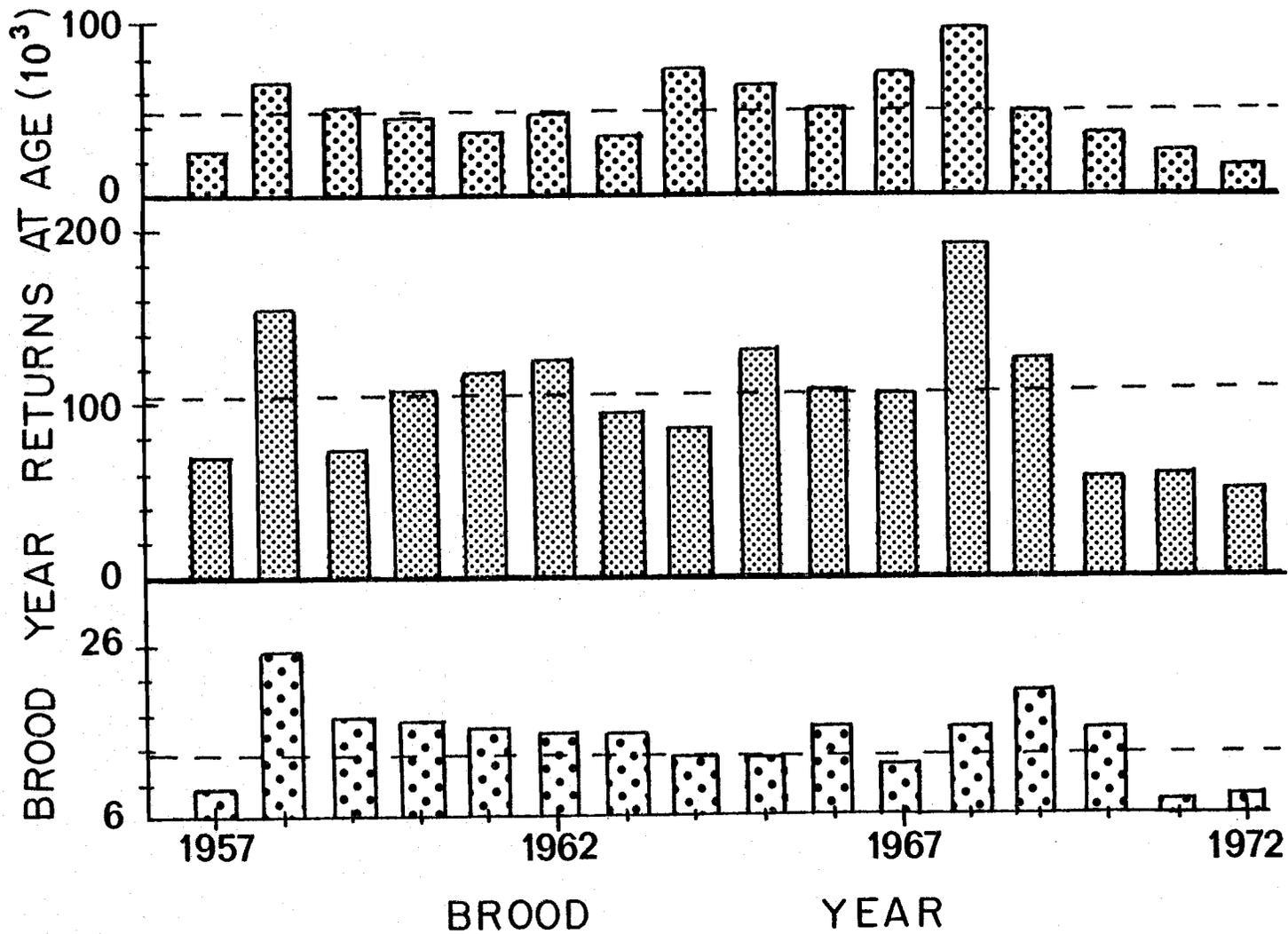


Figure 7.

brood year produced a large number of returning spawners. The number of returning three-, four-, and five-year-old fish produced by the strong 1963 brood year were above average (Fig. 8). The return of fish produced by the 1962, 1967, and 1968 brood years was also above average (Fig. 5). However, the 1969 and 1971 brood years produced very weak year classes. Only returns from the 1971 brood year were below average for all three age groups (Fig. 8).

Since all offspring from any one brood year share a common environment for the first 1 1/2 years, environmental conditions during this part of their life history may strongly influence the relative strength of the returning age classes. A consistently strong or weak year class contribution by both the Lemhi River and the upriver spring chinook salmon may reflect the effects of common environmental factors during outmigration. In addition, if the relative contributions from each of the three returning age classes for a single brood year are consistently strong or weak, the returning fish may be responding to similar environmental factors during the first 1 1/2 years.

Environmental conditions during the outmigration of strong and weak brood years for the upriver fish were analyzed to determine if specific trends could be isolated from these data. The 1957 year class contributed low numbers to the three-, four-, and five-year-old brood year returns (Fig. 7). The relative contribution of each age group

Figure 8. The number of spawning progeny of each of three age classes produced by parents spawning in the Lemhi River from 1962 to 1971. The dashed lines represent mean progeny abundances of 32 three (•••), 536 four (••••), and 518 five (•••••) year old fish.

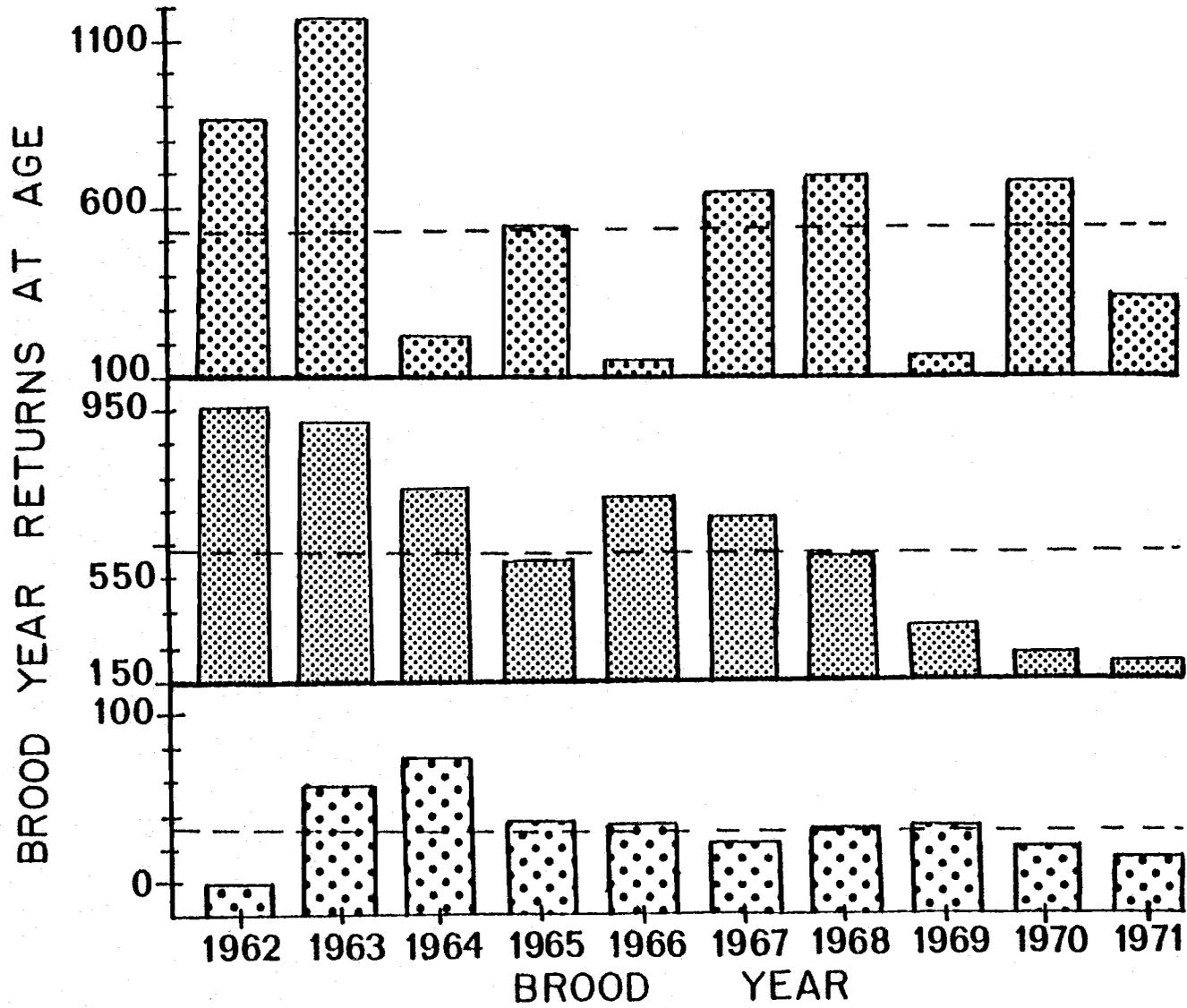


Figure 8.

produced by the 1971 and 1972 brood years was also low. During 1959, when the 1957 brood year migrated to sea, the Bonneville April-May turbidity and temperature and the June-July upwelling index were below average (Figs. 9-11). The Bonneville April-May flow and the August Columbia River discharge were above average (Figs. 12 and 13).

Similar environmental conditions were present in 1974 when the 1972 brood year migrated downstream (Figs. 9-13). In 1973, however, when the 1971 brood year migrated downstream, freshwater environmental conditions were unlike those present in 1959 (Figs. 9-13). For each of the three weak brood years, only June-July upwelling during the year of brood outmigration was consistently below average (Fig. 11). The 1958 brood year fish yielded above average returns from 1961 to 1963 and the contribution of the 1968 brood year to the upriver return of fish from 1971-1973 also was high. During the years of outmigration of both the 1958 and the 1968 brood years (1960 and 1970), the Bonneville Dam turbidities were above average and Bonneville Dam temperatures were below average (Figs. 9 and 10). No consistent trends were prevalent in the Columbia River discharge (Fig. 13), the upwelling index (Fig. 11) or the flow measured at Bonneville Dam (Fig. 12) during the outmigration of these broods. The qualitative analysis of the environmental conditions prevalent during the outmigration of upriver spring chinook salmon brood years suggested only that weak upwelling indices

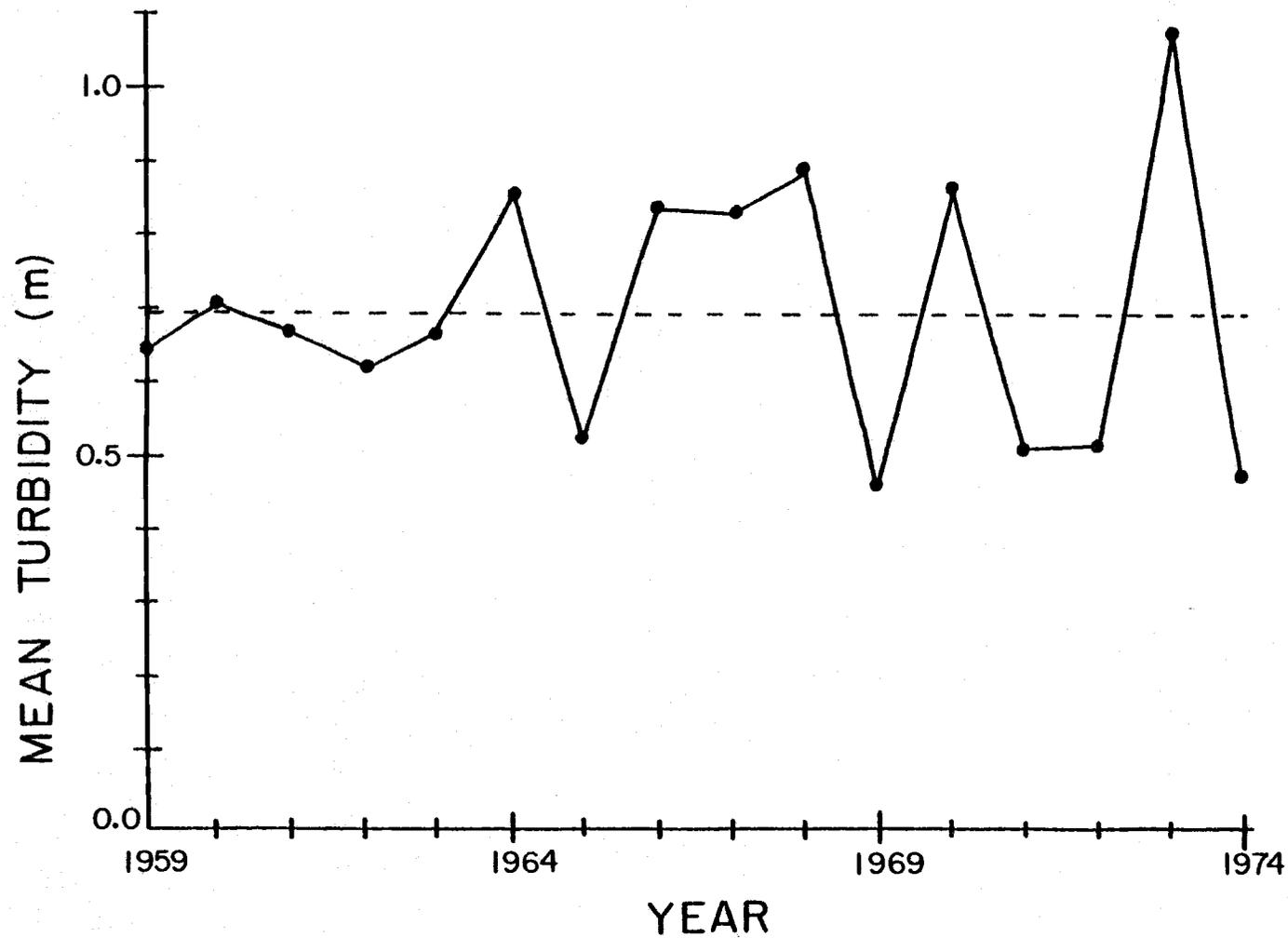


Figure 9. Mean April-May turbidity measurements recorded at Bonneville Dam from 1959 to 1974. The dashed line represents the 16-year mean of 0.69 m.

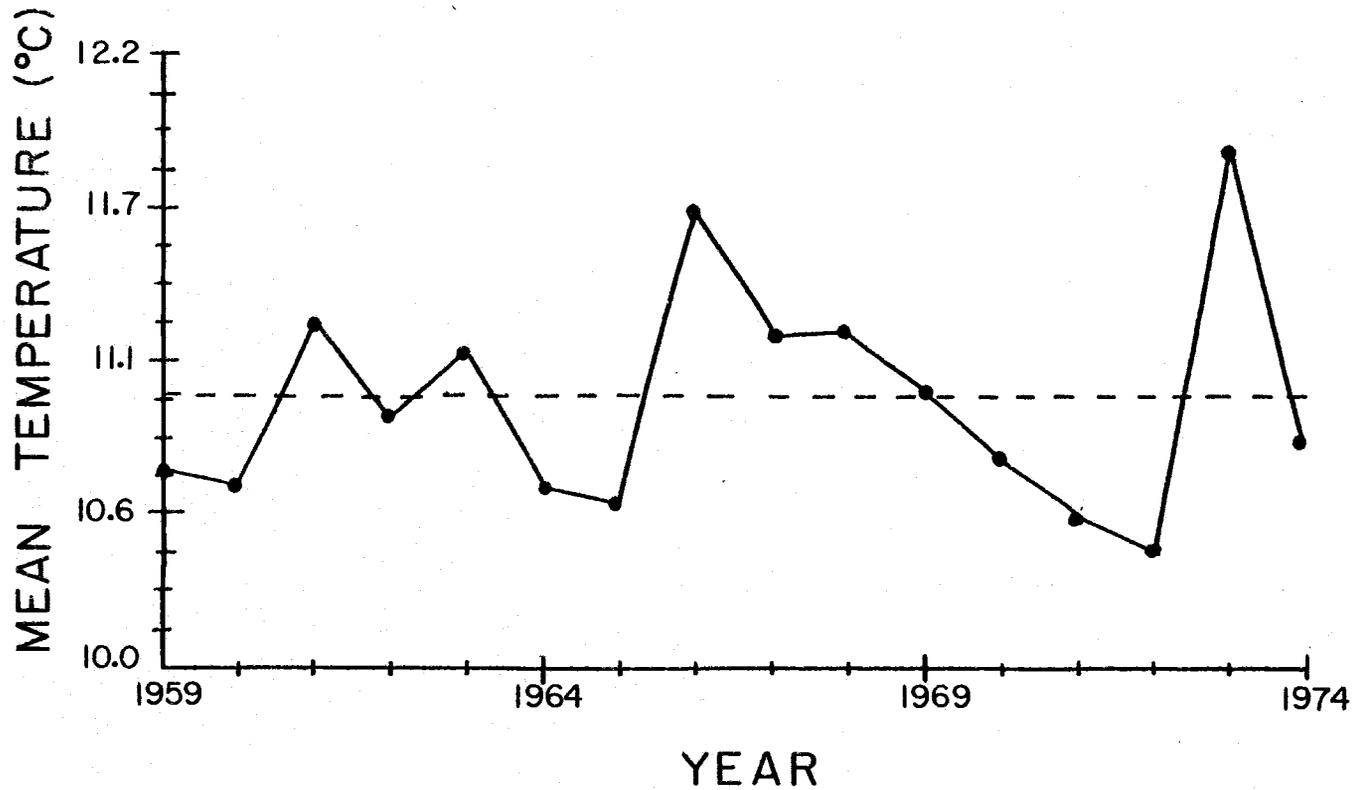


Figure 10. The mean April-May temperature recorded at Bonneville Dam from 1959 to 1974. The dashed line represents the 16-year mean of 11° C.

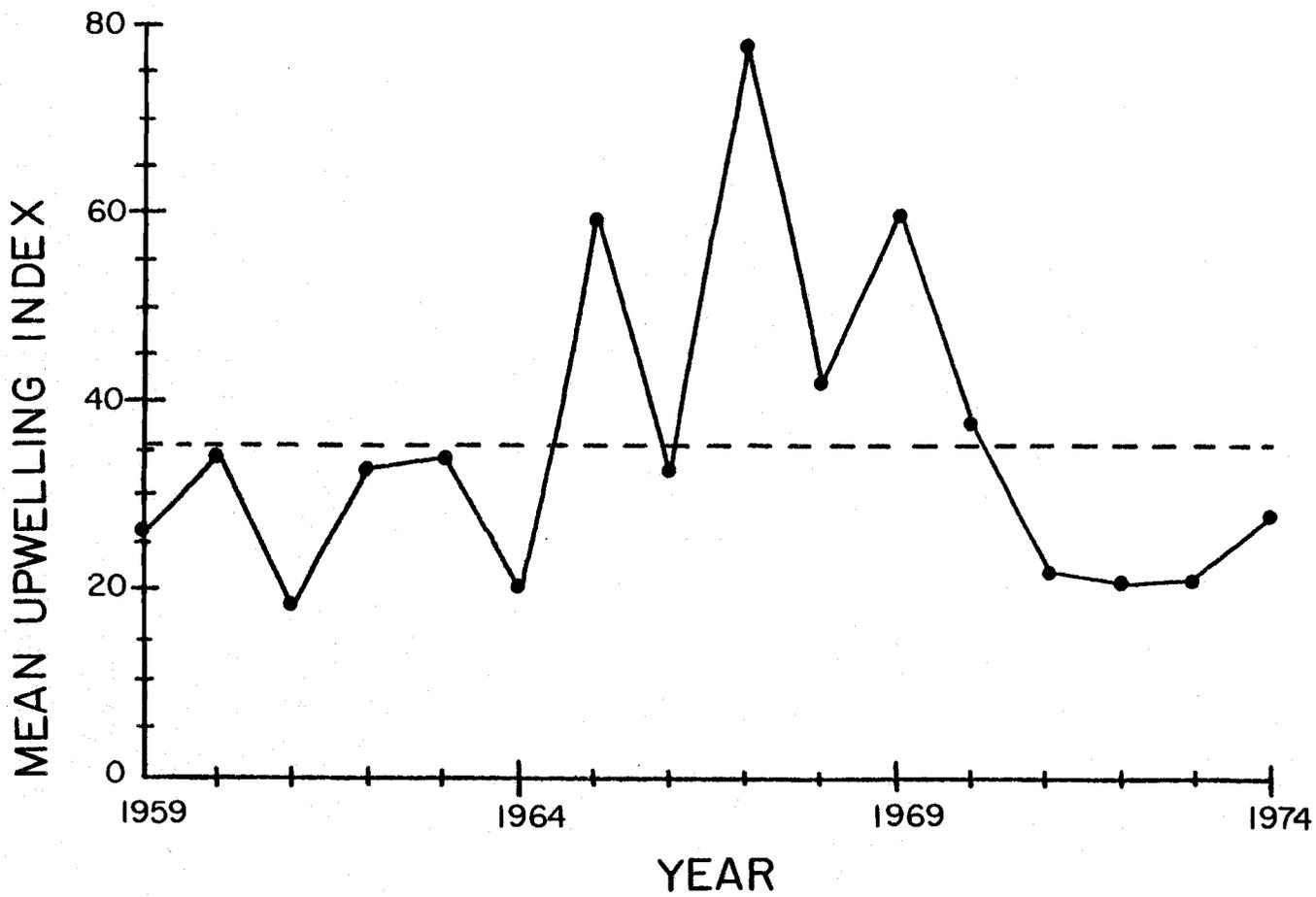


Figure 11. The mean June-July upwelling index calculated from atmospheric pressure data for  $48^{\circ}\text{N}$   $125^{\circ}\text{W}$  from 1959 to 1974. The dashed line represents the 16-year mean of 35.6.

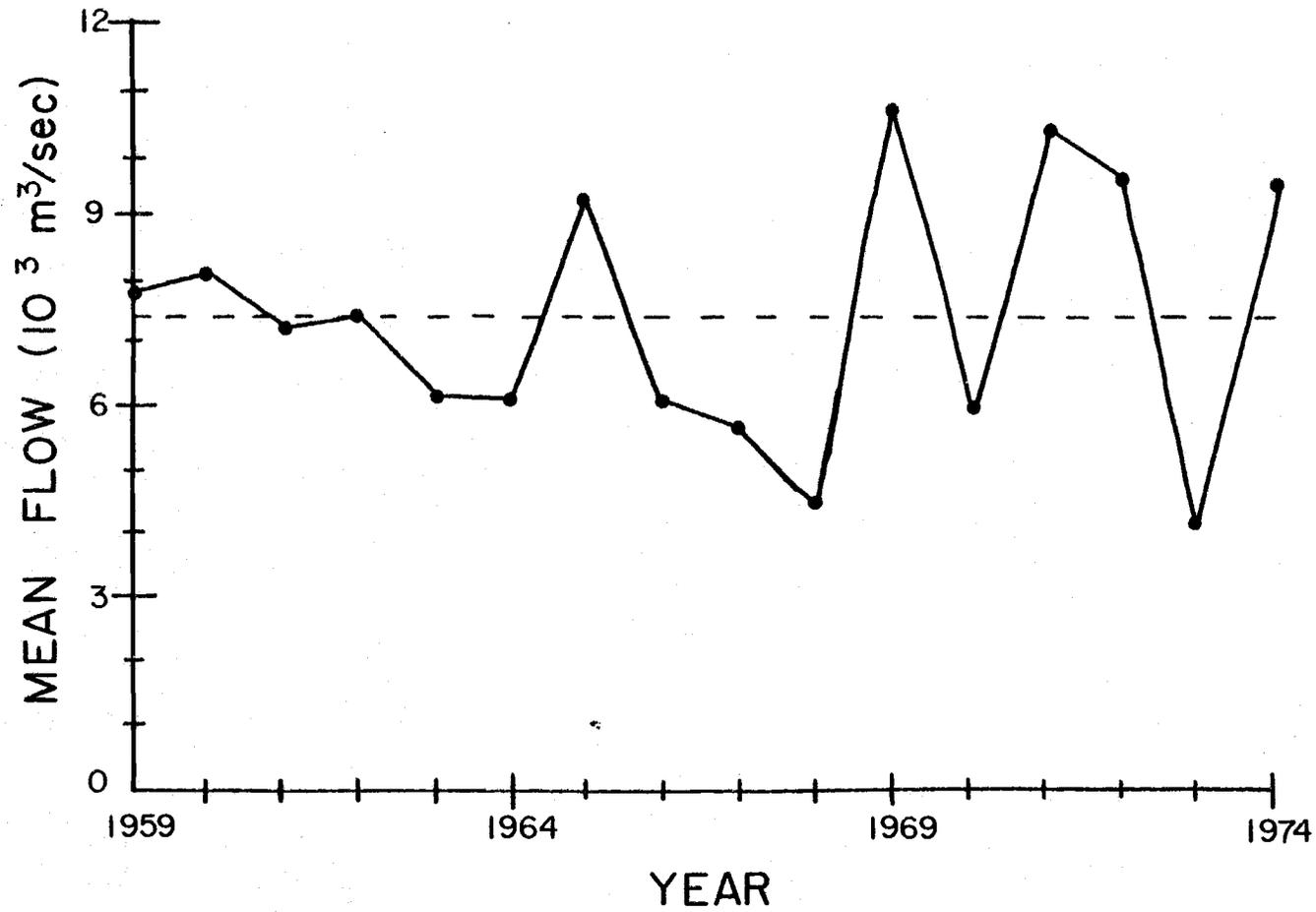


Figure 12. The mean April-May flow recorded at Bonneville Dam from 1959 to 1974. The dashed line represents the 16-year mean of  $7,380 \text{ m}^3/\text{sec}$ .

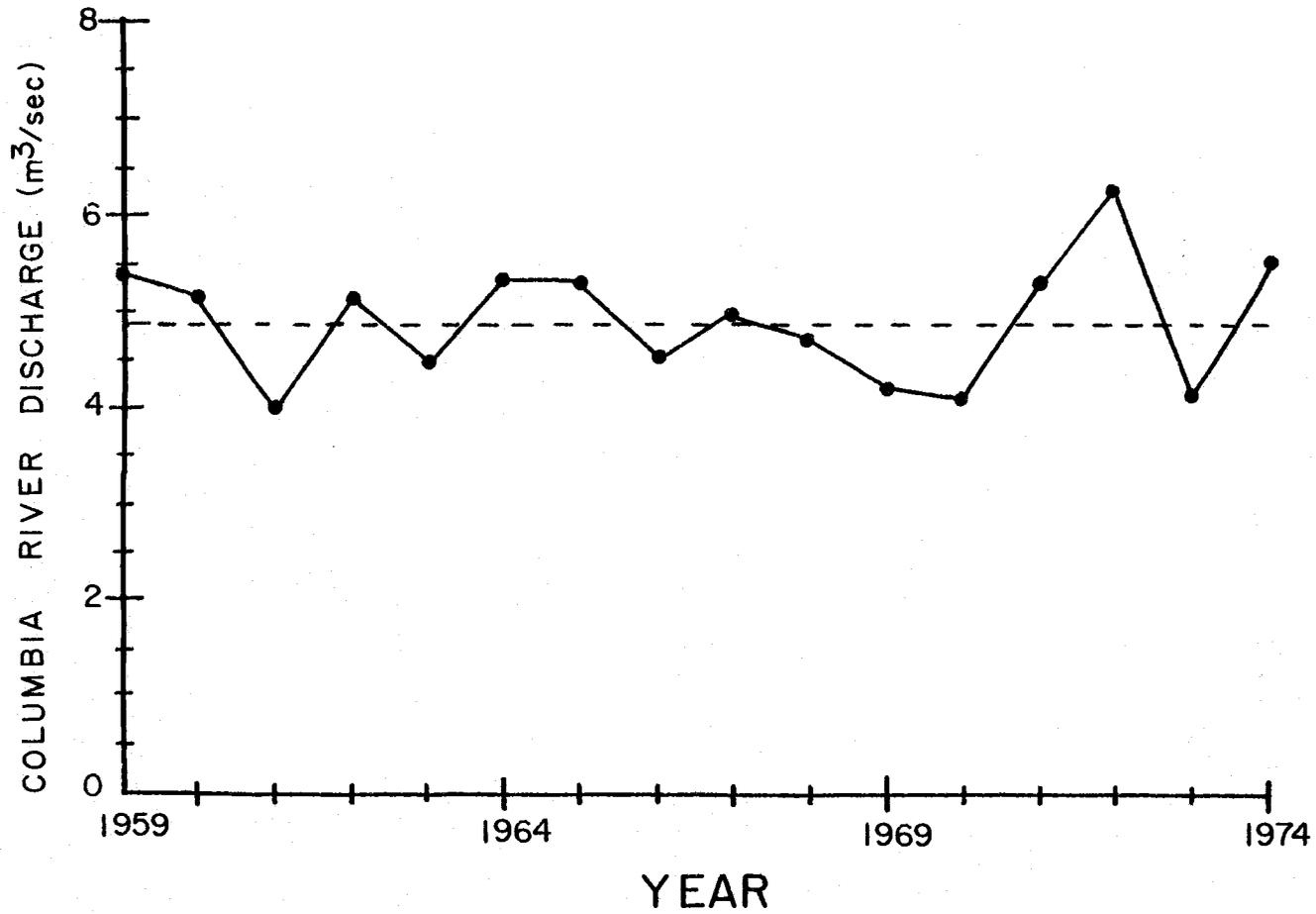


Figure 13. The mean August Columbia River discharges recorded at Astoria, Oregon, from 1959 to 1974. The dashed line represents the 16-year mean of  $4.88 \text{ m}^3/\text{sec}$ .

during outmigration may be associated with below average brood year returns.

Trends for all age groups from any single brood year could also be isolated from the relative contribution of specific brood years to subsequent runs for the Lemhi River spring chinook salmon (Fig. 8). The 1963 brood year contributed above average returns from 1966 to 1968. During the outmigration of this brood in 1965, both turbidity and temperature measured at Bonneville Dam were below average; the upwelling index, Columbia River discharge, and the flow at Bonneville Dam were above average (Figs. 9-13). As for the upriver fish, the 1971 brood year for Lemhi River spring chinook salmon yielded below average returns from 1974 to 1976 (Fig. 8).

The Ricker reproduction curve (Fig. 14) for the upriver spring chinook salmon was determined from the regression of  $\ln(R/S)$  on  $S$  (Fig. 15). For these data, the maximum number of progeny,  $R$ , is obtained when the parent spawner abundance is 58,000. The replacement abundance, where  $R=P$ , occurs when the spawners number 125,000. The years associated with the data points correspond to the years of parent escapement to the spawning ground. The straight line through the origin (Fig. 14) represents the one-to-one replacement line. Data points below this line indicate years when the return per spawner was less than one. Consecutive years of return per

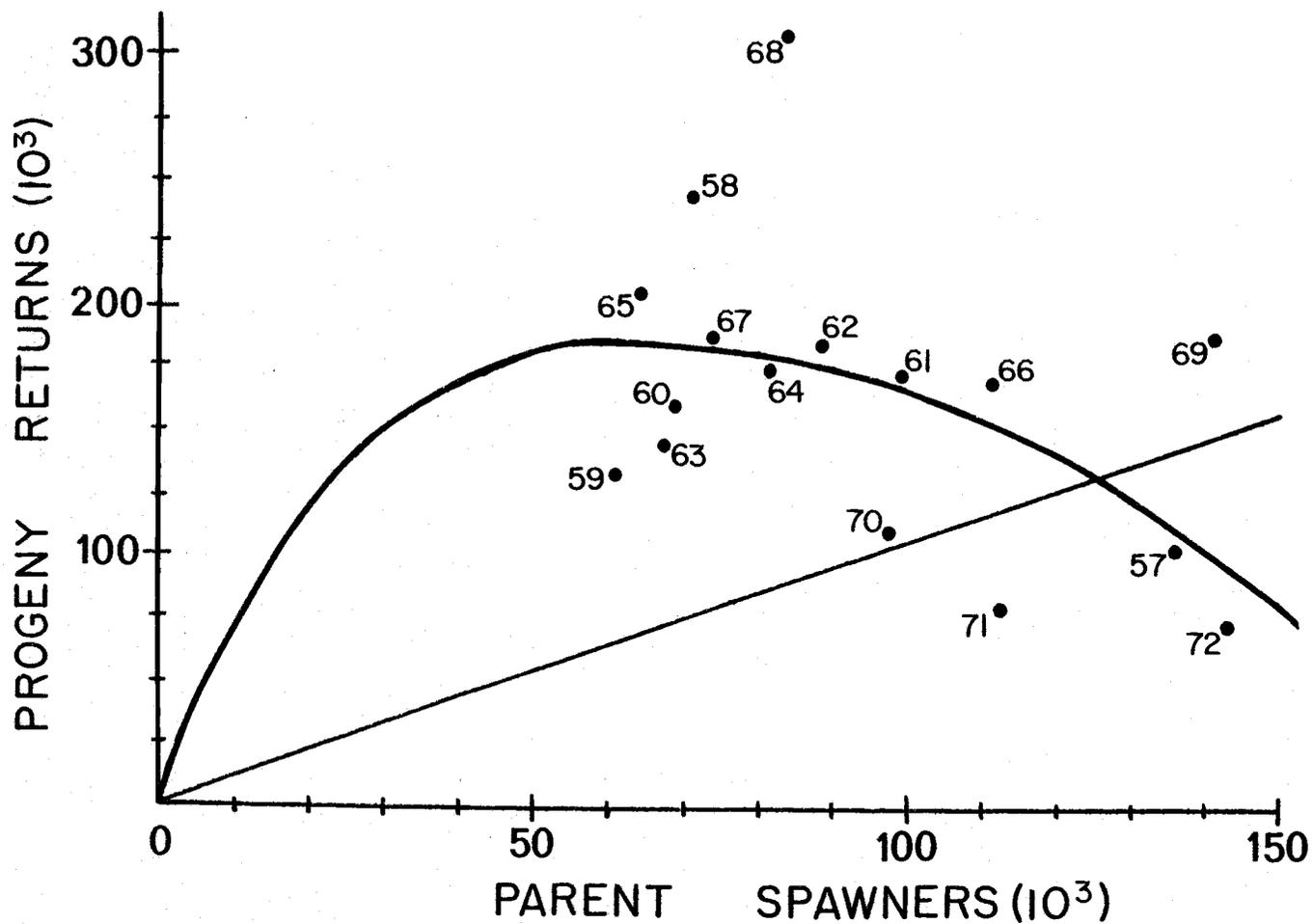


Figure 14. The Ricker reproduction curve for upriver spring chinook salmon. The year associated with each data point refers to the year of parent spawning.

Figure 15. The regression of the Ricker return per spawner index,  $\ln(R/S)$ , on spawning escapement for upriver spring chinook salmon. The year associated with each data point refers to the year of spawning escapement.

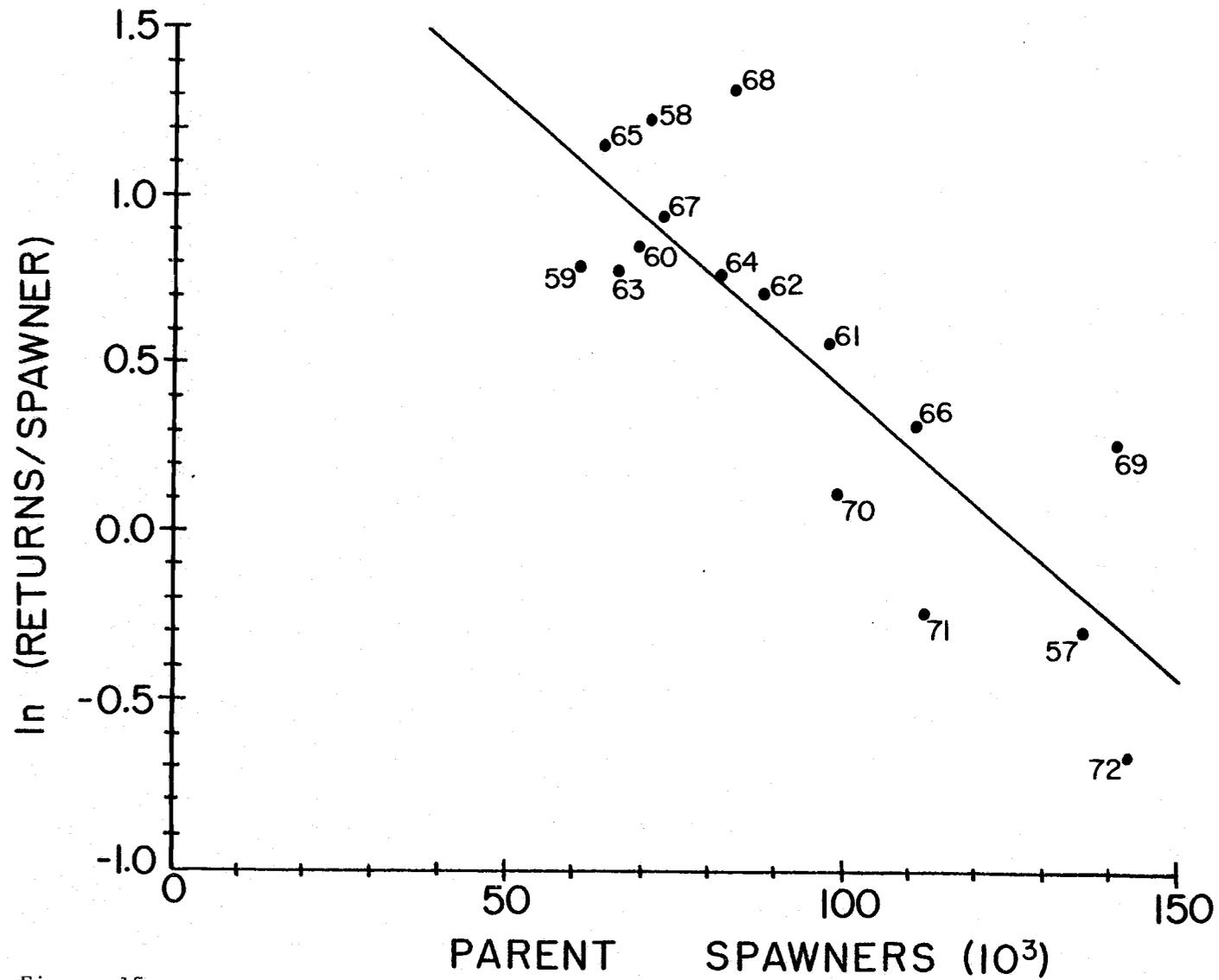


Figure 15.

spawner rates less than one result in the decline, and eventual extinction, of the population. For the upriver spring chinook salmon, the return per spawner rate was below the replacement line for the 1957, 1971, and 1972 brood years (Fig. 14). A very high return per spawner resulted from the 1968 brood year.

Most of the data from the Lemhi River indicated that the progeny returns were below the replacement line (Fig. 16). The solid line represents the one-to-one replacement line and the dotted line represents the linear regression line for the data points. Due to the limited range of the Lemhi River data set, the spawner-return relationship appears linear. That is, the available data points correspond to the ascending limb of a Ricker reproduction curve. Additional data points corresponding to the descending limb of this curve are necessary to generate a curve characterizing the spawner-recruit relationship for the Lemhi River.

### Correlation Analyses

Some significant ( $\alpha \leq .05$ ) correlations, indicated by asterisks (Tables 4 and 5), were found between the return per spawner index,  $\ln(R/S)$ , and parent escapement,  $S$ . This relationship was only negative and significant ( $\alpha \leq .05$ ) for the Columbia River data (Fig. 15). The Lemhi River brood year returns were positively and significantly ( $\alpha \leq .05$ ) correlated with the parent spawners (Fig. 16); however, the relationship between the Lemhi River return per spawner index and

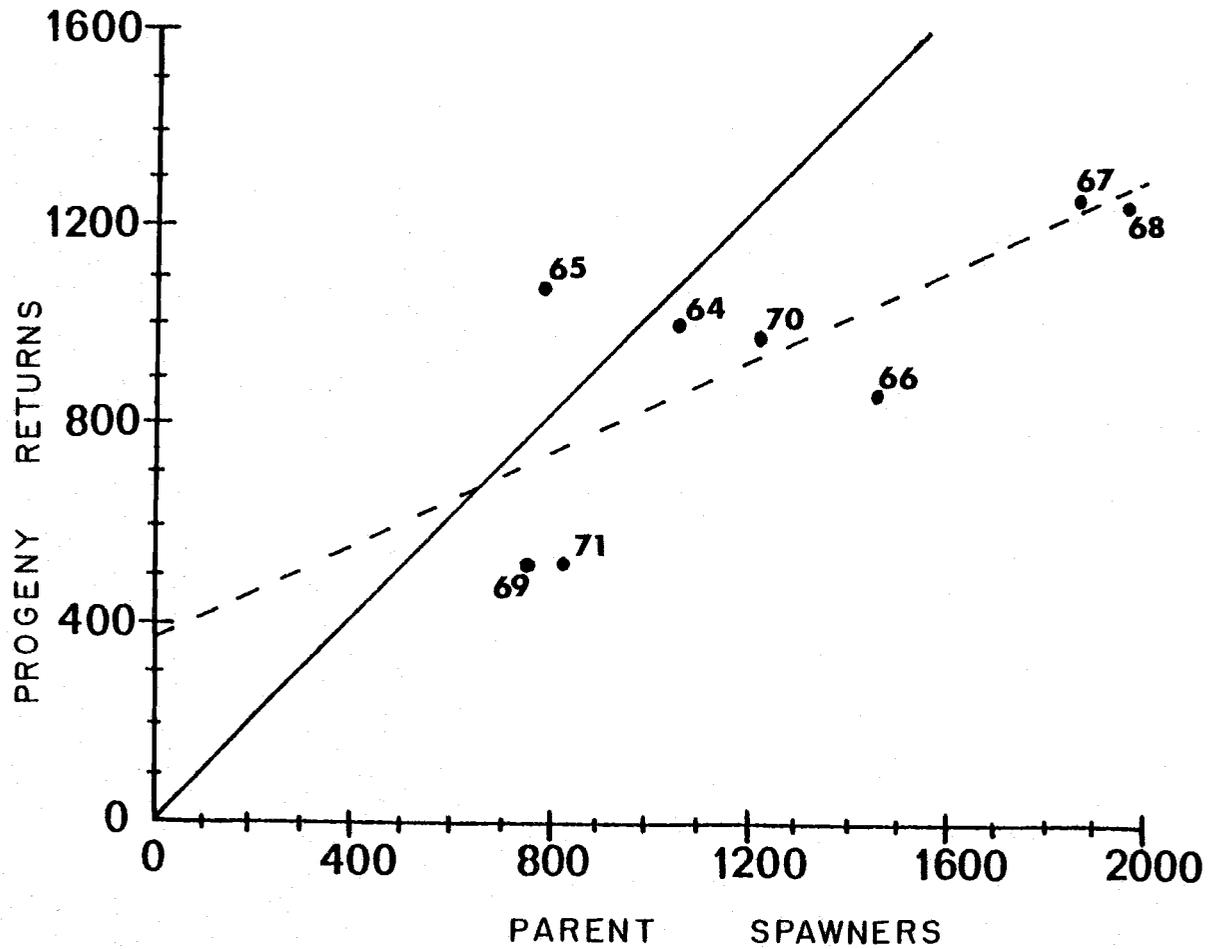


Figure 16. The regression of brood year returns on spawning parents for the Lemhi River fish. The year refers to the year of parent spawning. The dashed line is the regression line and the solid line is the one-to-one replacement line.

parent escapement (Fig. 17) was not significant ( $\alpha \leq .05$ ).

No significant ( $\alpha \leq .05$ ) correlations were observed (Tables 4 and 5) between either one of the two return per spawner indices and each freshwater environmental variable averaged over April and May during the year of outmigration. For the upriver data, flow and temperature recorded at Bonneville Dam were negatively correlated with the survival rate (Figs. 18 and 19); both the turbidity and nitrogen supersaturation at Bonneville Dam was positively related to the return per spawner index (Figs. 20 and 21). For the Lemhi River data, the flow at Ice Harbor Dam was positively related to the survival rate and both temperature and turbidity at the dam site were negatively related to this rate (Table 5). Because of the linear relationship between Lemhi River spawners and brood year returns, correlations between the brood year returns and density independent factors were also noted. For these data, flow at Ice Harbor Dam was positively related to the brood year returns (Fig. 22) and both temperature and turbidity were negatively related to the returns (Figs. 23 and 24).

The relationship between Lemhi River brood year returns and the flow at Ice Harbor Dam (Fig. 22) appeared curvilinear. This relationship suggested that the lowest brood year returns occurred when

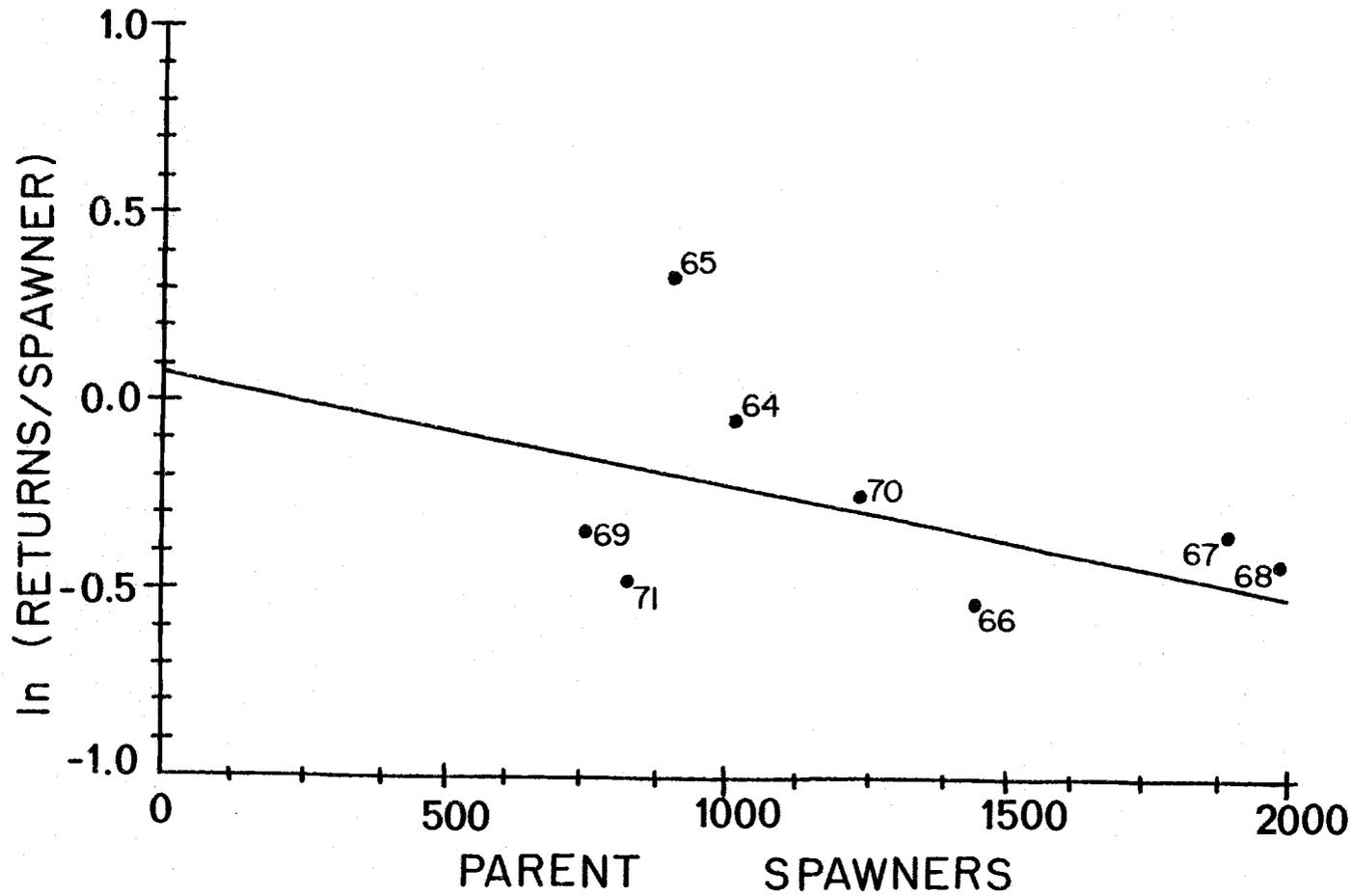


Figure 17. The regression of the Ricker return per spawner index,  $\ln(R/S)$ , on spawning escapement for Lemhi River spring chinook salmon. The year associated with each data point refers to the year of spawning escapement.

Table 4. Correlation coefficients calculated for selected factors influencing the upriver fish. Nitrogen supersaturation data are measured from 1967 to 1974; other environmental variables are measured from 1959 to 1974. The  $\ln(R/S)$ , S, and R are measured from 1957 to 1972.

Table 4.

	Bonneville												
	S	R	Flow	$\Delta$ Flow	Temp	Turb	N2	Columbia River Discharge				June-July upwelling	
ln (R/S)	**	**						June	July	August	Sept.	Oct.	
ln (R/S)	-.841	.845	-.144	-.298	-.036	.152	.056	.000	-.114	-.398	-.646	-.405	.482
Parent Spawners, S	1.0	-.450	.157	.350	-.132	-.111	-.036	-.033	.166	.391	.705	.526	-.456
Returning Offspring, R		1.0	-.152	-.216	-.166	.221	-.006	-.118	-.133	-.332	-.400	-.203	.341
Bonneville April-May Flow			1.0	**	**	**	.548	.444	.380	.502	.248	.079	.006
Bonneville April-May Transformed Flow ( $\Delta$ Flow)				1.0	-.372	-.646	.554	.065	.091	.176	.183	-.054	.060
Bonneville April-May Temperature (Temp)					1.0	.684	-.405	-.617	-.570	-.697	-.418	-.239	.056
Bonneville April-May Turbidity (Turb)						1.0	-.623	-.542	-.460	-.521	-.210	-.065	-.027
Bonneville April-May Nitrogen Supersaturation (N2)							1.0	.128	.185	.037	.254	.531	-.206
June Discharge								1.0	**	*	.236	.131	-.041
July Discharge									1.0	**	.400	.388	.142
August Discharge										1.0	*	.320	-.147
September Discharge											1.0	**	-.157
October Discharge												1.0	.026

\*Significant at 5% level

\*\*Significant at 1% level

Table 5. Correlation coefficients calculated for selected factors influencing the Lemhi River fish. Environmental variables are measured from 1966 to 1973. The ln(R/S), S, and R are measured from 1964 to 1971.

	Ice Harbor											
	S	R	April-May mean				Columbia River Discharge				June-July upwelling	
			Flow	$\Delta$ Flow	Temp	Turb	June	July	August	Sept.		Oct.
ln (R/S)	-.461	.261	.005	-.474	-.143	-.225	.544	.685	.270	-.366	-.238	.604
Parent Spawners, S	1.0	.734*	.069	-.479	-.229	.144	-.204	-.308	-.431	.002	.288	.159
Returning Offspring, R		1.0	.075	-.878**	-.338	-.020	.167	.169	-.272	-.305	.083	.618
Ice Harbor April-May Flow			1.0	.120	-.633	-.939**	.628	.498	.527	.248	.149	-.056
Ice Harbor April-May Transformed Flow ( $\Delta$ Flow)				1.0	.594	.139	-.494	-.416	-.122	.058	-.013	-.515
Ice Harbor April-May Temperature (Temp)					1.0	.542	-.753†	-.519	-.627	-.412	-.041	.132
Ice Harbor April-May Turbidity (Turb)						1.0	-.718*	-.645	-.658	-.230	-.055	-.026
June Discharge							1.0	.925**	.832*	.434	.249	.236
July Discharge								1.0	.724**	.257	.270	.419
August Discharge									1.0	.676	.079	-.258
September Discharge										1.0	.545	-.387
October Discharge											1.0	.361

\*Significant at 5% level

\*\*Significant at 1% level

Figure 18. The relationship between the upriver return per spawner rate for the 1957-1972 brood years and mean April-May flow recorded at Bonneville Dam from 1959-1974. The linear correlation coefficient calculated between the two variables is  $-.144$ . The year associated with each data point refers to the brood year. The solid line represents a parabolic transformation of the data.

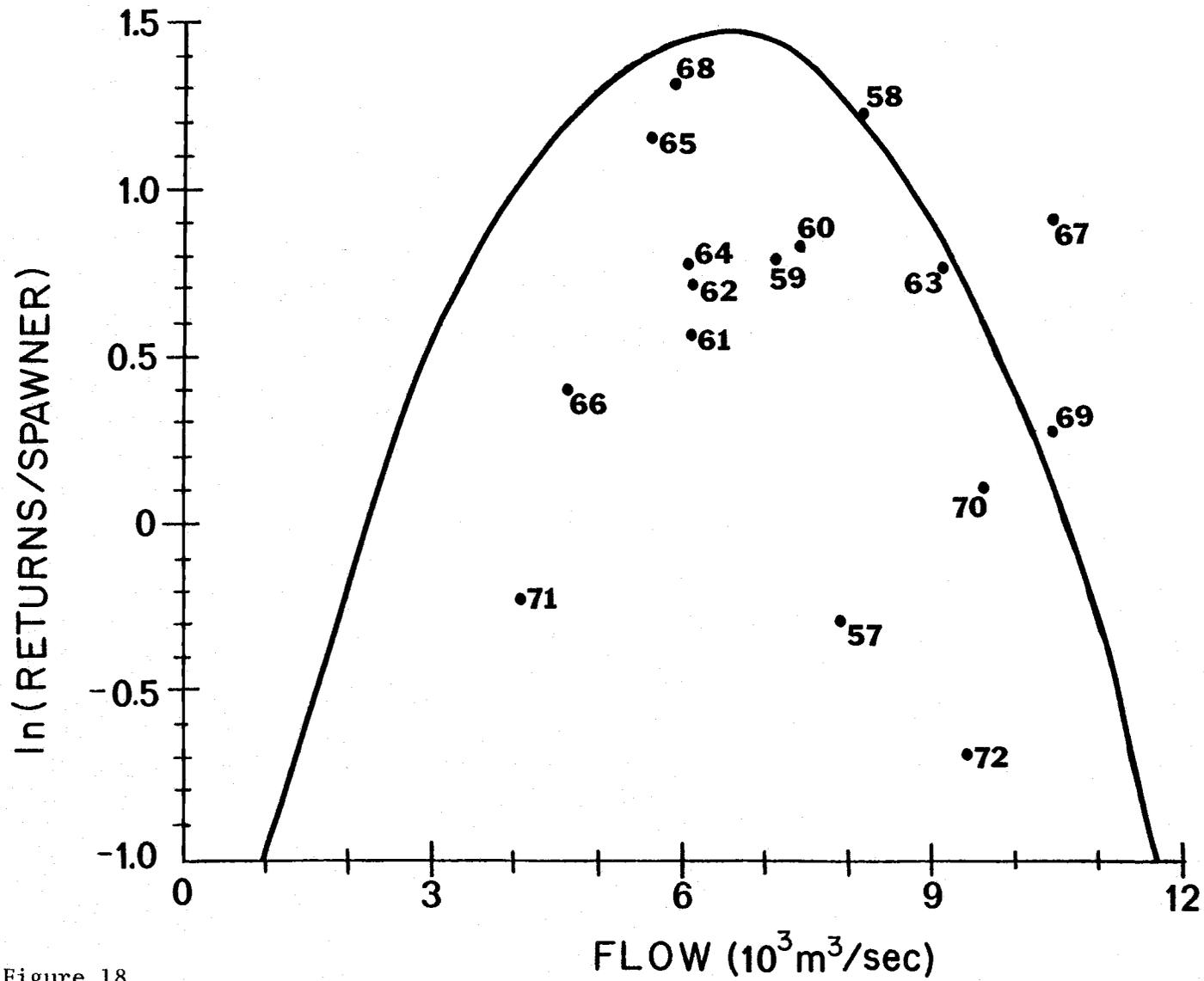


Figure 18.

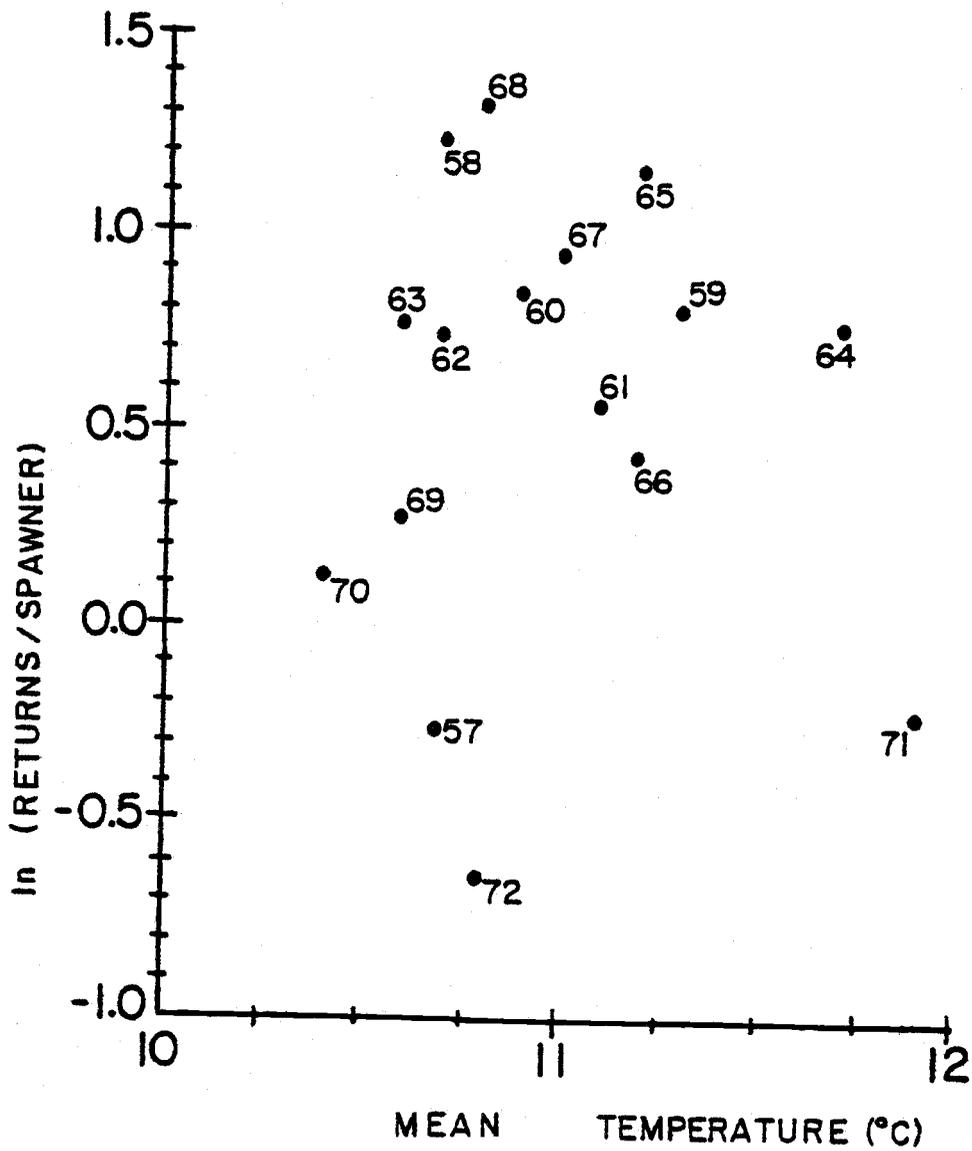


Figure 19. The relationship between the upriver return per spawner rate from 1957 to 1972 and the mean April-May temperature measured at Bonneville Dam from 1959 to 1974. The year associated with each data point refers to the brood year. The correlation coefficient calculated between the two variables is  $-.036$ .

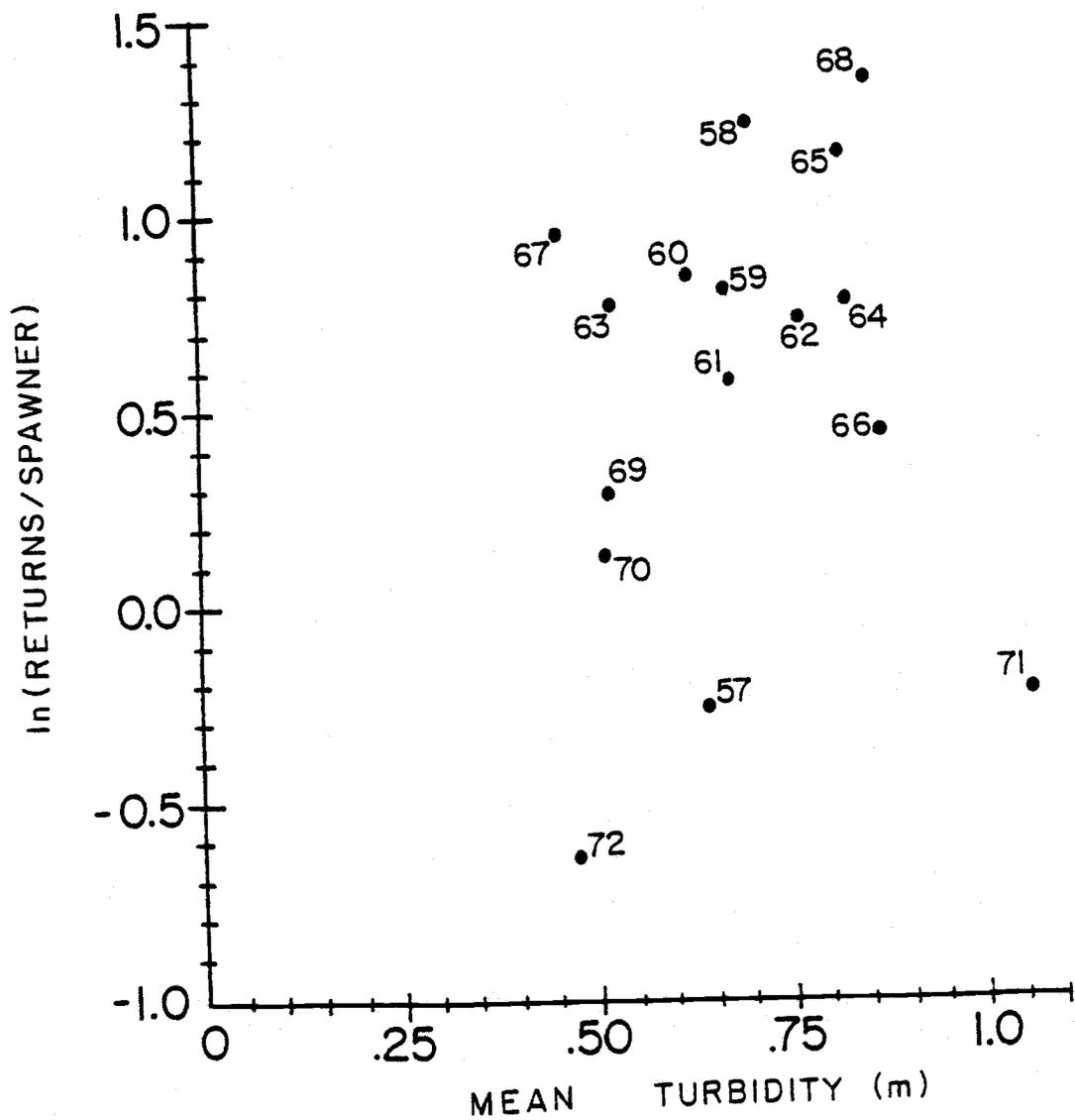


Figure 20. The relationship between the upriver return per spawner rate from 1957 to 1972 and the mean April-May turbidity measured at Bonneville Dam from 1959 to 1974. The correlation coefficient calculated between the two variables is .152. The year associated with each data point refers to the brood year.

Figure 21. The relationship ( $r = .056$ ) between the upriver return per spawner rate from 1965 to 1972 and the mean April-May nitrogen supersaturation at Bonneville Dam recorded from 1967 to 1974. The year associated with each data point refers to the brood year.

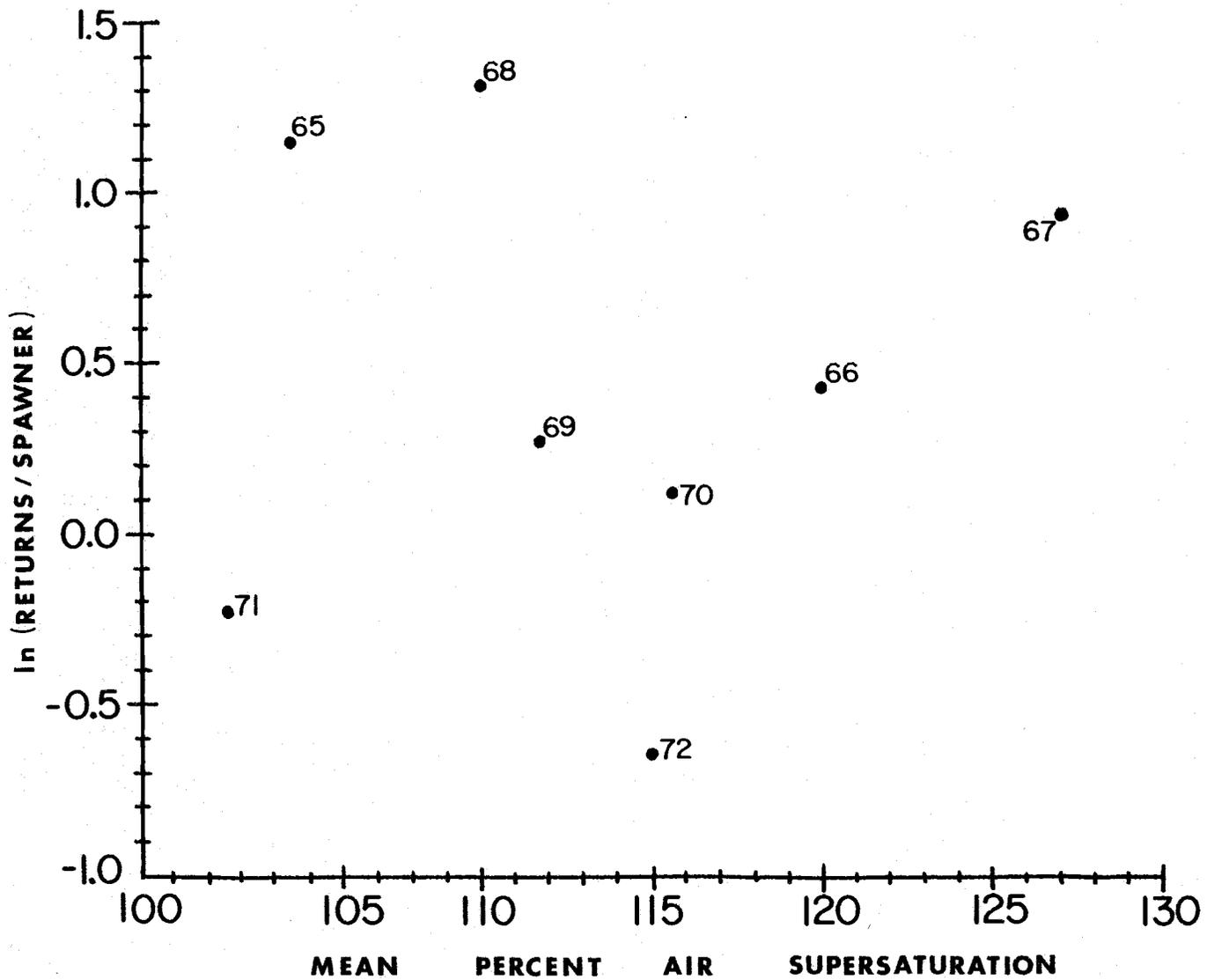


Figure 21.

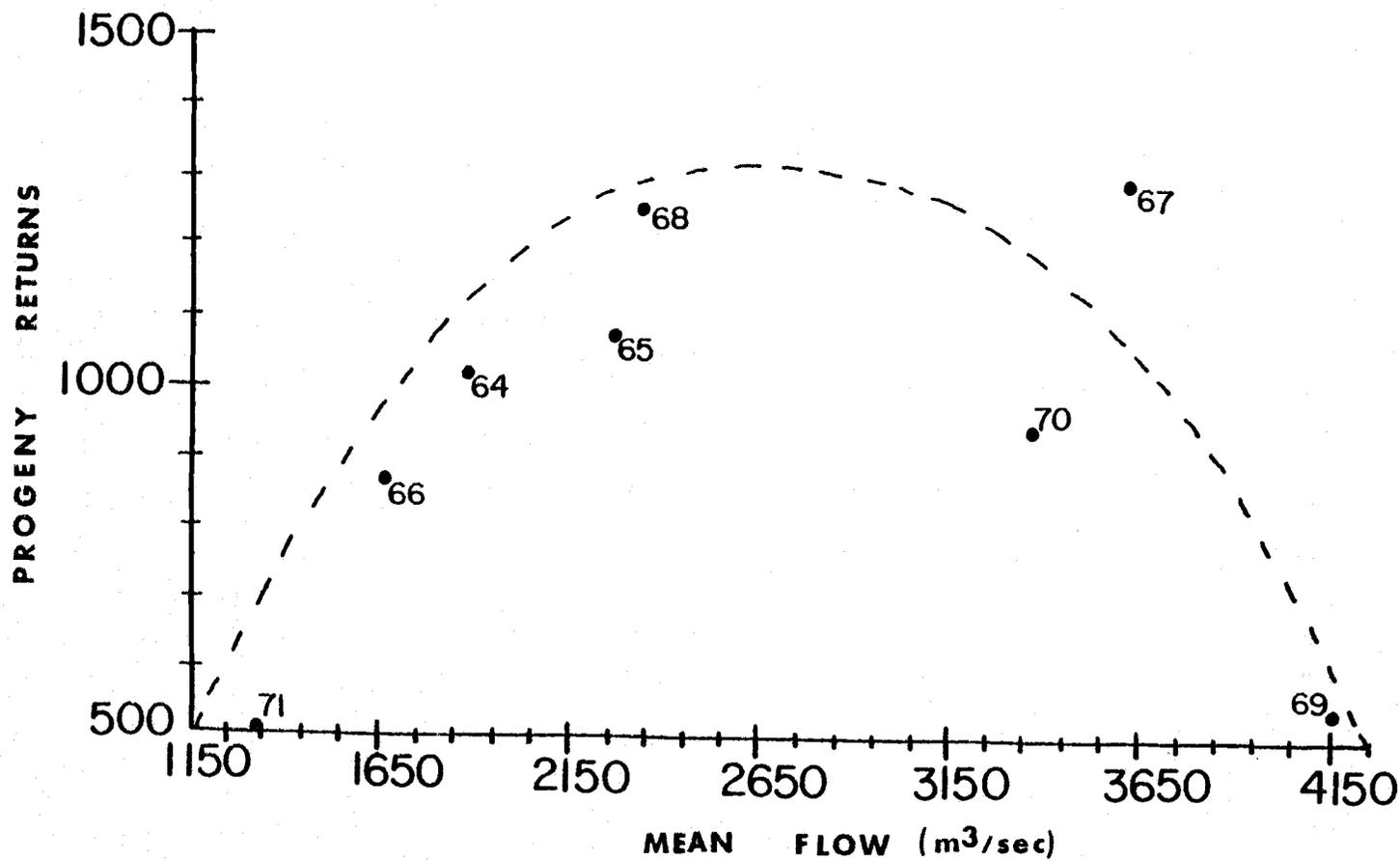


Figure 22. The relationship ( $r = .075$ ) between the Lemhi River brood year returns from 1964 to 1971 and the mean April-May flow measured at Ice Harbor Dam from 1966 to 1973. The year associated with each data point represents the brood year. The dashed curve represents the parabolic transformation fitted to the data.

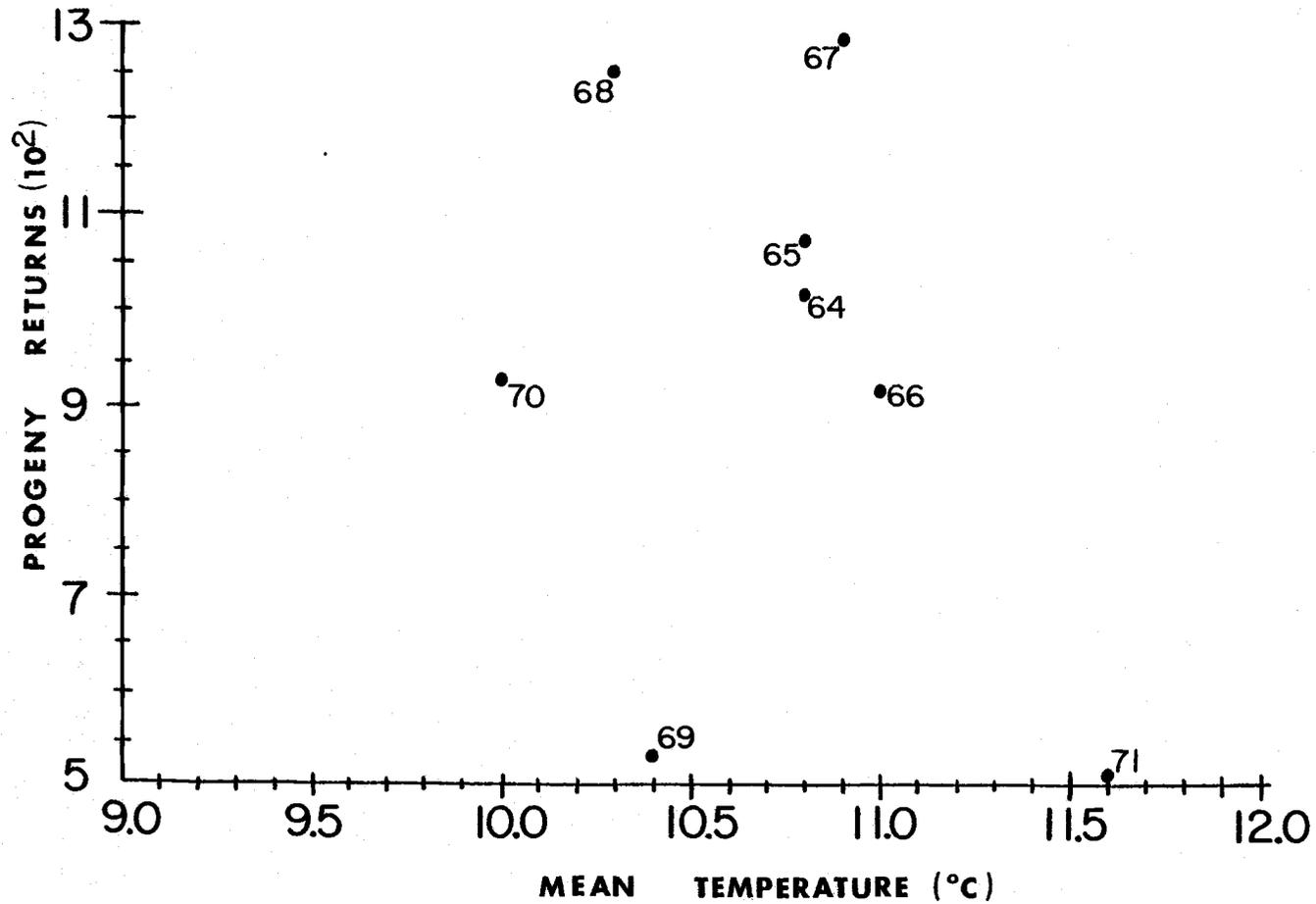


Figure 23. The relationship ( $r = -.338$ ) between the Lemhi River brood year returns from 1964 to 1971 and the mean April-May temperature measured at Ice Harbor Dam from 1966 to 1973. The year associated with each data point is the brood year.

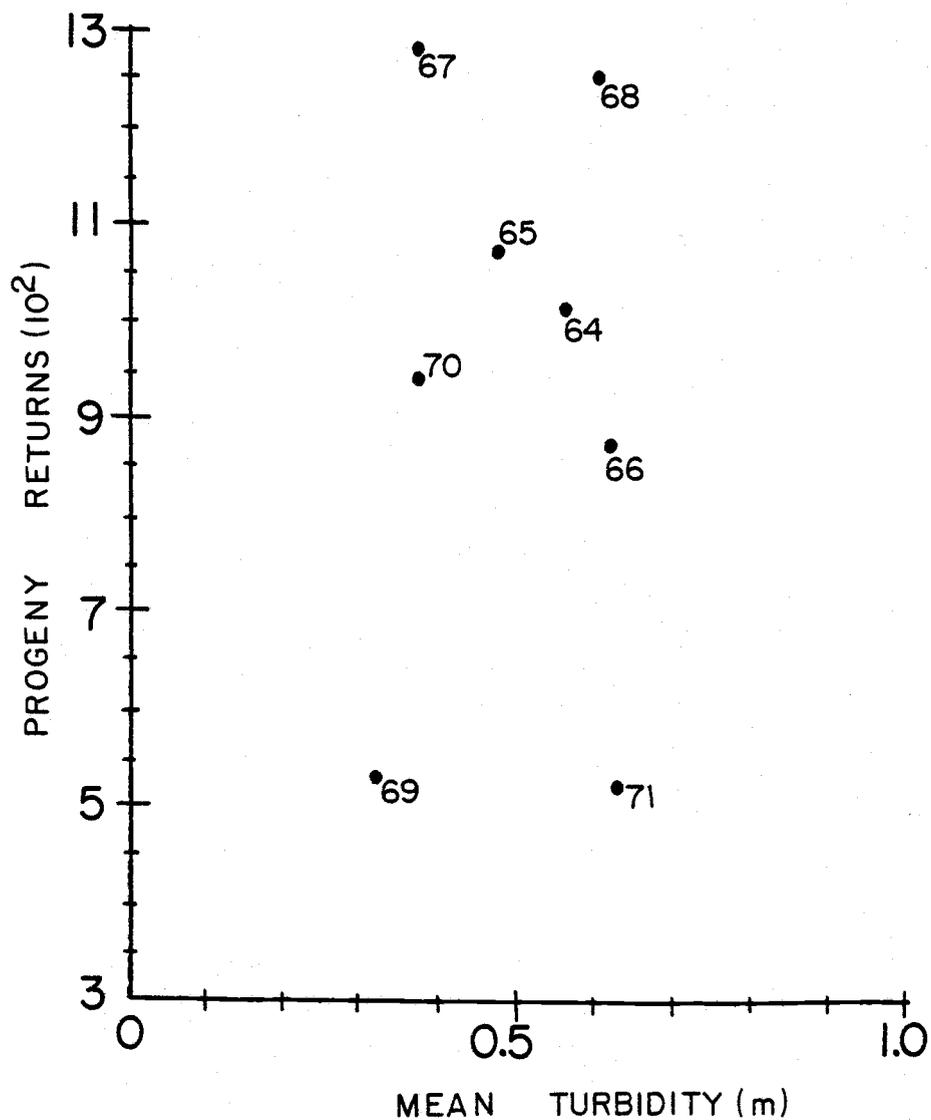


Figure 24. The relationship ( $r = -.0201$ ) between the Lemhi River brood year returns from 1964 to 1971 and the mean April-May turbidity measured at Ice Harbor Dam from 1966 to 1973. The year associated with each data point refers to the brood year.

outmigrants experienced either high or low flows. Raymond (1974) and Ebel et al. (1975) suggested that the highest juvenile mortality occurs when the outmigrating fish pass through turbines, during low flow years, or are exposed to high levels of nitrogen supersaturation during high flow years. Due to the curvilinear nature of the flow data, a parabolic transformation was fitted to the original flow data. The resulting transformation of these data was calculated as:

$$X' = (X-2830)^2$$

where  $X'$  is the transformed flow variable and  $X$  is the original flow variable. New correlation coefficients were calculated between selected biological indices and the transformed flow variable. The relationship between the transformed flow variable and Lemhi River brood year returns was statistically significant ( $r = -.878$ ; Fig. 25); however, the relationship with the Lemhi River return per spawner index (Fig. 26) was not significant statistically ( $r = -.474$ ;  $\alpha \leq .05$ ). To determine if a parabolic flow transformation was also appropriate for the Bonneville Dam data, the upriver correlation analysis was revised. The parabolic relationship determined for the Bonneville data (Fig. 18) was calculated as:

$$Y' = (Y-6370)^2$$

where  $Y'$  is the transformed flow variable and  $Y$  is the original flow

Figure 25. The relationship ( $r = -.878$ ) between the Lemhi River brood year returns from 1964 to 1971 and the transformed Ice Harbor April-May flow variable measured from 1966 to 1973. The year associated with each data point corresponds to the brood year. The solid line represents the linear regression calculated between the two variables.

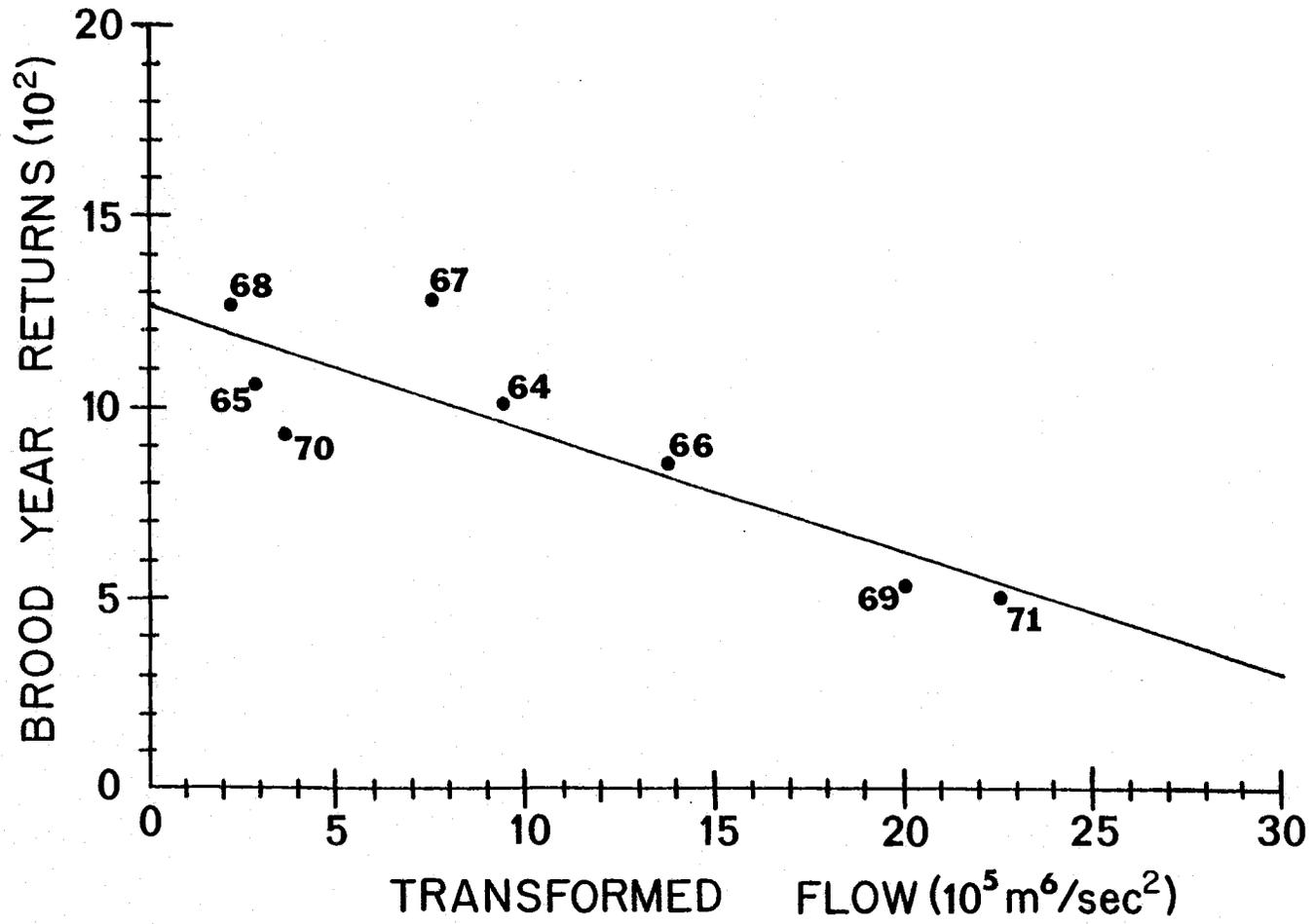


Figure 25.

Figure 26. The relationship ( $r = -.474$ ) between the Lemhi River return per spawner rate from 1964 to 1971 and the transformed Ice Harbor April-May flow variable measured from 1966 to 1973. The year associated with each data point refers to the brood year. The solid line represents the linear regression calculated between the two variables.

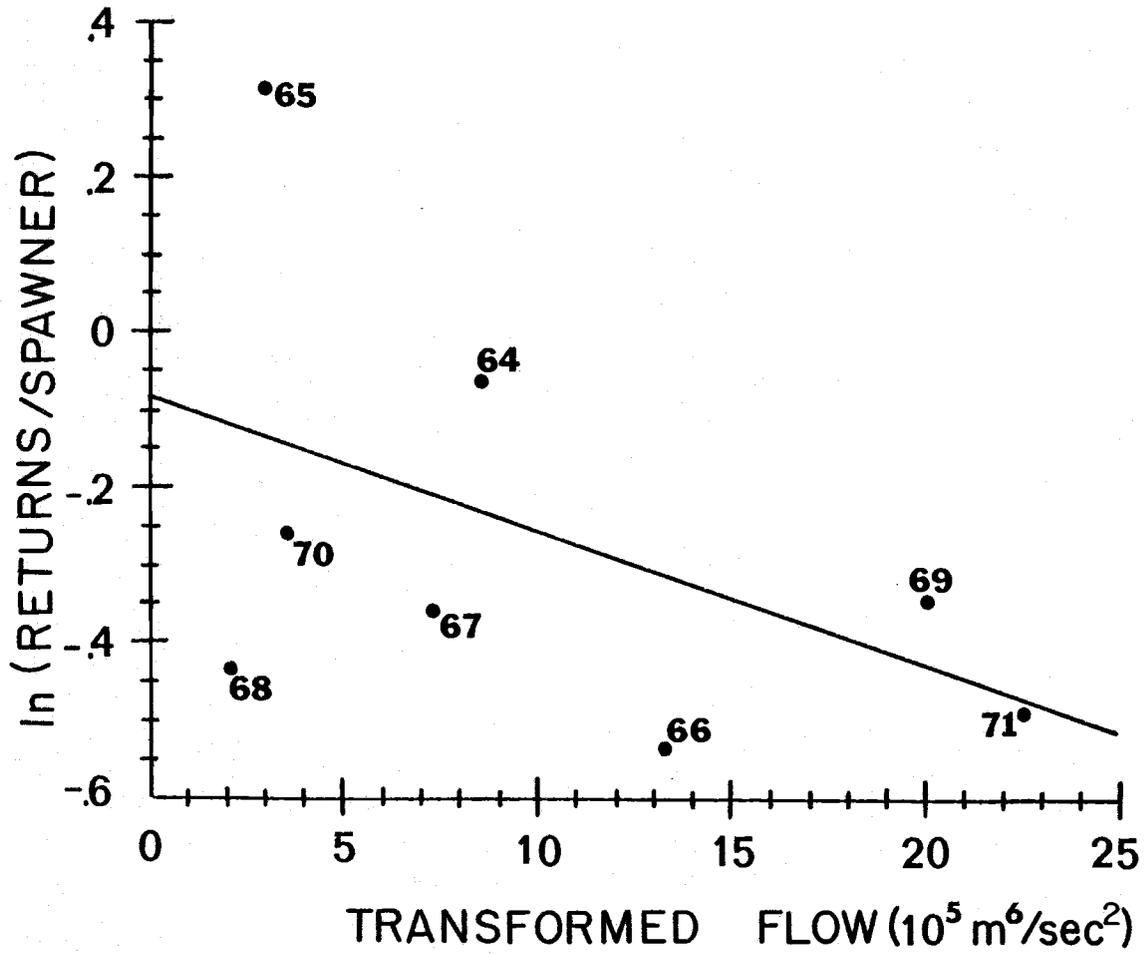


Figure 26.

variable. Although the transformed data improved the fit of the flow-survival rate relationship to a regression line ( $r = -.298$ ; Fig. 27), these data were not significantly ( $\alpha \leq .05$ ) correlated.

Of the selected measures of Columbia River discharge, only September discharge during downstream migration was significantly ( $\alpha \leq .01$ ) correlated with the upriver return per spawner index (Fig. 28). Columbia River discharge, measured from July through October, was negatively correlated with the survival rate and June discharge was positively related to this rate (Table 4). Since the numbers of parent spawners were also significantly ( $\alpha \leq .05$ ) correlated with September discharge (Table 4), the relationship between the upriver return per spawner index and September discharge may be spurious.

Neither the Lemhi River return per spawner index nor the brood year returns were significantly ( $\alpha \leq .05$ ) correlated with June through October Columbia River discharge during juvenile outmigration (Table 5). The survival rate was positively related to June through August discharges and negatively related to September and October discharges.

Initial results of the correlation analyses suggested that the strongest correlations with the upriver survival rate existed with the upwelling index averaged over June and July at  $48^{\circ}\text{N } 125^{\circ}\text{W}$  during the year of outmigration (Table 6). In addition, a significant relationship ( $r = .937$ ,  $\alpha \leq .01$ ) existed between the upwelling indices measured at

Figure 27. The relationship ( $r = -.298$ ) between the upriver return per spawner rate from 1957 to 1972 and the transformed Bonneville April-May flow variable measured from 1959 to 1974. The year associated with each data point refers to the brood year.

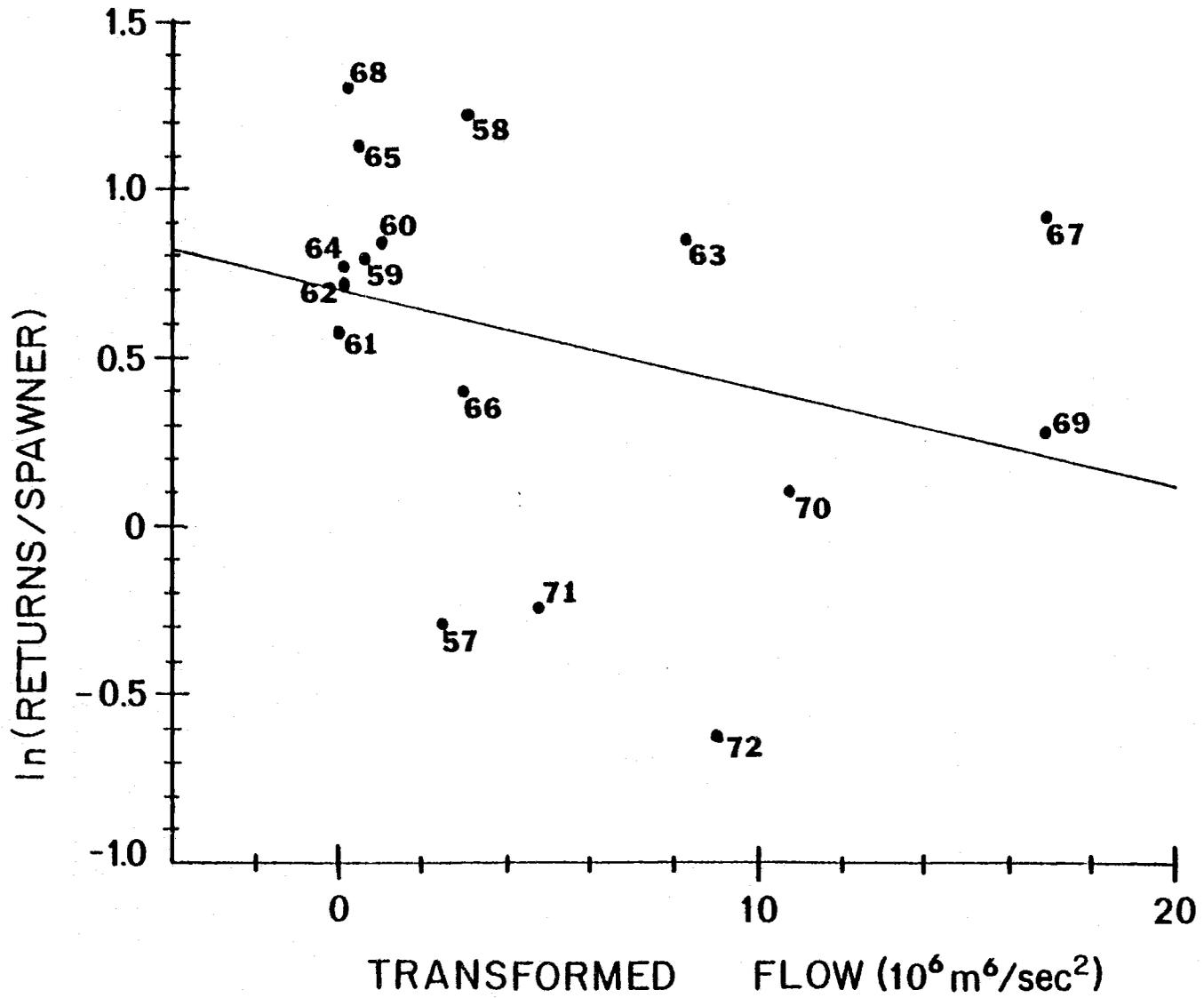


Figure 27.

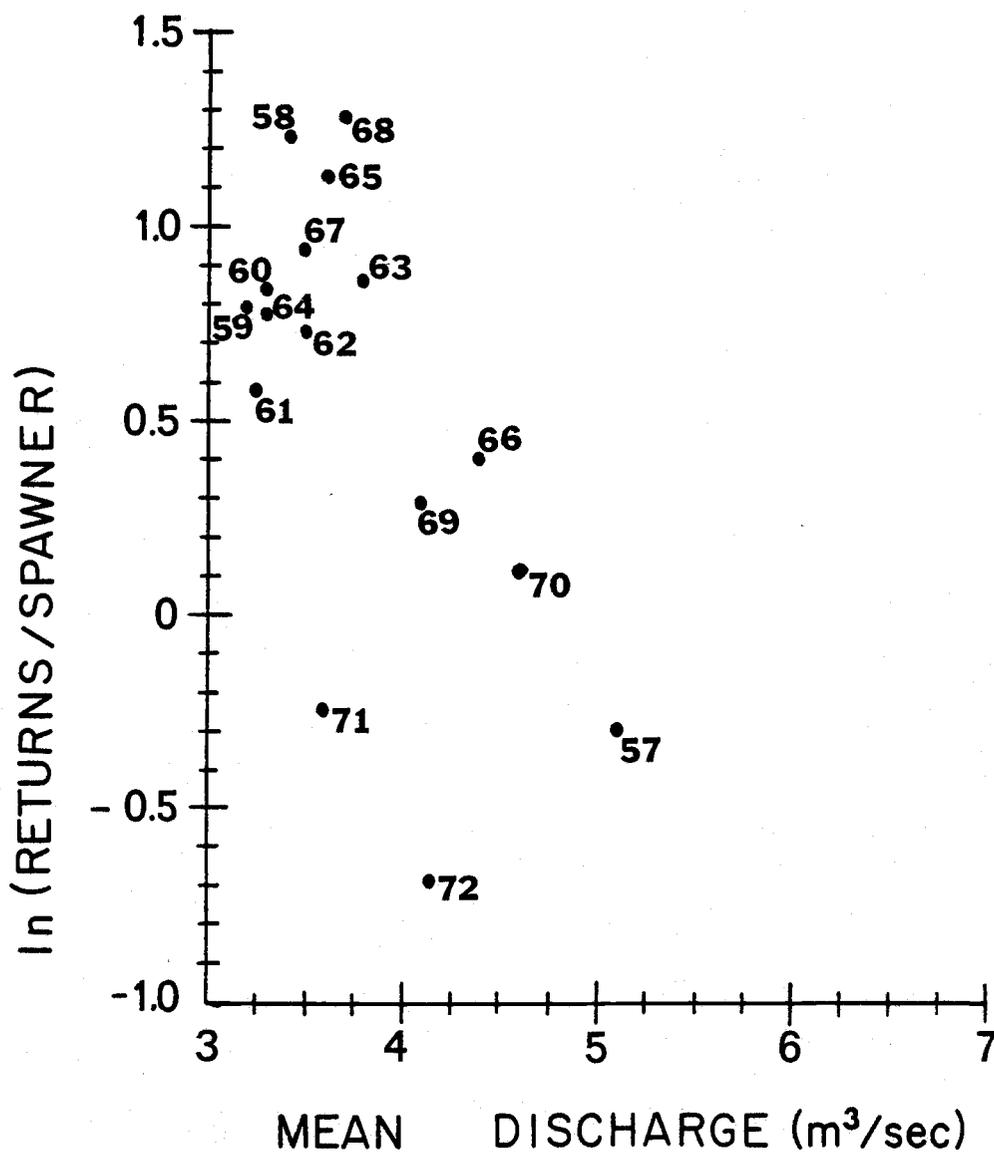


Figure 28. The relationship ( $r = -.646$ ) between the upriver return per spawner index for the 1957 to 1972 brood years and September Columbia River discharge measured from 1959 to 1974 at Astoria, Oregon. The years associated with each data point refer to the brood years.

Table 6. Correlation coefficients calculated between the upriver return per spawner rate,  $\ln(R/S)$ , and selected upwelling indices calculated for  $48^{\circ}\text{N } 125^{\circ}\text{W}$ . The upwelling indices are measured from 1959-1974 and the return per spawner index is measured from 1957-1972 brood years.

Upwelling Index	Correlation Coefficient
Mean March-April upwelling	.0144
Mean March through May upwelling	.077
Mean March through June upwelling	.219
Mean March through July upwelling	.314
Mean March through August upwelling	.227
Mean March through September upwelling	.246
Mean April through May upwelling	.0867
Mean April through June upwelling	.288
Mean April through July upwelling	.366
Mean April through August upwelling	.263
Mean April through September upwelling	.301
Mean May through June upwelling	.347
Mean May through July upwelling	.425
Mean May through August upwelling	.293
Mean May through September upwelling	.308
<u>Mean June through July upwelling</u>	<u>.480</u>
Mean June through August upwelling	.308
Mean June through September upwelling	.329
Mean July through August upwelling	.165
Mean July through September upwelling	.200
Mean August through September upwelling	-.120
Mean March upwelling	.118
Mean April upwelling	-.122
Mean May upwelling	.145
Mean June upwelling	.371
Mean July upwelling	.449
Mean August upwelling	.0996
Mean September upwelling	.136

each of the two sites. Based on these results, only the upwelling indices calculated for  $48^{\circ}\text{N } 125^{\circ}\text{W}$  were incorporated in the remainder of the study. The positive relationship between the upriver survival rate and the June-July upwelling index for  $48^{\circ}\text{N } 125^{\circ}\text{W}$  was nearly significant at the 5% level (Fig. 29). The Lemhi River return per spawner index was also positively related to this upwelling index (Fig. 30). For both sets of data, a high survival rate was noted for the 1965 brood year which experienced strong upwelling upon entering the ocean in 1967. Low survival rates were observed for the weak upwelling event in 1973 corresponding to the outmigration of the 1971 brood year offspring.

A study of the effects of ocean fishing pressures on the upriver spring chinook salmon was complicated by the lack of data separating age classes and chinook races in the fishery. In a single fishing year, three- and four-year-old fish from two different brood years may be landed. To circumvent this problem, the total number of adults (from two brood years) passing over Bonneville Dam were compared with landings in the troll fisheries the previous year. Although this type of analysis avoided the brood year contribution concept and thus precluded further inclusion of the results in a regression analysis, this method permitted an initial study of the importance of selected fisheries on the abundance of upriver spring chinook salmon. That is, the

Figure 29. The relationship between the upriver return per spawner index measured from 1957 to 1972 and the mean June-July upwelling index for  $48^{\circ}\text{N } 125^{\circ}\text{W}$  calculated from 1959 to 1974 data. The year associated with each data point is the brood year. The correlation coefficient calculated between the two variables is .482.

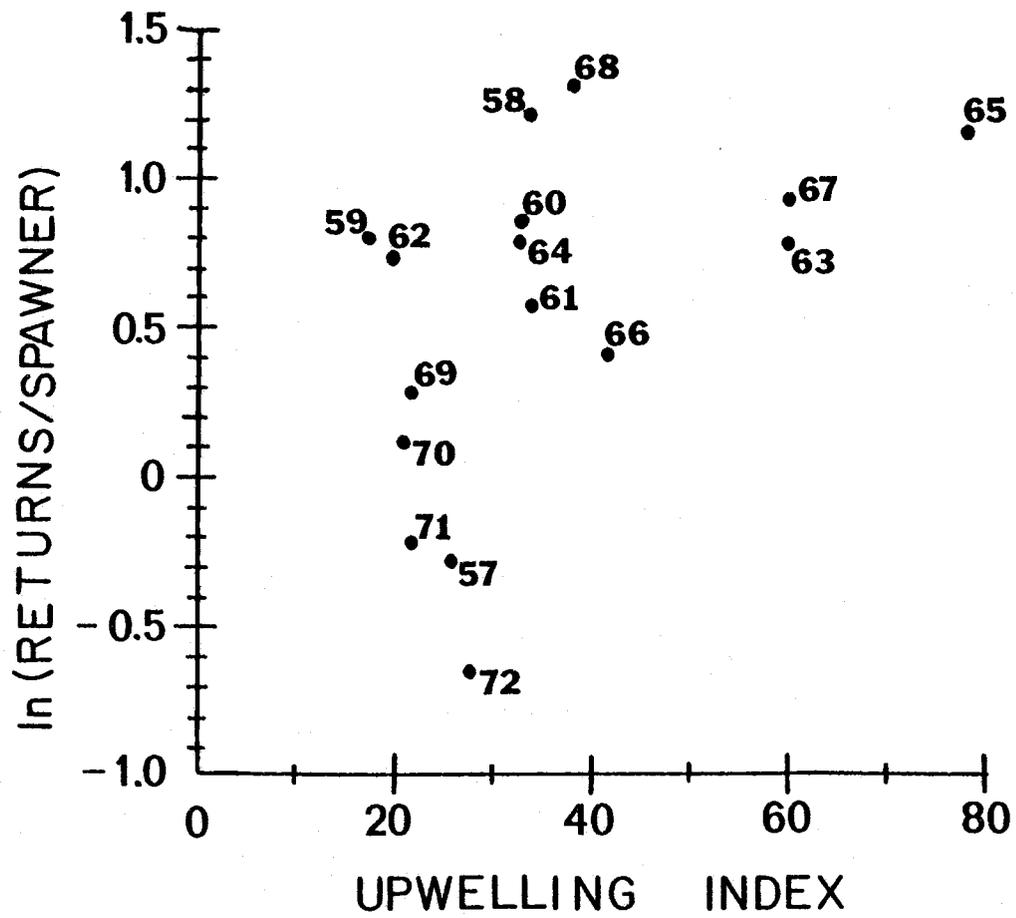


Figure 29.

Figure 30. The relationship ( $r = .604$ ) between the Lemhi River return per spawner rate from 1964 to 1971 and the mean June-July upwelling index at  $48^{\circ}\text{N } 125^{\circ}\text{W}$  calculated from 1966 to 1973 data. The year associated with each data point is the brood year.

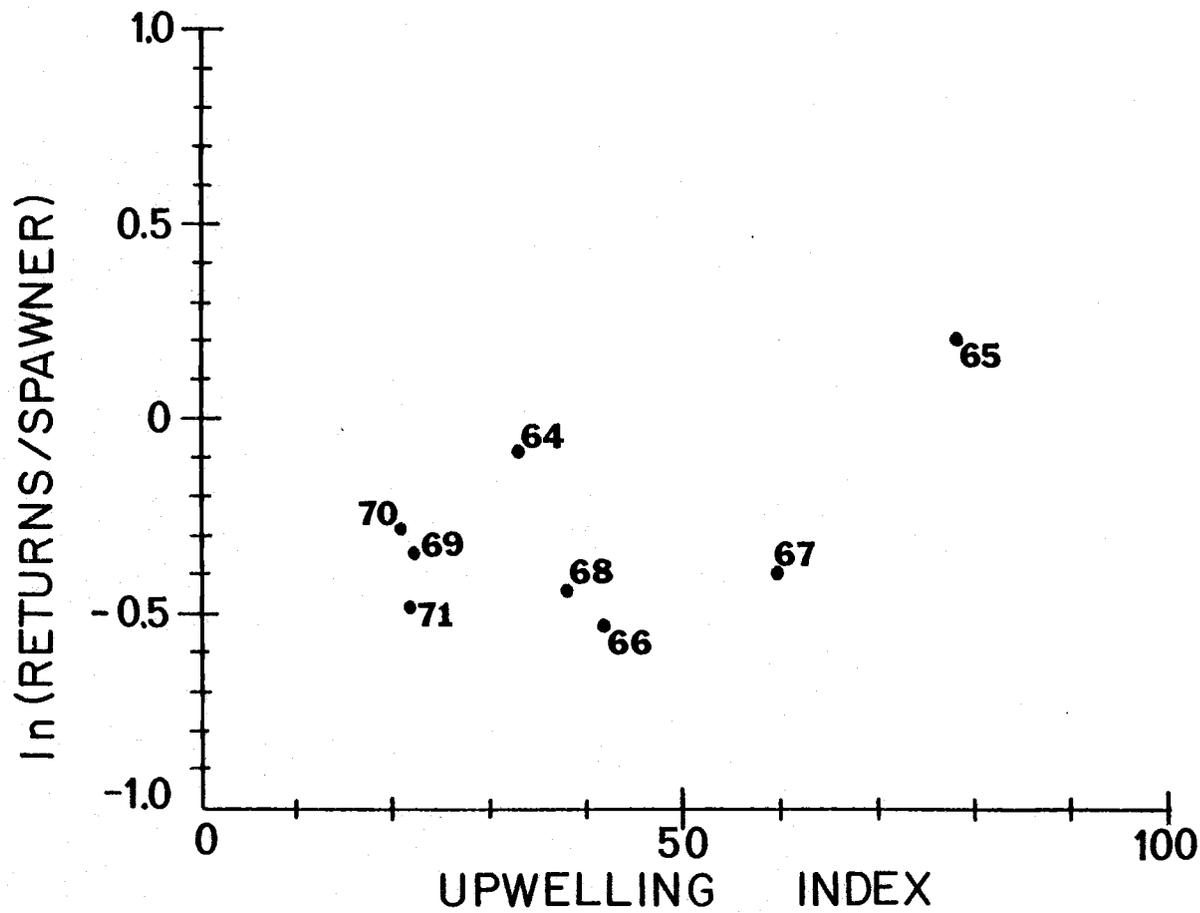


Figure 30.

method suggested those fisheries that merited in-depth studies. The results of these correlation analyses (Table 7) indicated that a significant ( $\alpha \leq .05$ ) relationship existed only between the adult fish count at Bonneville Dam and the annual landings in the Canadian troll fishery (Fig. 31).

Since annual landings in the Canadian troll fishery were recorded as weight rather than numbers, the significant correlation with the adult spring chinook salmon count over Bonneville Dam could reflect annual variability in the average size of the fish landed. To test this hypothesis, the average weight per fish of salmon caught annually (Environment Canada, 1977) was used to calculate the average number of fish landed each year. The mean weight per fish fluctuated in the 1960's and has declined since 1970 (Appendix I). A significant ( $\alpha \leq .01$ ,  $r = .811$ ) correlation existed between the annual landings in pounds and numbers. In addition, the correlation coefficient ( $r = .473$ ) determined between the calculated numbers of fish landed annually and the adult spring chinook salmon count over Bonneville Dam was nearly significant at the 5% level.

Since the adult dam count used in the correlations with the troll fishery landings included returns from two brood years, it was not possible to separate brood year effects from fishing effects. To further investigate the influence of the Canadian troll fishery on brood

Table 7. Selected correlation coefficients calculated between the adult spring chinook salmon count over Bonneville Dam and annual chinook salmon landings in selected troll fisheries. American troll landings are recorded as numbers of fish caught; Canadian troll landings are recorded as pounds of fish caught.

Variable I	Variable II	Correlation Coefficient
Bonneville Adult Count 1961-1975	California Troll Landings 1960-1974	-.284
Bonneville Adult Count 1961-1975	Oregon Troll Landings 1960-1974	.312
Bonneville Adult Count 1961-1975	Washington Troll Landings 1960-1974	.288
Bonneville Adult Count 1964-1977	Canadian Troll Landings 1963-1976	.554*
Bonneville Adult Count 1961-1975	S. E. Alaskan Troll Landings 1960-1974	.372

\*Significant at the 5% level

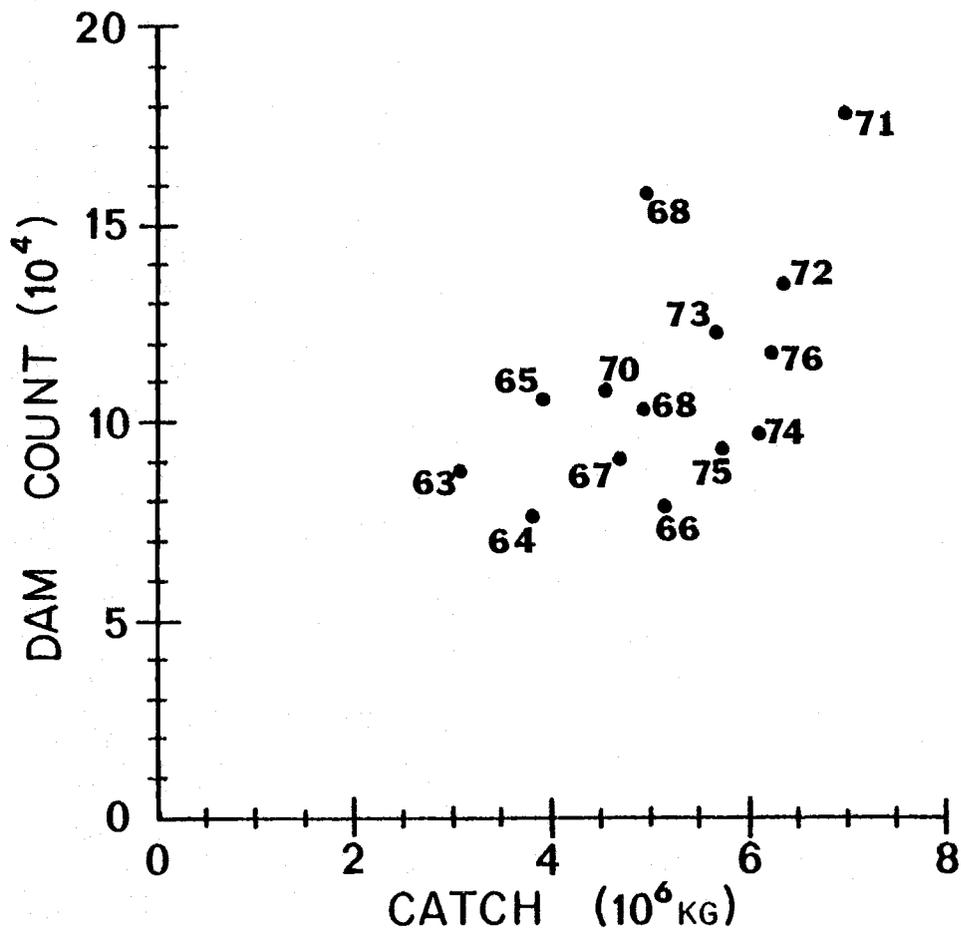


Figure 31. The relationship ( $r = .554$ ) between the adult spring chinook salmon count at Bonneville from 1964 to 1977 and annual troll landings in the Canadian chinook salmon fishery from 1963 to 1976. The year associated with each data point refers to the year of landing.

year returns, a new return per spawner index was generated for the return of only four-year-old upriver spring chinook salmon from each brood year. In this way, brood year effects were separated from the influence of the troll fishery and the effect of fishing could be incorporated in a multiple regression study. The return per spawner index used in the preliminary correlation analyses could not be correlated against the fishing data since the progeny from one brood year contribute to several years in the troll fishery.

The data considered in the revised correlation analyses included the revised return per spawner index, annual landings and annual effort for the Canadian troll fishery, and the environmental variables considered in the preliminary analyses. Since the fishery data was only available from 1963; only upriver brood years from 1960 to 1972 were considered in this analysis. Since 1963, annual landings in the Canadian fishery have increased and effort has fluctuated (Fig. 32). The decrease in effort noted in 1972 is most likely related to the initiation of a limited entry fishery. The mean catch per unit effort was less than 31 kg per day from 1963 to 1970 and has been greater than 44 kg per day since 1971 (Fig. 32). In the correlation analysis between Canadian troll landings and the four-year-old return per spawner index, it is assumed that the fishing effort is evenly distributed over all age classes and both races. A negative relationship was determined

Figure 32. Annual landings (—●—), effort, and catch per unit effort in the Canadian chinook salmon troll fishery and adult spring chinook salmon count (—◄—) over Bonneville Dam from 1963 to 1977.

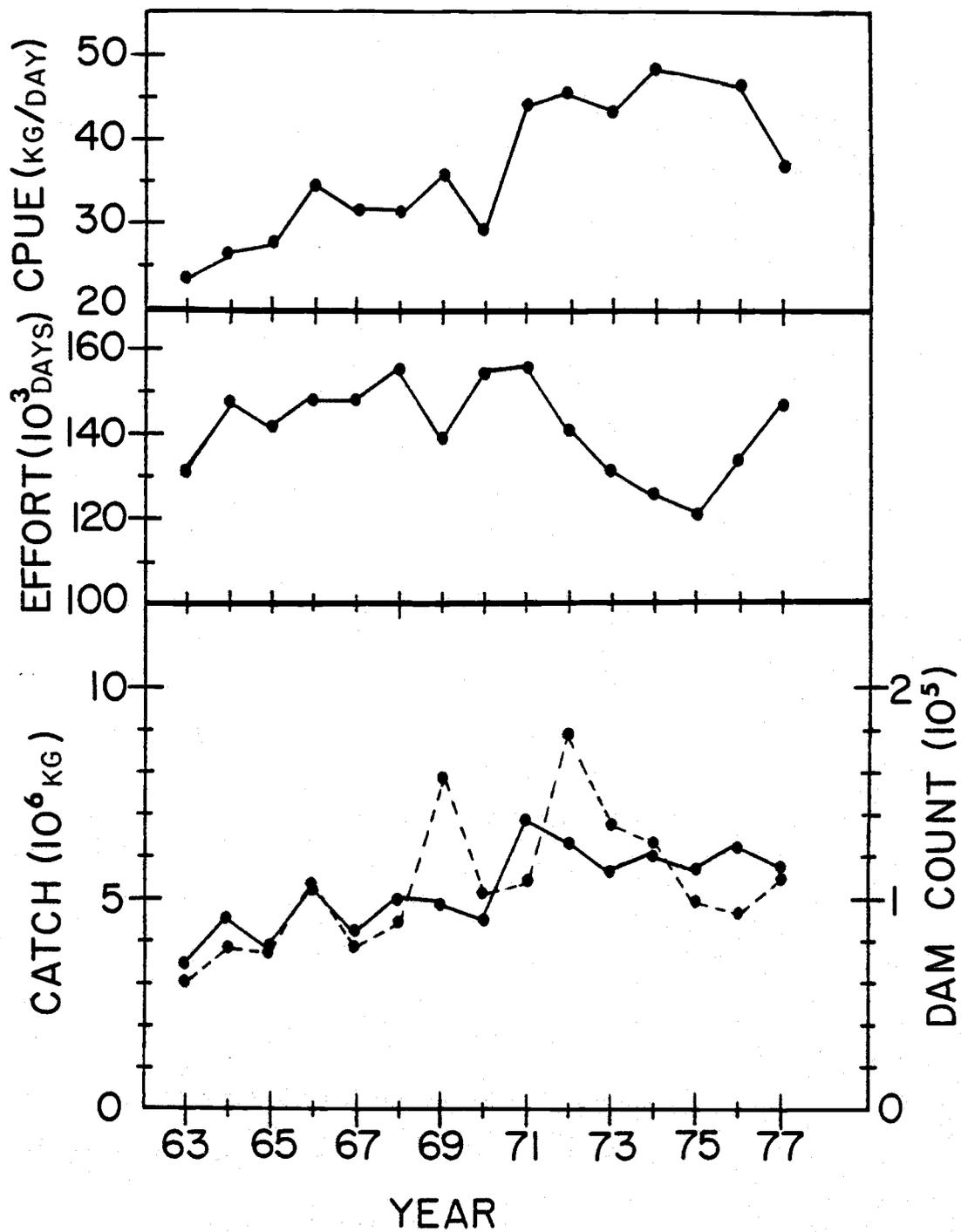


Figure 32.

between the spawners and the four-year-old return per spawner index (Fig. 33). The Ricker reproduction curve generated from these data (Fig. 34) has a replacement abundance of 97,980 fish and a maximum progeny abundance when the number of parent spawners is 62,145 fish.

No significant correlations were noted between the four-year-old return per spawner index and freshwater environmental variables (Table 8). The survival rate was negatively related to both flow and temperature recorded at Bonneville Dam and positively correlated with turbidity measured at this site. Columbia River discharge measured in June and July was positively correlated with the survival rate and August through October discharge was negatively related to this rate. A significant ( $\alpha \leq .05$ ) relationship was noted between the June-July upwelling index for  $48^{\circ}\text{N}$   $125^{\circ}\text{W}$  and the four-year-old return per spawner index. Canadian effort was significantly ( $\alpha \leq .01$ ) and positively related to the index. The relationship between the survival rate for four-year-old fish and Canadian landings was negative.

Cross correlations were calculated (Tables 4, 5, and 8) among environmental variables to insure that the environmental variables included in the regression analyses were independent. At Bonneville Dam, flow was negatively correlated ( $\alpha \leq .01$ ) with temperature and turbidity and positively correlated ( $\alpha \leq .05$ ) with August discharge (Table 4); temperature at this site was positively correlated ( $\alpha \leq .01$ )

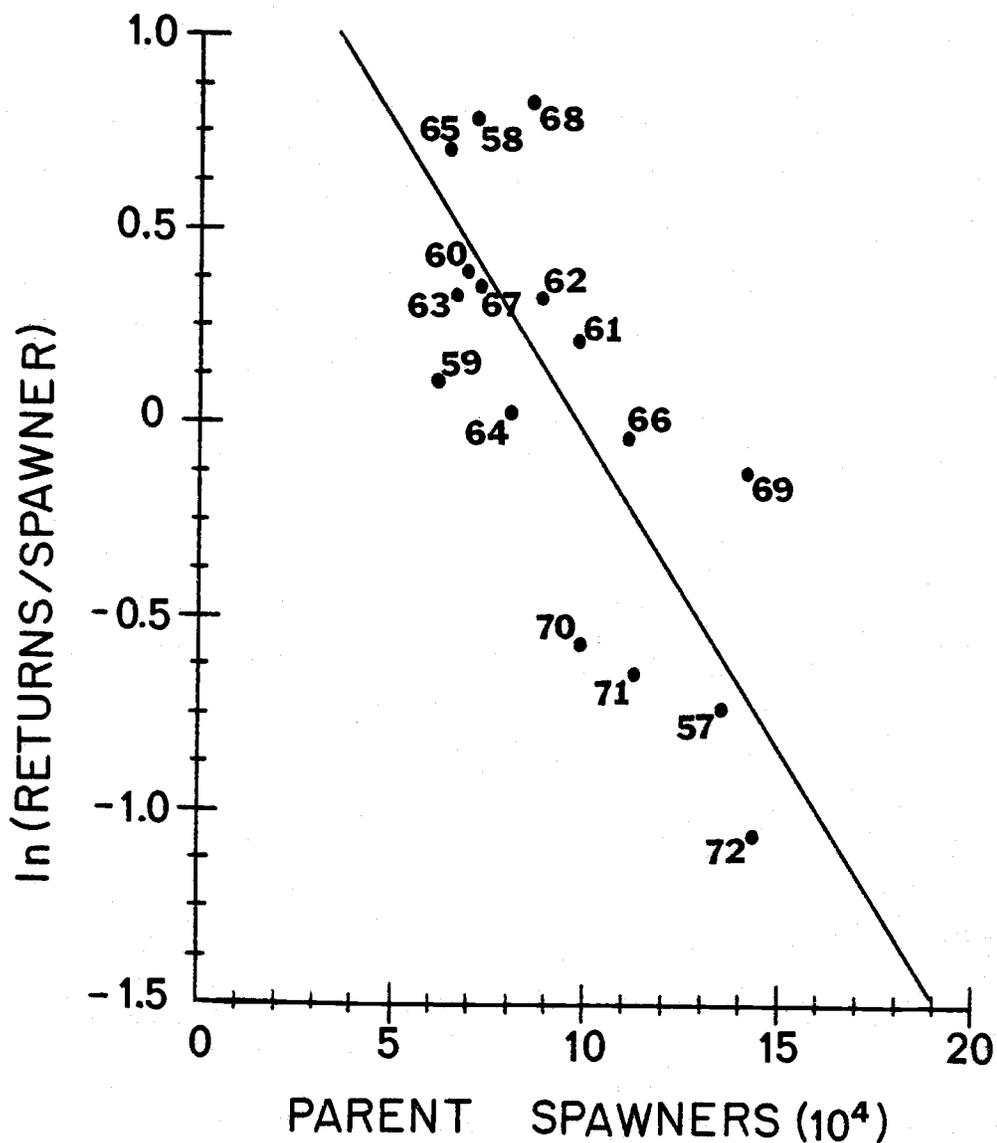


Figure 33. The linear regression ( $r = -.765$ ) between the upriver four-year old return per spawner index from 1957 to 1972 and the parent spawners. The solid line represents the regression line. The year associated with each data point refers to the brood year.

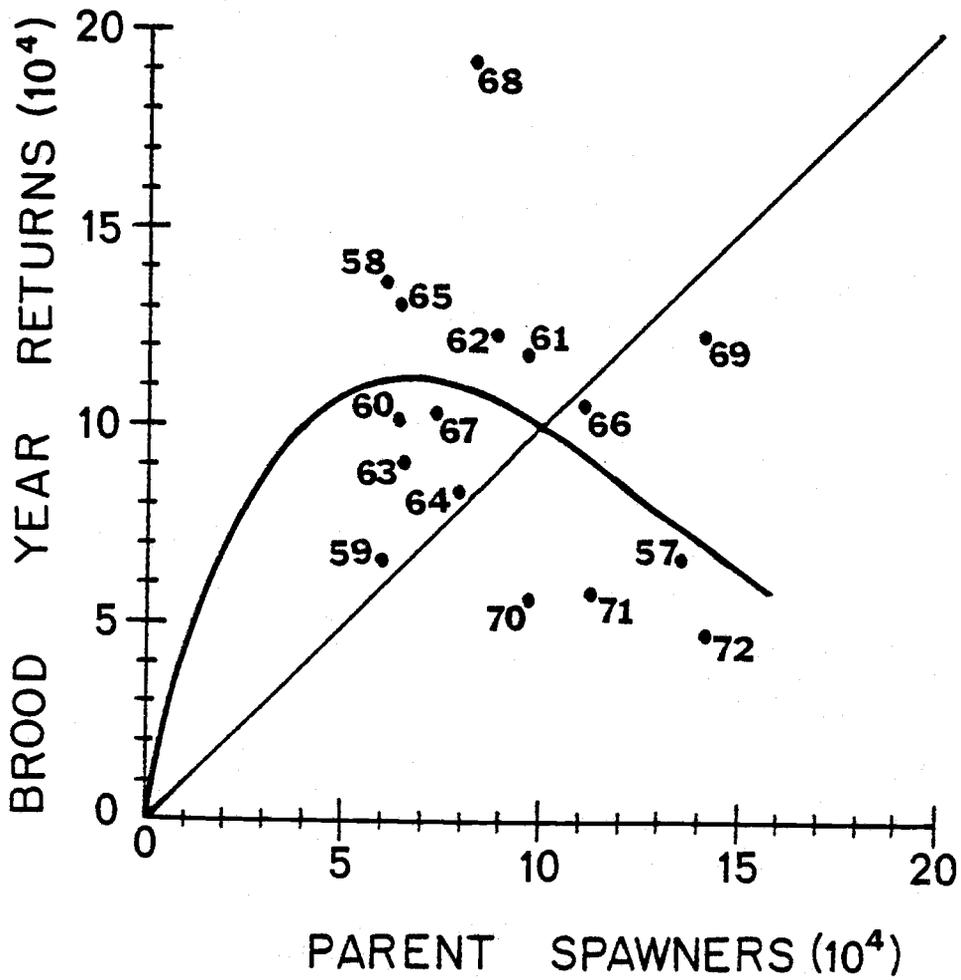


Figure 34. The Ricker reproduction curve for the upriver four-year old returns and the parent spawners from 1957 to 1972. The year associated with each data point represents the brood year. The straight line represents the one-to-one replacement line.

Table 8. Correlation coefficients calculated for selected factors influencing the four-year-old brood year returns of upriver fish. Environmental variables are measured from 1962 to 1974. Canadian catch and effort in the chinook troll fishery are measured from 1963 to 1975. The  $\ln(R/S)$ , S, and R are measured from 1960 to 1972.

Table 8.

	Bonneville													
	S	RF	April-May mean				Columbia River Discharge				June-July upwelling	Canadian Troll Catch	Troll Effort	
In (RF/S)	**	**	Flow	Δ Flow	Temp.	Turb.	June	July	August	Sept.	Oct.	*	*	*
	-.765	.841	-.207	-.381	-.092	.169	.058	.038	-.387	-.543	-.004	.567	-.288	.847
Parent Spawners, S	1.0	-.334	.166	.384	-.065	-.107	-.005	-.011	.264	.570	.232	-.612	.475	-.620
Returning four-year-old offspring, RF		1.0	-.227	-.319	-.194	.230	.037	-.044	-.400	-.302	.151	.289	.076	**
Bonneville April-May Flow			1.0	**	**	**	.486	.379	.530	.299	.064	.016	.110	-.048
Bonneville April-May Transformed Flow (Δ Flow)				1.0	-.406	-.681	.162	.104	.275	.436	.246	-.021	.347	-.127
Bonneville April-May Temperature					1.0	**	**	-.547	-.674	-.445	-.211	.081	-.108	-.043
Bonneville April-May Turbidity						1.0	*	-.476	-.584	-.242	-.027	-.046	.123	.071
June Discharge							1.0	**	**	.334	.161	.084	-.120	.054
July Discharge								1.0	**	.223	.160	.183	-.257	.091
August Discharge									1.0	.542	.108	-.254	-.036	-.445
September Discharge										1.0	.538	-.213	.537	-.408
October Discharge											1.0	.164	.141	-.086
June-July upwelling												1.0	-.158	.644
Canadian Troll Catch													1.0	-.050

\*Significant at 5% level

\*\*Significant at 1% level

with turbidity and negatively correlated with June ( $\alpha \leq .05$ ), July ( $\alpha \leq .05$ ), and August ( $\alpha \leq .01$ ) discharge (Table 4). Turbidities recorded at Bonneville Dam were negatively correlated ( $\alpha \leq .05$ ) with both June and August discharge (Table 4). July discharge was positively correlated ( $\alpha \leq .01$ ) with both June and August discharge and August discharge was positively correlated ( $\alpha \leq .05$ ) with June and September discharge. September discharge also was positively correlated ( $\alpha \leq .01$ ) with October discharge. Since flow at Bonneville Dam was correlated with nearly all freshwater environmental variables, only this factor was included in the regression analyses about these data.

#### Multiple Regression Analyses

Three multiple regression models were generated from the results of the correlation analyses. The overall objective of the multiple regression analyses was to determine if density independent factors acting in concert could improve the linear relationship between indices of progeny abundance and spawner abundance. In each regression model, a Ricker return per spawner index was used as the measure of progeny abundance for the dependent variable. The total progeny return per spawner for both the upriver and the Lemhi River fish constituted dependent variables for models not considering the effect of

the troll fishery. The return of four-year-old progeny per spawner for the upriver fish constituted the dependent variable in a model which included the Canadian troll fishing effort as an independent variable.

Initially, a regression model was generated using the total progeny return per spawner for the upriver fish as the dependent variable (Table 9). The independent variables included in the full model were parent spawners, mean April-May flow recorded at Bonneville Dam, June-July upwelling at 48°N 125°W, and Columbia River discharge measured in June and September. The return per spawner index,  $Y$ , was best described by parent spawners ( $X_1$ ), the upwelling index ( $X_2$ ), and the September discharge ( $X_3$ ):

$$Y = 2.25 - .135 \times 10^{-4} X_1 + .528 \times 10^{-2} X_2 - .468 \times 10^{-2} X_3$$

This best model was chosen based on the highly significant ( $\alpha \leq .01$ ) F-statistic and the lack of a large increase in  $R^2$  with the inclusion of additional independent variables. The best model accounted for 73.1% of the variability about the dependent variable; however, the parent spawners alone accounted for nearly 71% of this variability. In the stepwise procedure used to generate the best model, parent spawners entered as the first variable, upwelling as the second variable, and September discharge as the third variable.

Table 9. The full model from the forward stepwise regression analysis using the upriver return per spawner index as the dependent variable, Y. Environmental variables are lagged to reflect environmental conditions during the outmigration of the brood year.

Entering Variable	Time Period	F-Statistic	R <sup>2</sup>	Regression Model
X <sub>1</sub> : Parent spawners	1957-1972	33.72**	.707	$Y = 2.16 - .172 \times 10^{-4} X_1$
X <sub>2</sub> : Mean June-July upwelling index at 48°N 125°W	1959-1974	16.62**	.718	$Y = 1.90 - .161 \times 10^{-4} X_1 + .418 \times 10^{-2} X_2$
X <sub>3</sub> : September Columbia River discharge	1959-1974	10.85**	.731	$Y = 2.25 - .135 \times 10^{-4} X_1 + .528 \times 10^{-2} X_2 - .468 \times 10^{-2} X_3$
X <sub>4</sub> : June Columbia River discharge	1959-1974	7.48**	.731	$Y = 2.22 - .132 \times 10^{-4} X_1 + .545 \times 10^{-2} X_2 - .514 \times 10^{-2} X_3 + .119 \times 10^{-3} X_4$
X <sub>5</sub> : Mean April-May flow at Bonneville Dam	1959-1974	5.45*	.732	$Y = 2.23 - .131 \times 10^{-4} X_1 + .553 \times 10^{-2} X_2 - .514 \times 10^{-2} X_3 + .155 \times 10^{-3} X_4 - .143 \times 10^{-6} X_5$

\*Significant at 5% level

\*\*Significant at 1% level

Six independent variables were considered in the multiple regression analysis using the Lemhi River return per spawner index as the dependent variable,  $Y$  (Table 10). The variables included in the full model were parent spawners, the parabolic transformation of the mean April-May flow at Ice Harbor Dam, the mean June-July upwelling index at  $48^{\circ}\text{N } 125^{\circ}\text{W}$ , September Columbia River discharge, and mean April-May turbidity and temperature recorded at Ice Harbor Dam. The high correlation between the return per spawner index and upwelling (Table 5) favored the introduction of this independent variable in the first step of the analysis. Since the objective of this analysis was to isolate those independent variables contributing to the variability about the  $\ln(R/S)$ -spawner relationship, parent spawners were "forced" in as the first independent variable entering the model.

The choice of a best model for the Lemhi River data was difficult. Due to the short time-series for these data, few significant correlations existed between selected pairs of independent variables (Table 5). However, the relationships between pairs of independent variables may contribute to the unexpected increase in the value of the  $F$ -statistic in the stepwise regression procedure (Table 10). Also, the short time series for these data prevented the inclusion of more than three independent variables in the best regression model. Based on these restrictions, the dependent variable was best described by

Table 10. The results of forward stepwise regression analysis using the Lemhi River return per spawner index as the dependent variable, Y. Environmental variables are lagged to reflect environmental conditions during the outmigration of the brood year.

Entering Variable	Time Period	F-Statistic	R <sup>2</sup>	Regression Model
X <sub>1</sub> : Parent spawners	1964-1971	1. 62	. 212	$Y = .782 - .277 \times 10^{-4} X_1$
X <sub>2</sub> : Parabolic transformation of mean April-May flow at Ice Harbor Dam	1966-1973	13. 13*	. 840	$Y = .733 - 5.38 \times 10^{-4} X_1 - 2.64 \times 10^{-2} X_2$
X <sub>3</sub> : Mean June-July upwelling index at 48°N 125°W	1966-1973	23. 96*	. 947	$Y = .406 - 5.12 \times 10^{-4} X_1 - 2.00 \times 10^{-2} X_2 + 5.40 \times 10^{-3} X_3$
X <sub>4</sub> : September Columbia River discharge	1966-1973	52. 38**	. 986	$Y = .989 - 5.12 \times 10^{-4} X_1 - 2.12 \times 10^{-2} X_2 + 3.94 \times 10^{-3} X_3 - 3.72 \times 10^{-3} X_4$
X <sub>5</sub> : Mean April-May turbidity at Ice Harbor Dam	1966-1973	33. 06*	. 988	$Y = 1.06 - 5.06 \times 10^{-4} X_1 - 2.08 \times 10^{-2} X_2 + 3.91 \times 10^{-3} X_3 - 3.94 \times 10^{-3} X_4 - 3.57 \times 10^{-2} X_5$
X <sub>6</sub> : Mean April-May temperature at Ice Harbor Dam	1966-1973	14. 43	. 989	$Y = 2.47 - 5.04 \times 10^{-4} X_1 - 1.87 \times 10^{-2} X_2 + 4.51 \times 10^{-3} X_3 - 4.21 \times 10^{-3} X_4 - 1.06 \times 10^{-2} X_5 - 2.85 \times 10^{-2} X_6$

\*Significant at 5% level

\*\*Significant at 1% level

parent spawners ( $X_1$ ), flow ( $X_2$ ), and upwelling ( $X_3$ ):

$$Y = .406 - 5.12 \times 10^{-4} X_1 - 2.00 \times 10^{-2} X_2 + 5.40 \times 10^{-3} X_3$$

This best model accounted for 94.7% of the total variability about the dependent variable.

To consider the interactive effects of the Canadian troll fishery on upriver returns, a regression model was generated using the return of four-year-old fish per spawner for upriver salmon as the dependent variable (Table 11). The return per spawner of four-year-old fish to the Columbia River was best described by the abundance of parent spawners ( $X_1$ ), annual effort in the Canadian chinook troll fishery ( $X_2$ ), and the parabolically transformed Bonneville flow variable ( $X_3$ ):

$$Y = -3.65 - 6.26 \times 10^{-6} X_1 + .0310 X_2 - 1.31 \times 10^{-10} X_3$$

Additional independent variables considered in the full model were June-July upwelling at 48°N 125°W and August mean Columbia River discharge. Due to the high correlation between effort and the return per spawner index, effort should have entered the model in the first step of the analysis. However, the objective of the analysis required that parent spawners be "forced" in as the first independent variable entering the model. The best model explained greater than 84% of the variability about the dependent variable. Parent spawners alone

Table 11. The results of forward stepwise regression analysis using the upriver return of four-year-old fish per spawning parent as the dependent variable, Y. Environmental variables are lagged two years to reflect environmental conditions during the outmigration of the brood year. Canadian effort is lagged three years to reflect the effect of the troll fishery one year prior to the return of spawners. The parent spawners were forced in as the first independent variable.

Entering Variable	Time Period	F-Statistic	R <sup>2</sup>	Regression Model
X <sub>1</sub> : Parent spawners	1960-1972	15.56**	.586	$Y = 1.58 - 1.61 \times 10^{-5} X_1$
X <sub>2</sub> : Canadian effort	1963-1975	21.57**	.812	$Y = -3.33 - 8.20 \times 10^{-6} X_1 + 2.94 \times 10^{-2} X_2$
X <sub>3</sub> : Parabolic transformation of mean April-May flow at Bonneville Dam	1962-1974	15.82**	.841	$Y = -3.65 - 6.26 \times 10^{-6} X_1 + 3.10 \times 10^{-2} X_2 - 1.31 \times 10^{-10} X_3$
X <sub>4</sub> : Mean June-July upwelling index at 48°N 125°W	1962-1974	10.71**	.843	$Y = -3.70 - 6.86 \times 10^{-6} X_1 + 3.22 \times 10^{-2} X_2 - 1.23 \times 10^{-10} X_3 - 1.97 \times 10^{-3} X_4$
X <sub>5</sub> : August Columbia River discharge	1962-1974	7.55**	.844	$Y = -4.00 - 6.73 \times 10^{-6} X_1 + 3.31 \times 10^{-2} X_2 - 1.29 \times 10^{-10} X_3 - 1.93 \times 10^{-3} X_4 + 9.60 \times 10^{-4} X_5$

\*\*Significant at 1% level

explained nearly 60% of this variability.

Of the three regression models generated in this study, the model using the return of four-year-old fish per spawner for upriver salmon as the dependent variable (Table 11) was most useful. This model explained a greater proportion of the variability about the dependent variable than the full upriver model that did not consider fishing effects (Table 9). In addition, the long time series in the upriver model made it more reliable than the model generated from the Lemhi River data (Table 10). To eliminate any temporal effects that might contribute to the results of this regression analysis, an analysis of the residuals was performed. Since the residuals from the best model using the upriver four-year-old survival rate as the dependent variable appeared randomly distributed (Fig. 35), temporal effects did not confound the results of the analyses.

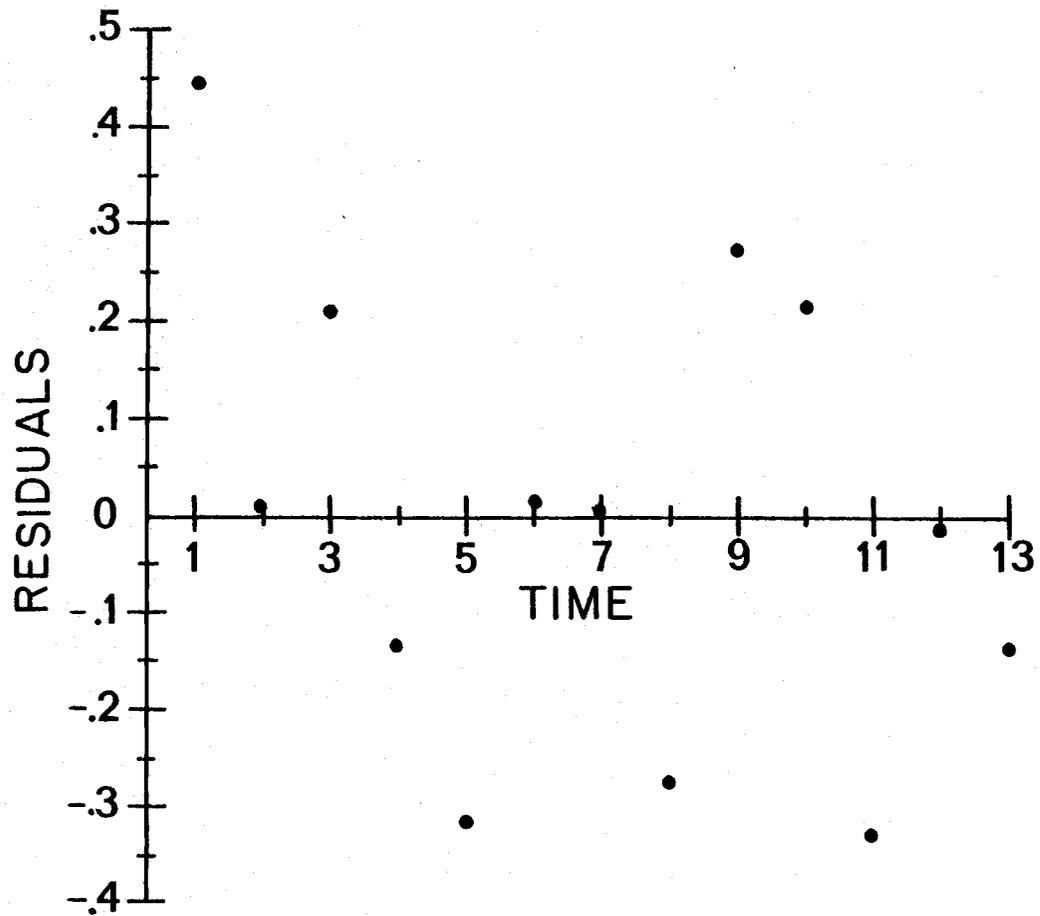


Figure 35. The residuals from the best model using the four-year old survival rate as the dependent variable plotted against time.

## DISCUSSION

### Statistical Analyses

The impact of the density independent factors considered herein on the fluctuations in upriver and Lemhi River spring chinook salmon abundance is not clear. Significant ( $\alpha \leq .05$ ) correlations were noted between the return per spawner indices and the flow at Bonneville Dam, the coastal upwelling index, and effort in the Canadian troll fishery. Since the upriver multiple regression models accounted for only 73% (Table 9) and 84% (Table 11) of the total variability about the dependent variable, the influence of unmeasured factors, such as hatchery releases, on the survival rate of the upriver spring chinook salmon could also influence these relationships.

Since the mid-1950's, the number of hatcheries releasing salmon into the Columbia River watershed has increased (Wahle et al., 1975). Although the emphasis of this fish culture effort has been on fall chinook salmon and coho salmon, several facilities have been constructed for the rearing of upriver spring chinook salmon (Appendix II). The major production facilities for upriver spring chinook salmon are in the Snake River drainage; in addition, the majority of these hatchery releases have occurred since the mid-1960's.

The density-dependent relationship between parent spawners and

offspring described by the Ricker reproduction curve is only characteristic of salmonids spawning in a wild stream habitat. Specifically, hatchery production could contribute to the deviations of data points from such a reproduction curve. In this study, the upriver Ricker reproduction curve was calculated from data including fish of both hatchery and wild origins. Since hatchery releases of upriver spring chinook salmon have increased since the mid-1960's, any deviations attributed to hatchery effects should vary with time. In the multiple regression analysis of four-year-old returning fish, the random distribution of residuals over time (Fig. 35) suggested that the temporal effects associated with hatchery compensation of upriver spring chinook salmon are negligible.

Although long-term effects of hatcheries on the upriver reproduction curve appear negligible, short-term effects may exist. Specifically, if a non-native egg source is used in the hatchery, the observed spawner escapement underestimates the actual number of spawners. That is, the number of parent spawners,  $S$ , actually counted is less than the total number of spawners available due to the importation of non-native fish (or eyed eggs) to the hatchery. Under these conditions, an unexpectedly high return per spawner rate would be noted. This unusually high rate of return would only be noted for one brood year unless importation of adult spawners from

non-native streams continued. The very high return per spawner noted for upriver fish from the 1968 brood year (Fig. 6) may reflect the initial impact of the Snake River hatchery production.

Environmental conditions in tributaries prior to the outmigration of a brood year also may significantly influence the run-strength of native spring chinook salmon. The potential influence of the freshwater environment on early juvenile survival may be related to factors such as flow or temperature. Certain Idaho streams are characterized by reduced carrying capacities during low flow years (Sekulich and Bjornn, 1977). Also selected laboratory studies (Bishai, 1960; Olson and Foster, 1955) have demonstrated that high water temperatures contribute to high egg and larval mortality among salmonid species. Such factors, aside from density dependent events influencing the shape of the Ricker reproduction curve, were not considered in the analysis due to the lack of adequate escapement data for selected streams. If freshwater conditions prior to outmigration were critical factors determining the success of a brood year, consistent contributions would be noted in the brood year returns for each of the three age classes (Figs. 7 and 8). The five brood years (1957, 1958, 1968, 1971, 1972) for the upriver fish which were characterized by specific trends for the relative age class contribution may exemplify the importance of freshwater environmental conditions prior to outmigration.

Additional data must be collected at selected spawning streams to test the hypothesis that environmental conditions prior to outmigration strongly influence year class survival of upriver spring chinook salmon.

The results from this study suggest that freshwater environmental conditions during brood year outmigration may be most important during extreme conditions. The parabolic distribution of the flow data suggested particularly by the Lemhi River analyses (Fig. 22) exemplifies this hypothesis. Specifically, the Lemhi River data illustrate that low brood-year returns were associated with years of very high (1969 brood year) and very low (1971 brood year) flows during the outmigration of the brood. Ebel et al. (1975) strongly suggested that nitrogen gas supersaturation associated with high flow years, contributed to juvenile mortalities attributed to gas bubble disease. In recent years, the U. S. Army Corps of Engineers has recognized the need for modifications to dams in the form of "flip-lips" designed to reduce the levels of supersaturation in the Columbia River watershed. As such devices are installed and become operational, the parabolic relationship described between downstream migrants and flow (Figs. 18 and 22) should become asymptotic. The low contribution from the 1971 brood year for both upriver (Fig. 6) and Lemhi River (Fig. 5) fish may reflect the influence of unfavorable environmental conditions prevalent in the

entire Columbia River watershed during the 1972-73 winter season. Raymond (1974) indicated that the low run-off in 1973 resulted in low flows over dams contributing to the high mortality of the 1971 brood year progeny which were forced to migrate downstream through the power turbines. The low returns from the 1972 brood year (Fig. 6) may be attributed to abnormally low survival of eggs and a reduction in available spawning habitat associated with the low flows (Fig. 12) and below average water levels associated with the 1972-73 winter season.

Among the brood years studied, some variability existed in the relative age-class contribution of returning fish. For example, from the 1964 brood year of upriver fish (Fig. 7), below average numbers of fish returning as three- and four-year-old spawners were compensated for by the above average returns of five-year-old fish. The 1961 brood year, conversely, yielded above average returns of three- and four-year-old progeny but below average returns of five-year-old fish. These results may be influenced by mechanisms determining the age at which a spring chinook salmon returns to spawn. If such a mechanism is size-related, environmental conditions in either freshwater or the ocean may control both the individual growth rate and the age at which the fish return to spawn. Thus, the relative contribution of three- and four-year-old returns from the brood year might be poor but the return of five-year-old progeny would be high.

Recent analytical studies have suggested the correlations between coastal upwelling and salmon abundances. The study described herein demonstrated a significant ( $\alpha \leq .05$ ) relationship between the June-July upwelling index at  $48^{\circ}\text{N } 125^{\circ}\text{W}$  and the return of four-year-old fish per spawner (Fig. 36). In addition, Gunsolus (1978) noted a strong ( $r=.628$ ,  $\alpha \leq .01$ ) positive relationship between an April through July upwelling index and a production index for Oregon coho salmon. The upwelling index considered was measured at  $42^{\circ}\text{N } 125^{\circ}\text{W}$  (offshore from Brookings, Oregon) and the production index was a summation of total coho landings in the sport and troll fisheries and total adult escapement to both hatcheries and wild spawning grounds. He found that years of strong adult production were characterized by years of strong April through July upwelling during the outmigration of the juvenile fish. Since Gunsolus did not consider a production rate (i. e. progeny produced per spawner), his relationships are confounded by factors such as increased hatchery releases.

Relationships between salmon abundances and upwelling indices may reflect the importance of a good food supply to juvenile salmon first entering the ocean. Craddock et al. (1976) determined that salmonids feed on zooplankton during their first months at sea and Peterson and Miller (1975) found a positive relationship between zooplankton abundances and upwelling indices. Since Peterson and

Figure 36. The relationship ( $r = .567$ ) between the four-year old return per spawner rate from 1957 to 1972 and the mean June-July upwelling index for  $48^{\circ}\text{N } 125^{\circ}\text{W}$  from 1959 to 1974. The year associated with each data point represents the brood year.

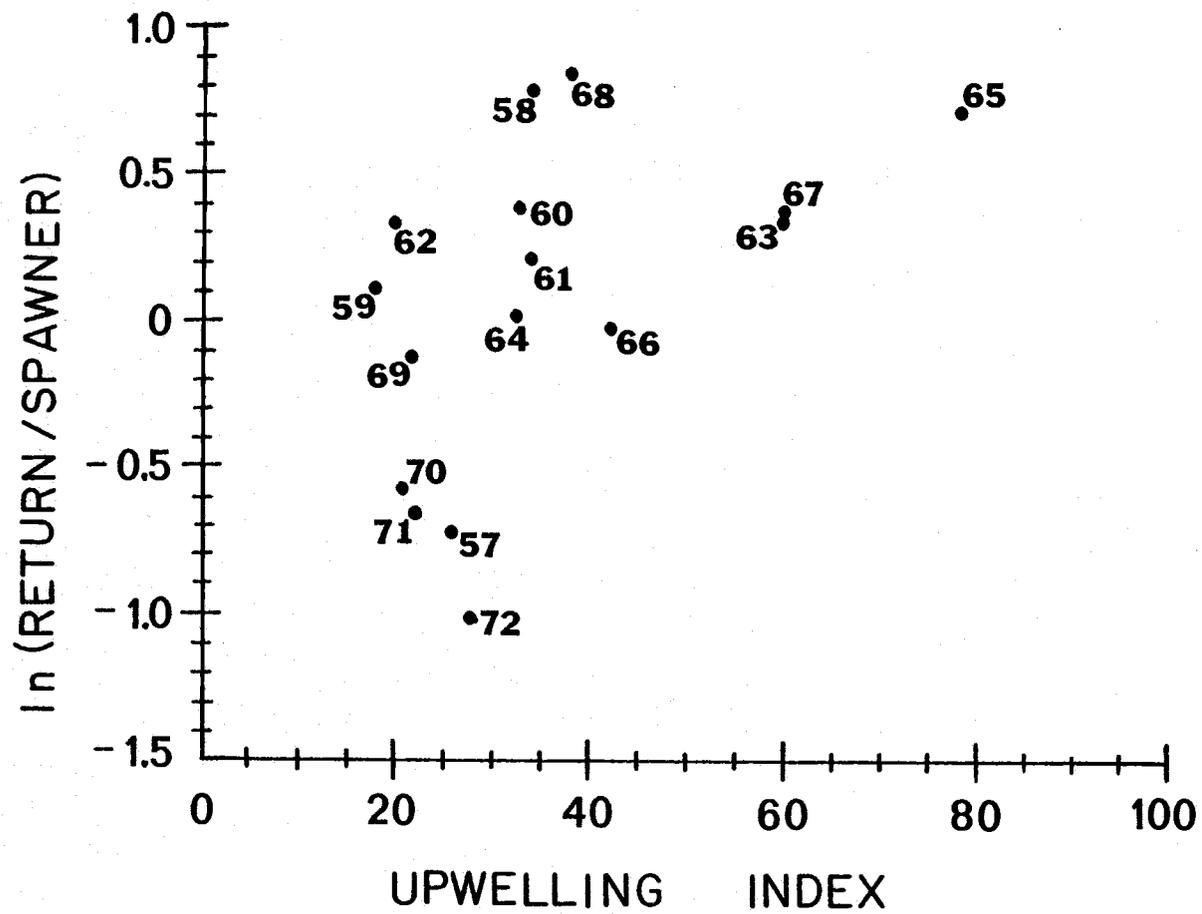


Figure 36.

Miller (1975) considered sizes of zooplankton that may not have been part of the salmon food supply, a direct relationship between upwelling and the presence of a good food supply for juvenile salmon can not be made. Temporal differences (i. e. April-July vs. June-July) were noted in the correlations between upwelling indices and coho and spring chinook salmon abundances. These differences may be related to the timing of the outmigration characteristic of each species. Coho salmon, predominantly found in the lower Columbia River and in coastal streams, migrate shorter distances during outmigration than upriver spring chinook salmon. Thus, coastal coho salmon may enter the salt water significantly earlier than upriver spring chinook salmon.

The correlations with the upwelling indices may also be related to other ocean events, such as current patterns. Both upwelling indices and currents are influenced by wind direction and speed. The positive relationships between salmon abundances and upwelling indices may suggest that favorable current patterns influence the survival of the outmigrating juveniles. Currents along the coast of the Pacific Northwest are strongly influenced by local winds (Reid et al., 1958). The predominant current, the California Current, flows southward to about 20°N. A northward flowing current, the Davidson Current, occurs along the California and Oregon coasts during the winter when southwesterly winds prevail. If the survival of Pacific salmon is

dependent upon the proper ocean orientation of juvenile outmigrants, the direction and strength of the California Current system may significantly influence these fish.

Since the early 1970's, the Canadian chinook salmon troll fishery has been characterized by a decreasing effort, associated with the initiation of a limited entry fishery, and an increasing catch per unit effort (Fig. 32). The variability in the mean catch per unit effort seems to center about two different levels. From 1963-1970, the catch per unit effort vasculated about the mean value 66.4 kg/day and from 1971-1977, the catch per unit effort fluctuated about the mean 98.5 kg/day. If the overall survival of hatchery fish is better than that of wild fish, these data may reflect increased hatchery compensation associated with the late 1960's.

The significance of the correlations with both the landings and effort in the Canadian chinook salmon troll fishery are unclear. The relationship between the Bonneville Dam count and total landings indicates that the greater the landings in the troll fishery, the larger the dam count at Bonneville Dam. In addition, the significant ( $\alpha \leq .05$ ) relationship between parent spawners and Canadian troll effort (Table 8) confounded the results of the positive ( $\alpha \leq .01$ ) correlation between the return per spawner index and effort. The positive relationship between the four-year-old survival rate and Canadian effort

suggests that the harder the Canadians fish, the greater the survival of upriver fish! Since a low survival rate would intuitively be anticipated from a high effort due to the removal of fish by the fishery, the significant correlation between these variables may be spurious. In this study, on the other hand, the fishing effort data refers to the total effort expended on all chinook salmon originating from many different river systems. Additional data pertinent to the capture of upriver spring chinook salmon by the Canadian troll fishery is necessary to fully understand any influence this fishery may have on upriver salmon survival. The influence of factors such as economic and social pressures on fishing effort further complicate the interpretation of the effort-survival rate relationship.

#### Conceptual Life History Model

The statistical analyses presented in this study do not adequately describe the types of factors influencing the abundance of upriver spring chinook salmon. Since insufficient data currently exist to isolate factors significantly influencing the abundance of upriver spring chinook salmon, a compartmental model was developed to suggest the types of relationships affecting these fish. This conceptual model was developed using an alternative hypothesis approach. Due to the lack of a strong data base for the upriver spring chinook salmon, the

types of functional relationships describing the life history of these fish is unclear. In the development of the conceptual model, several different hypotheses were incorporated to describe life history events. Thus, verification of the model can serve as a tool for testing the various hypotheses and can suggest those relationships best describing the life history of the modelled organisms. An anticipated outcome of this model construction was to improve the current conceptual understanding of upriver spring chinook salmon life history events.

The strategy used in this model construction relied partially upon guidelines described by Overton (1977). The overall goal of the model was formulated:

To build a realistic model of the life history of a single upriver spring chinook salmon stock spawning in a natural stream that would sufficiently account for factors that influence the abundance of adults returning to the spawning ground.

Since the outcome of the model should only be evaluated within the constraints of the goal, it is important to clearly understand this goal. The term "realistic" is used to signify that the model will rely primarily upon existing data. Since insufficient data have been collected for the upriver spring chinook salmon, the model will be based upon data relevant to several species of Pacific salmon. In addition, verification of the model through simulation, though not considered in this study, should result in reasonable adult returns to the spawning

ground given an adequate data base. An actual simulation run should also reproduce survival and growth rates representative of the modelled fish in a natural situation.

To simplify the initial model construction, the model was restricted to the consideration of a single "stock" of upriver spring chinook salmon. Recent salmonid literature (cf. Ricker, 1972) has dealt extensively with the problem of stock identification. It is not within the scope of this dissertation to deal with this problem. For the purposes of this study, the term "stock" was considered to encompass all fish of one species spawning in a single stream with common growth and survival parameters. Since offspring from natural spawners are influenced by mortality factors during the first year that are not characteristic among hatchery juveniles, the model was restricted to the consideration of a hypothetical stock of naturally spawned fish.

To understand the anticipated outcome of this modelling effort, the specific objectives of the model were outlined:

- 1) to incorporate the types of events influencing the brood year strength of upriver spring chinook salmon into a compartmental model designed to enhance the understanding of these fish;
- 2) to describe the types of functional relationships depicting specific life history events; and
- 3) to propose alternative hypotheses as explanations for the types of events influencing the life history of upriver spring chinook salmon in the absence of concrete data.

Thus, the model will serve as a conceptual tool in suggesting the types of factors influencing the major life history events of the studied species.

Within the defined goal and objectives of the model, the temporal, geographic and conceptual constraints must clearly be understood. The model only considers a hypothetical stock of spring chinook salmon spawning above Bonneville Dam in the Columbia River watershed. The outcomes of this model do not relate necessarily to other species or to other watersheds. Conceptually, the modeller must assume that the events influencing the growth and survival of these fish can be simplified as a series of functional relationships described in subsequent sections. Furthermore, the types of relationships considered are based upon data collected over the past 15 years; the model is not designed to predict future events unrelated to events of the past 15 years. The types of questions the model is designed to address are entirely defined by the goal, objectives, and constraints of the model.

The compartmental model consists of the state variables, the driving variables, and the major processes internal to the state variables (Fig. 37). The state variables, which describe the state of the model components at one time, were defined as AGE(1) juveniles, AGE(2) ocean smolts, AGE(3) ocean fish, AGE(4) ocean fish, SPAWNING adults, JACK salmon spawners, ocean TROLL landings, and

Figure 37. The major components and their interactions as considered in a simulation model of a hypothetical stock of upriver Columbia River spring chinook salmon.

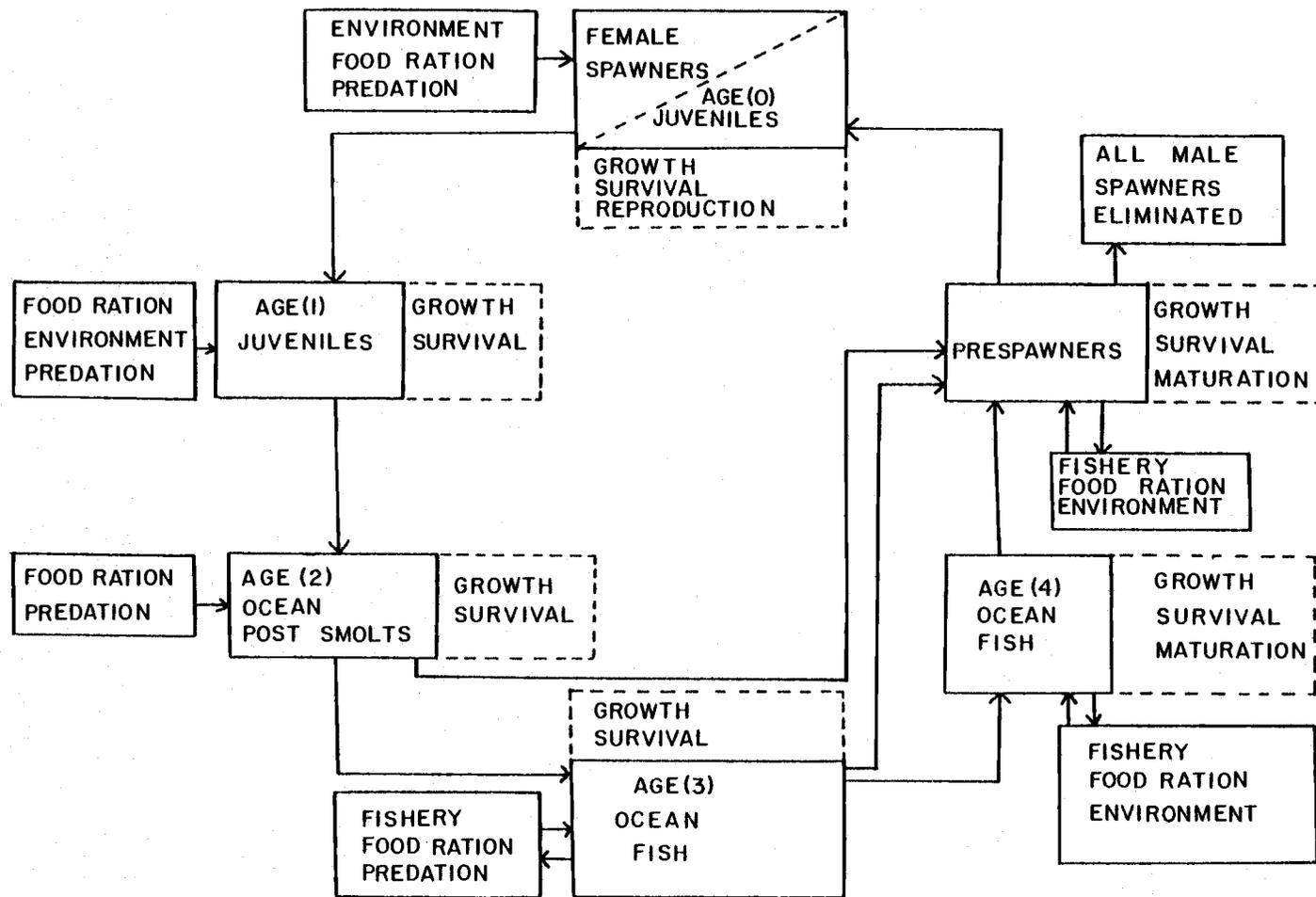


Figure 37.

Columbia River GILL NET landings. The capitalized names depict the computer variables relevant to the model. Both the numbers and the mean size of fish in a state variable are output from the model. Since the model considers the return of spawners older than five years of age as negligible, all ocean fish return as spawners after AGE(4). Internal to the model is a compartment designated as "prespawners." Since spring chinook salmon can return as three-, four-, or five-year-old fish, the prespawner category is used to distinguish immature and maturing fish within age groups. The four major processes, influencing the output from the state variables, were defined as growth, survival, reproduction, and maturation. Driving variables, which determine the rates at which these processes operate, included food ration, environmental events, predation/natural mortality processes, and fishing pressures.

Initially, the numbers and mean sizes of fish internal to most state variables are randomly generated. Fishery landings are only generated from information provided in the model. Due to the number of fish internal to each age group, the model does not track individual fish; however, individual body sizes can readily be generated from the mean and standard deviation describing normal frequency distributions of size at age. The model operates on an annual time increment but finer temporal resolution is achieved within each

compartmental submodel. Updating of the model occurs in the fall of each year when spawning occurs. Functional relationships internal to each compartment describe the influence of the driving variables on the state variable output. Once the model has been initialized, the inputs and outputs to each state variable are generated internally (Table 12). The elements of this "information table" depict the specific variables that must be generated in each annual iteration of the model to move from one compartment to the next. To best comprehend the conceptual aspects of the model, each compartment submodel will be separately described.

#### Spawner Submodel

Update Subroutine. Initially, the spawner submodel (Appendix III-1) calls the UPDATE subroutine. This subroutine, which is also called at the end of the main program in the final iteration, performs several major functions (Appendix III-2). On the first annual iteration, the numbers and mean weights are generated for each age class and assigned to designated variable names (Tables 13-14). The variables generated represent the state of the model in the fall of the year just prior to spawning. It is assumed that the numbers in each age group are normally distributed with respect to size in a natural population (Table 13). Mean weights at age are randomly selected from

Table 12. An information table specifying the types of information necessary to move from one system variable to another system variable in the model. An "O" indicates that the specified pair of variables are not connected within the model. An "X" indicates that the specified variables are the same.

	AGE (1)	AGE (2)	AGE (3)	AGE (4)	TO ADULT SPAWNERS	JACK SALMON	OCEAN TROLL FLEET	GILLNET FLEET	
AGE (1)	X	Natural mortality Mean weight per individual S. D. of mean weight	O	O	O	O	O	O	
AGE (2)	O	X	Natural mortality Mean weight per individual S. D. of mean weight	O	O	Number of male fish returning to spawn Size at return	O	O	
FROM	AGE (3)	O	O	X	Natural mortality Mean weight per individual S. D. of mean weight	Number of fish returning to spawn Size at return Sex ratio at return	O	Number of fish landed Size at capture	O
	AGE (4)	O	O	O	X	Number of fish returning to spawn Size at return Sex ratio at return	O	Number of fish landed Size at capture	O
	ADULT SPAWNERS	Fecundity Number of females Natural mortality Spawner body size Mean weight per individual offspring	O	O	O	X	O	O	Number of fish landed Size at capture
JACK SALMON	O	O	O	O	O	X	O	Number of fish landed Size at capture	
OCEAN TROLL FLEET	O	O	Number of fish removed by fishery Size at capture	Number of fish removed by fishery Size at capture	O	O	X	O	
GILLNET FLEET	O	O	O	O	Number of fish removed by fishery Size at capture	Number of fish removed by fishery Size at capture	O	X	

Table 13. A description of selected variable names and the normally distributed populations used in the initial generation of the variables in the simulation model.

Variable Name	Variable Description	Mean	Variance
SPAWN	The total number of fish available for spawning	2, 000	700
AGE (4)	The total number of four-year-old fish in the ocean	2, 000	500
AGE (3)	The total number of three-year-old fish in the ocean	10, 000	5, 000
AGE (2)	The total number of two-year-old fish in the ocean	800, 000	400, 000

Table 14. A description of size-related variable names and the lower and upper bounds of the uniformly distributed populations used in the initial generation of the variables in the simulation model.

Variable Name	Variable Description	Lower Bound	Upper Bound
SIZE(4)	The mean weight (kg) of fish in AGE(4)	4.8	8.8
SIZE(3)	The mean weight (kg) of fish in AGE(3)	2.0	4.0
SIZE(2)	The mean weight (kg) of fish in AGE(2)	0.4	0.6
SIZE(1)	The mean weight (kg) of fish in AGE(1)	0.008	0.012
SPSIZE(5)	The mean weight (kg) of five-year-old spawners	9.6	17.6
SPSIZE(4)	The mean weight (kg) of four-year-old spawners	4.8	8.8
SPSIZE(3)	The mean weight (kg) of three-year-old spawners	2.0	4.0
SPSIZE(2)	Dummy Variable	0.0	0.0
SPSIZE(1)	Dummy Variable	0.0	0.0

uniformly distributed populations (Table 14). Initially, the variances associated with each mean weight variable are assigned specific values in the UPDATE subroutine (Table 15). For immature individuals, the number in each age class is stored in the array AGE(I). To maintain consistency in the model presentation, the subscript "I" always designates one of five age classes. The mean weights at age of immature fish are stored in the array SIZE(I) and the variance associated with each mean weight is stored in the array VSIZE(I). For mature individuals, both adult and jack salmon, the total number of fish is stored in the variable SPAWN and the mean weights and variances associated with these fish are stored in the arrays SPSIZE(I) and VSPSIZE(I) respectively. Since no spring chinook salmon spawn as one- or two-year-old fish, SPSIZE(1), SPSIZE(2), VSPSIZE(1), and VSPSIZE(2) are 0.

Data from selected Idaho stream studies (Bjornn, 1978; Sekulich and Bjornn, 1977) constitute the basis for the normally distributed populations chosen to describe the abundance and mean size at age (Tables 13-15). The numbers of adults spawning over ten years were counted at a weir on the Lemhi River in Idaho (Bjornn, 1978). From these data, a normal distribution for SPAWN was generated. The estimates (Bjornn, 1978) of juvenile freshwater fish in the Lemhi River during summer and fall months provided a basis for the distribution

Table 15. A description of variance variable names associated with mean sizes. The initial values represent the values assigned to each variable in the initial iteration of the simulation model.

Variable Name	Variable Description	Initial Value
VSIZE(4)	The variance associated with SIZE(4)	2
VSIZE(3)	The variance associated with SIZE(3)	1
VSIZE(2)	The variance associated with SIZE(2)	0.1
VSIZE(1)	The variance associated with SIZE(1)	0.002
VSPSIZE(5)	The variance associated with SPSIZE(5)	4
VSPSIZE(4)	The variance associated with SPSIZE(4)	2
VSPSIZE(3)	The variance associated with SPSIZE(3)	1
VSPSIZE(2)	Dummy Variable	0
VSPSIZE(1)	Dummy Variable	0

describing AGE(1). No population estimates were available for fish in the ocean; however, ocean mortality estimates suggested in the literature (cf. Ricker, 1976) provided a basis for selecting the designated distributions. Mean weights for spring chinook salmon landed in the Washington troll fishery (Wright et al., 1972) provided estimates of mean sizes for AGE(3), AGE(4), and AGE(5) fish. Only for the purposes of initial variable generation, it was assumed that mean body weights for both immature and mature fish of the same age could be described from a single normally distributed population. Sekulich and Bjornn (1977) surveyed numerous streams in the Snake River drainage and found that one-year-old spring chinook salmon had a mean weight of nine grams in the fall. At the time of hatchery release in the spring, chinook salmon have a mean weight of .05 kg. Based on these data, it seemed reasonable to assume that ocean smolts have a mean weight ranging from 0.40 kg to 0.60 kg in the fall of the first year at sea.

In the initial iteration of the model, the number of mature fish in each age class is determined and stored in the array MATURE(I):

$$\text{MATURE(I)} = \text{SPAWN} * \text{PCT(I)}$$

where PCT(I) is an array designating the percentage of spawners of age I. Based on the return of spring chinook to the Lemhi River over a ten year span (Bjornn, 1978), the values of the PCT array were

assigned as follows:  $PCT(1) = 0$ ,  $PCT(2) = 0$ ,  $PCT(3) = .03$ ,  
 $PCT(4) = .54$ ,  $PCT(5) = .43$ . The mean weight and associated vari-  
 ance of individuals in the MATURE array are stored in the SPSIZE  
 and VSPSIZE arrays respectively.

On subsequent annual iterations, the age class structure is  
 updated to reflect the numbers and mean weights of fish in each age  
 class in the fall of the year. The procedure for updating the numbers  
 of individuals in each age class is:

$$AGE(4) = AGE(3)$$

$$AGE(3) = AGE(2)$$

$$AGE(2) = AGE(1)$$

$$AGE(1) = SPAWN$$

$$SPAWN = \sum_{i=1}^5 MATURE(I)$$

At this time, the mean weight of fish in each age class must also be  
 updated to correspond with the updated age class structure. The pro-  
 cedure for updating the mean size at age is:

$$SIZE(4) = SIZE(3)$$

$$SIZE(3) = SIZE(2)$$

$$SIZE(2) = SIZE(1)$$

$$SIZE(1) = YOUNG$$

The variable YOUNG stores the mean size of fish spawned the previ-  
 ous fall. The sizes of spawning fish, stored in the array SPSIZE are

internally generated and updated in the ocean adult submodels.

Once all updating has been completed, designated variables become available as output. The variables that can be output from each annual iteration are: MATURE(I), JACK(I), AGE(I), SPSIZE(I), SIZE(I), TROLL, GILLNET, TRSIZE, GNSIZE. The annual catch in the troll fishery and the mean size of the catch are stored in the variables TROLL and TRSIZE respectively. The annual landings in the Columbia River gillnet fishery and the mean size of the catch are stored in the variables GILLNET AND GNSIZE. Since these latter four variables are internally calculated, no landings are generated in the initial year of print out from the model.

Spawn Subroutine. The major part of the spawner submodel calculates 1) the fecundity of the spawning females and 2) the number and mean weights of the emerging fry (Appendix III-1). The model assumes that a sufficient number of male spawners are present on the spawning ground to insure maximum fertilization. Based on several years of data, Bjornn (1978) determined that the relative contribution of females to four- and five-year-old spawning adults was 45% and 53% respectively. From these data, the total number of female spawners is calculated. The mean body size associated with only the female spawners reflects the largest individuals among all spawners and is determined from the upper 50 percent of the

normal distribution describing body size for all spawners. Each body size is converted from weight (kg) to fork length (cm).

The maximum egg deposition for each female spawner is determined from the body size of the spawners (Fig. 38). Fecundity, defined as the total number of eggs per female spawner, is considered to increase curvilinearly with spawner body size (Fowler, 1972; Stauffer, 1976; Galbreath and Ridenhour, 1964). Spawning chinook salmon less than 46 cm long are classified as jacks and spring chinook salmon as large as 102 cm long have been recorded in the Washington troll fishery (Wright et al., 1972). Galbreath and Ridenhour (1964) noted a range of 2,000 to 8,000 eggs per female spawner for Columbia River spring chinook salmon.

The successful fertilization and survival of the eggs depends on the density of eggs per unit area. Since the amount of stream bed available for spawning depends partially upon the river level, a linear relationship, based on data presented by Sekulich and Bjornn (1977), was considered between the stream carrying capacity and flow (Fig. 39). If the maximum egg deposition is greater than the stream carrying capacity, the actual egg deposition is set equal to the carrying capacity of the stream. If the stream is below the carrying capacity for eggs, the maximum egg deposition is not adjusted. The range of values used to represent the carrying capacity and the flow was based on data for selected Idaho streams (Sekulich and Bjornn,

Figure 38. The functional relationship between fecundity and the individual body size (fork length) associated with spawning females (based on data from Galbreath and Ridenhour, 1964).

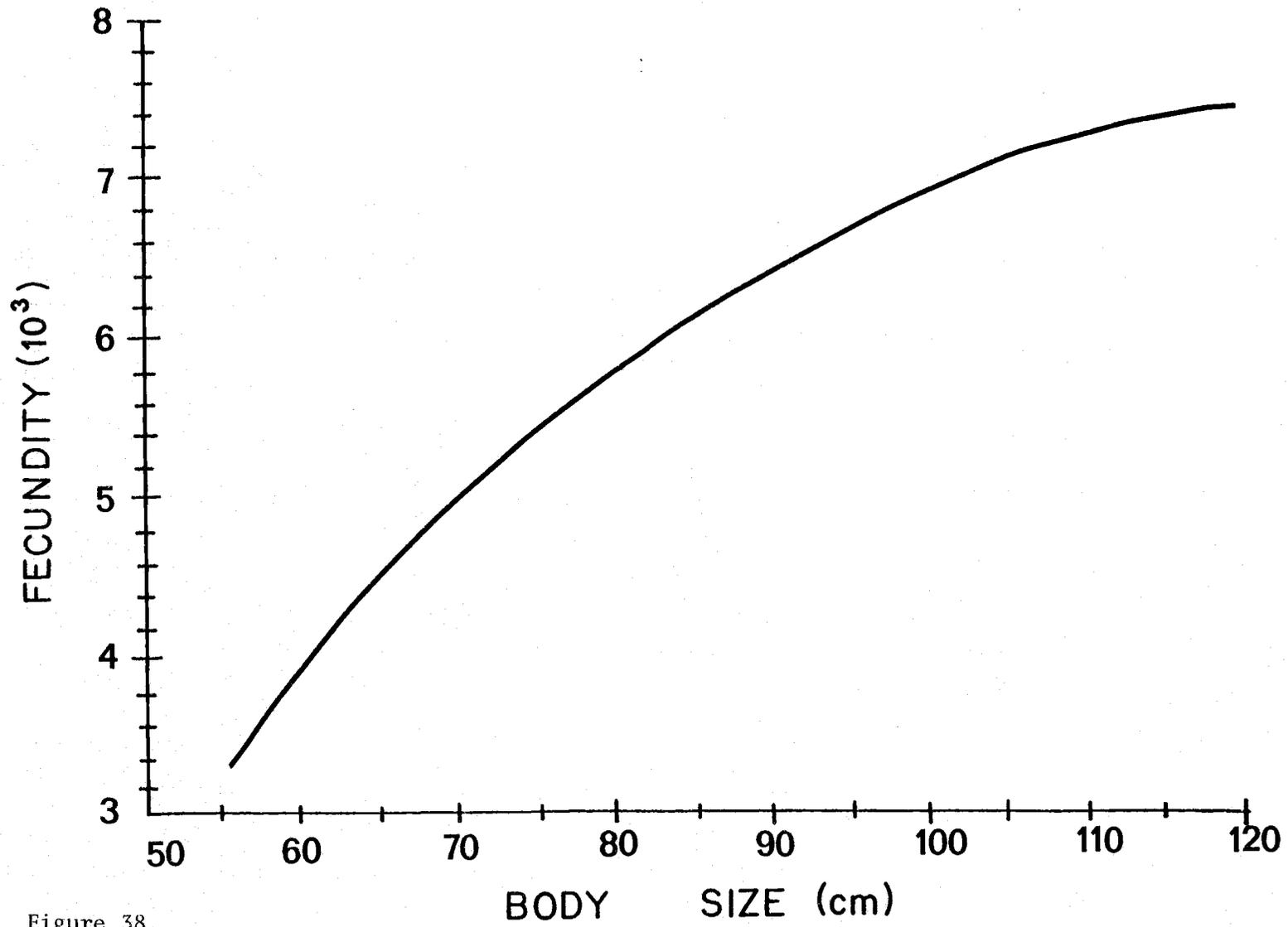


Figure 38.

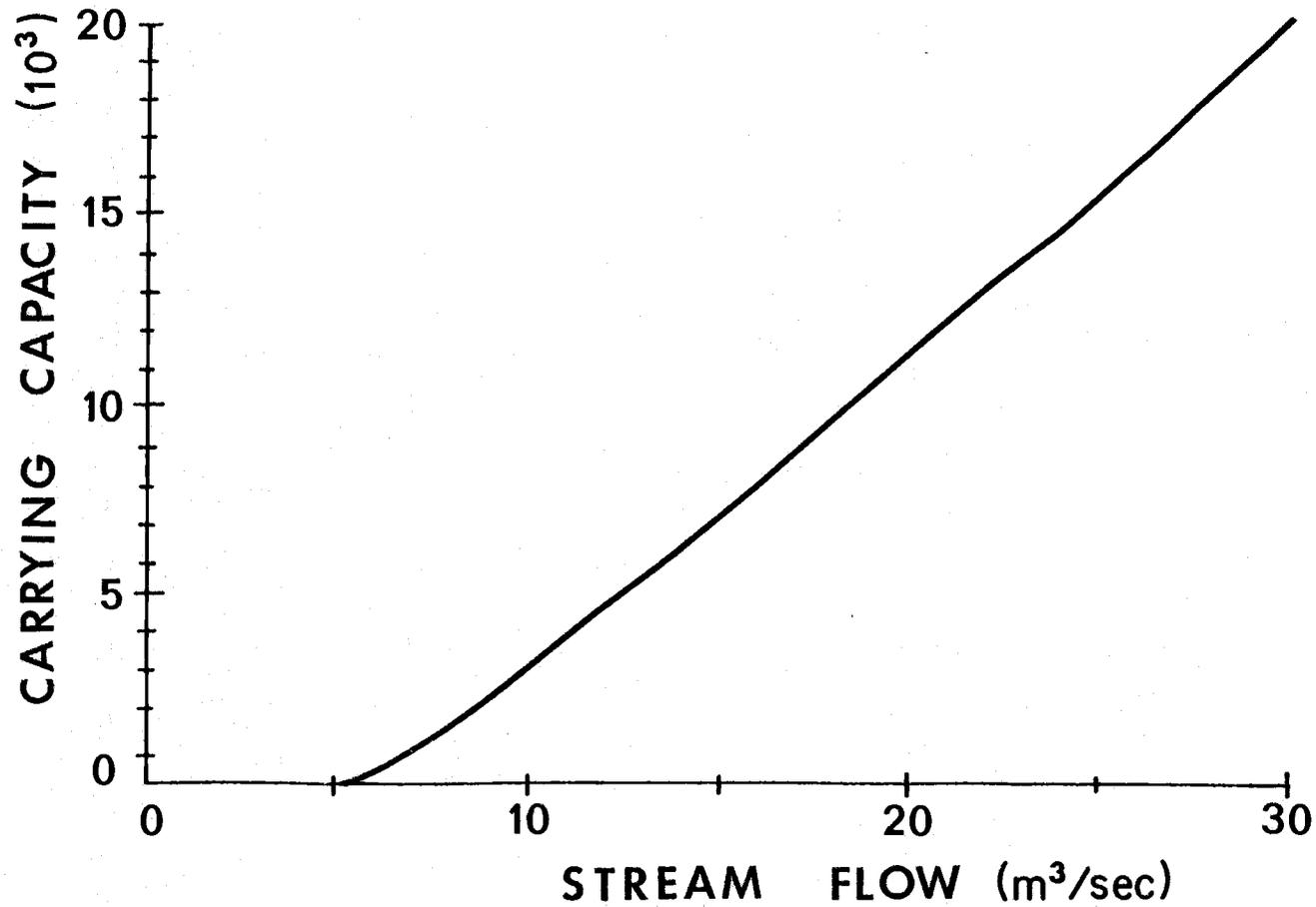


Figure 39. The functional relationship between the carrying capacity of the stream and the flow in the stream at the time of spawning.

1977). The magnitude of the river flow, internally simulated, is greatest in the spring, lowest in the late summer and early fall, and intermediate in the late fall and winter. Initially, the modeller supplies the range (high and low values) of flows pertinent to the native stream under consideration to account for streams of all sizes.

Experimental studies (Bishai, 1960; Olson and Foster, 1955) with various species of Pacific salmon (Oncorhynchus sp.) and trout (Salmo sp.) suggest that water temperatures above 21°C contribute to the mortality of eggs and larval fish. To incorporate this factor in the model, an exponential mortality rate is calculated if the river temperature is greater than 21°C (Fig. 40). The simulation of stream temperatures within the model is based upon seasonal variations in temperatures for the Lemhi River during the months of egg incubation. The range of temperatures considered in the simulation is initially supplied by the modeller to permit consideration of rivers larger than the Lemhi River. Since egg incubation occurs over the fall and winter months, it is anticipated that the temperature-related mortality would only be significant during abnormally warm years.

From the time that eggs are laid until the young fish absorb the yolk sac, commonly referred to as the "button-up" stage, growth of the fish is not considered. It is assumed that a density dependent mortality (Fig. 41) affects the survival of fish to the button up stage

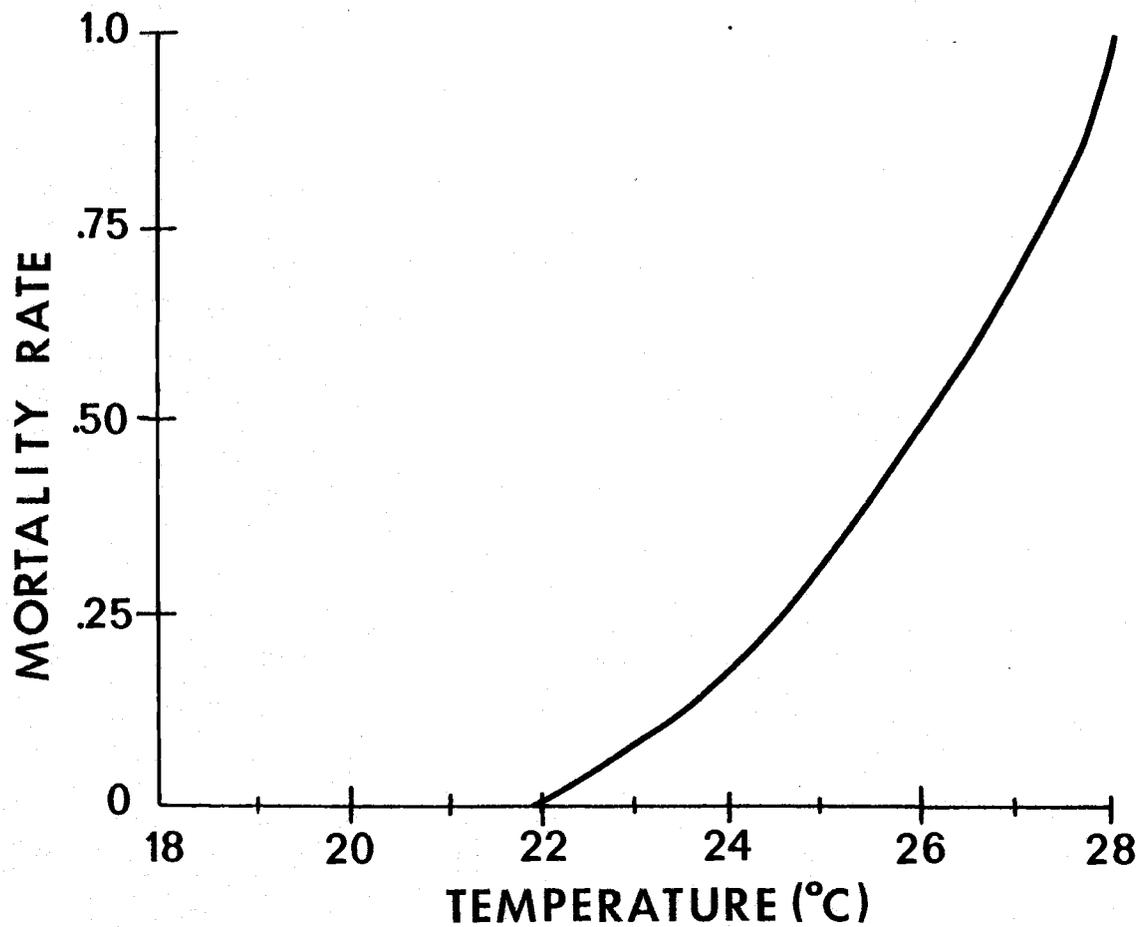


Figure 40. The functional relationship between stream temperatures and the instantaneous mortality rate of salmonid eggs and larval fish in the native spawning stream.

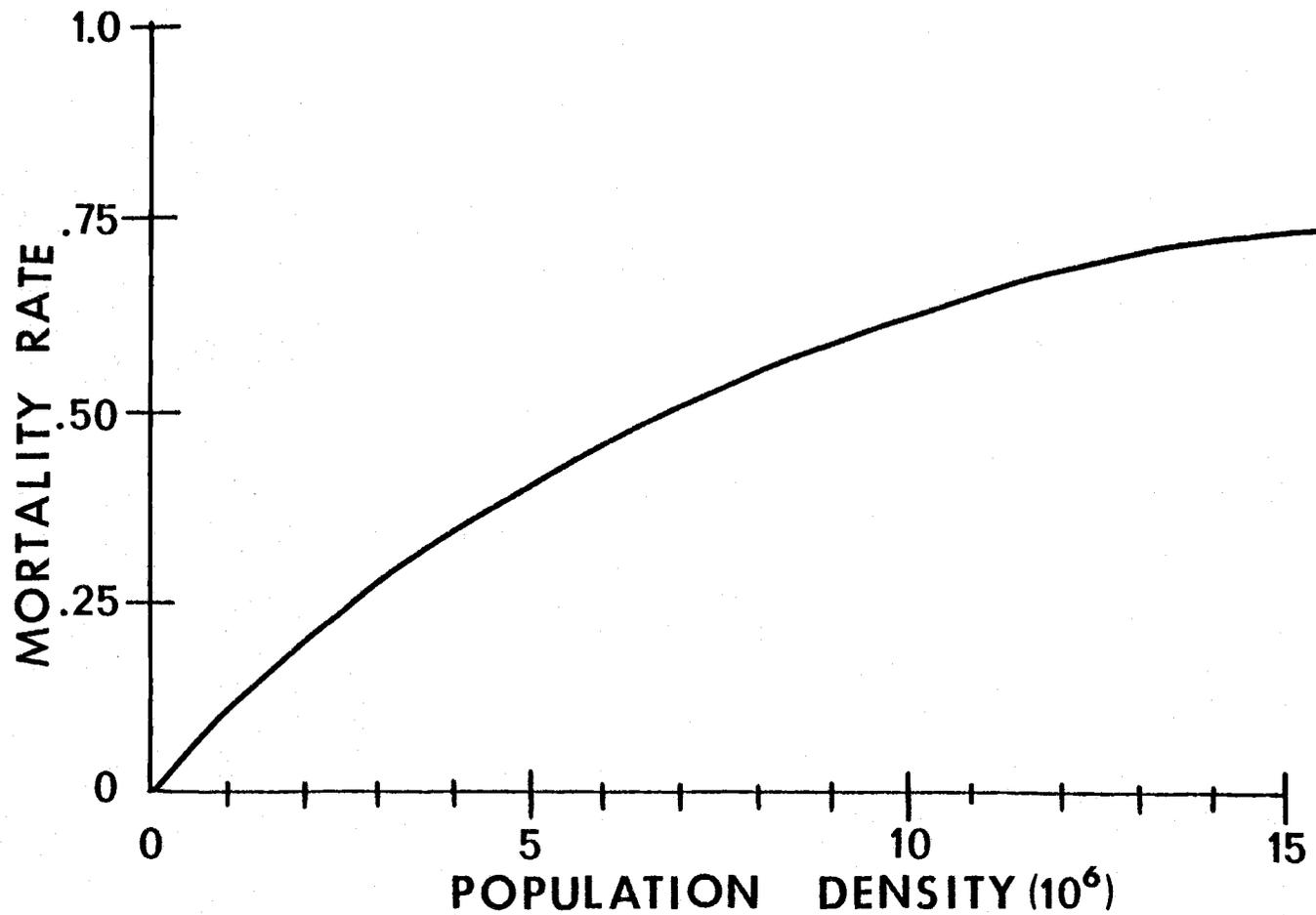


Figure 41. The effect of larval fish density on the instantaneous natural mortality rate incorporated in the simulation model.

when feeding first occurs. Recent studies (Sekulich and Bjornn, 1977) of chinook salmon in a natural stream indicated a natural mortality rate ranging from .723 to .971 during the first year of life. Since the larval fish feed only on the attached yolk sac until the button up stage is reached, this natural mortality appears unrelated to competition for food with resulting starvation. Presumably, then, the primary mortality to emergent larval fish would be density-dependent predation.

When the fish button up, the weight per individual fish is calculated as a function of the female spawner body size (Fig. 42). Experimental studies (Fowler, 1972) with Columbia River fall chinook salmon demonstrated that large female spawners produced large eggs which tended to develop into large alevins. To calculate the total number of surviving fish associated with each spawner body size, it is assumed that mortality during the larval and egg stages is not related to the size of individual fish. Individual body sizes are assigned to all female spawners based on the frequency distribution for size at age. The total fecundity of all adult spawners of body size K (in BODSIZE array) is multiplied times the overall survival of juvenile offspring to determine the total number of fish surviving from parent spawners of body size K (in FISH array):

$$\text{BODSIZE}(K) * \% \text{ Survival} = \text{FISH}(K)$$

Figure 42. The functional relationship between the mean weight per individual emerged alevin and the body size of the female spawner expressed as fork length.

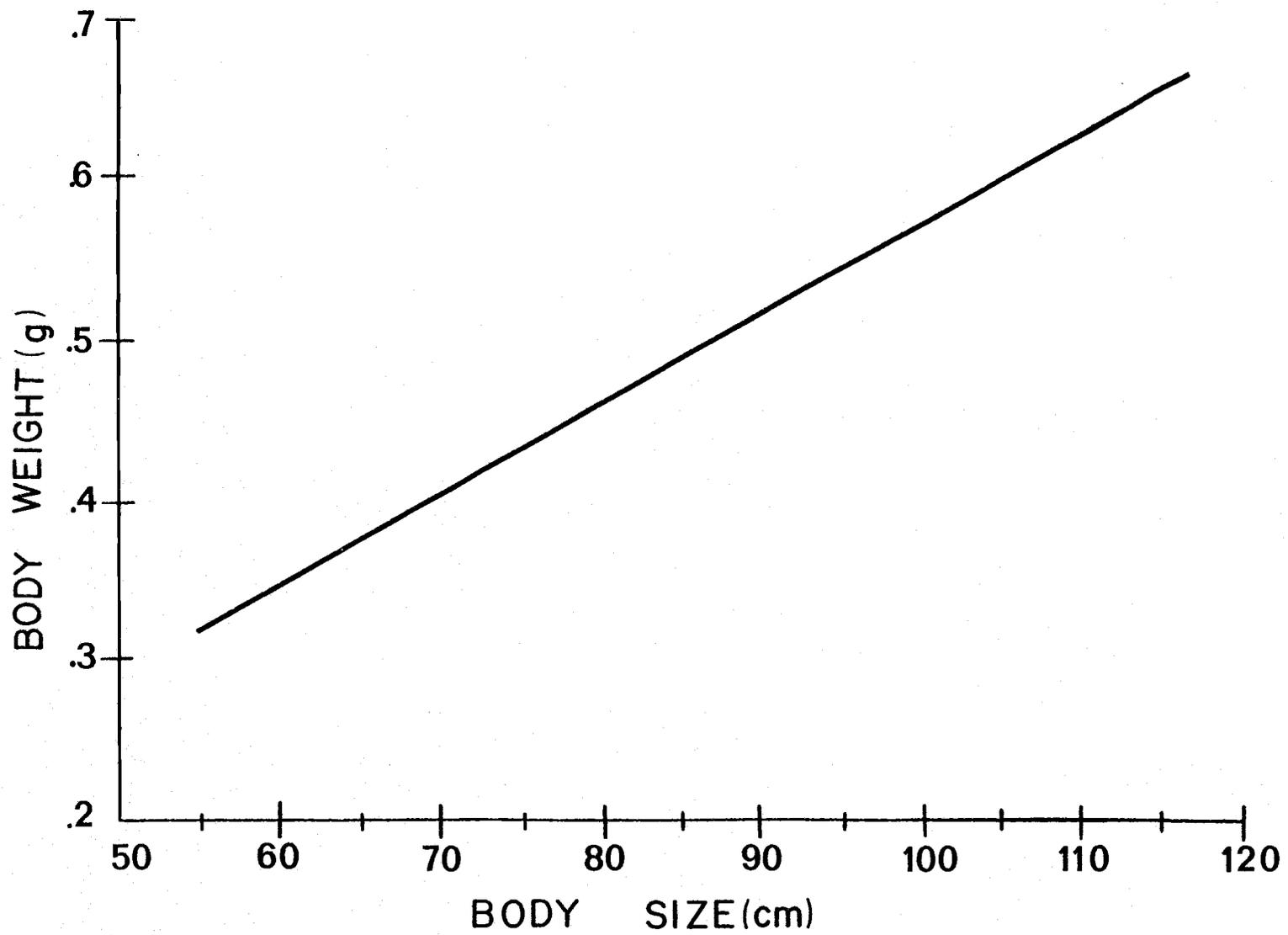


Figure 42.

For all offspring (FISH(K)) from one spawner body size K, the weight per individual fish is determined as a linear function of the female spawner body size (Fig. 42; Fowler, 1972). The mean body weight and associated variance are calculated for the juvenile offspring and stored in the variables YOUNG and VYOUNG respectively.

Juvenile Growth Subroutine. Many studies (cf. Paloheimo and Dickie, 1966a; Paloheimo and Dickie, 1966b; Brett et al., 1969) have concentrated on understanding the growth of fish. The approach used in this modelling effort greatly simplifies the results of these studies. The approach used to model salmon growth at each life history stage is based upon empirical results of laboratory studies (Brett et al., 1969; Brett, 1974; Brett, 1976).

The JGROWTH subroutine (Appendix III-3) is called from both the SPAWNER submodel and the AGE(1) submodel to calculate the growth and survival of juvenile fish from the button-up stage until out-migration. The subroutine operates on a weekly iteration with new growth and survival rates calculated each week. A counter variable, MXCNT, stores the total number of weekly iterations through the JGROWTH subroutine. A second variable, MCNT, stores the number of weekly iterations that have been simulated in the current accessing of the JGROWTH subroutine. Initially, the subroutine checks the counter variable, MXCNT, against the week variable, MCNT, to

determine if additional iterations through the subroutine are required.

Two alternative hypotheses, related to the influence of river flow on growth and survival are presented in the JGROWTH subroutine. One hypothesis is developed under the assumption that river flow in the native stream does not directly influence juvenile growth or survival. Several studies (cf. Reimers, 1973; Erman and Leidy, 1975) have illustrated that young salmonids exhibit behavioral adaptations, such as short distance emigration, in response to critically low river levels. Under the alternative hypothesis, however, river flow can indirectly influence the juvenile growth rate by controlling the quantity of food that drifts by the young fish. Thus, the prey abundance becomes functionally related to river flow (Fig. 43).

Stomach analyses (Sekulich and Bjornn, 1977) of juvenile spring chinook salmon indicate that both aquatic insect larvae and fish contribute to the diet of these fish. Since fish species ranked only tenth in importance out of 13 total food items, insect larvae were considered the dominant prey item during the juvenile life history. The net prey abundance potentially available for consumption by the juvenile fish is internally simulated in the JGROWTH subroutine. Since this prey abundance is partially dependent upon the size of the native stream and the abundance of competitive predators, the maximum and minimum bounds of abundance are initially determined by the

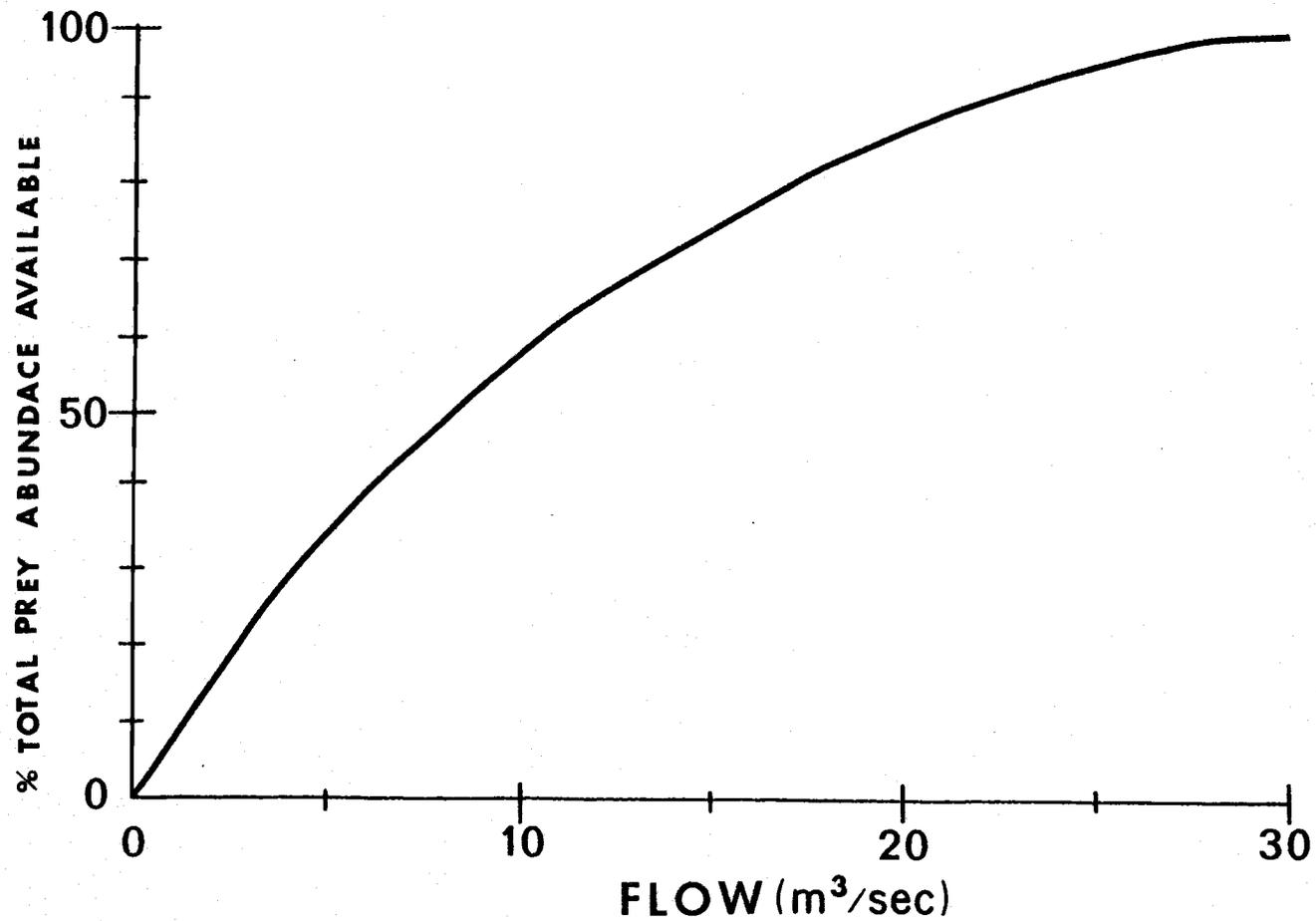


Figure 43. The percentage of the total prey abundance potentially available as food to the modelled stock expressed as a function of the stream flow.

modeller. The simulation of prey abundance varies seasonally with peak abundance during the early summer, intermediate abundances during the fall and spring and lowest abundance in the winter. When the prey availability is flow-dependent, under the second hypothesis previously discussed, the net prey abundance is multiplied times the proportion available to the predator given the strength of the river flow (Fig. 43).

To calculate the growth rate in freshwater, the mean maximum ration is determined from the mean body weight (Fig. 44) and stored in the variable MAXEAT. A logarithmic transformation is used for both the ration level and the growth rate. Experimental studies (Brett, 1974; Brett, 1976) with juvenile sockeye salmon suggested a linear relationship between these variables. The body weights in this functional relationship reflect the range of sizes characteristic of upriver spring chinook salmon up to two years of age. The range of ration levels considered reflect plausible ration levels consumed by the juvenile fish based on the growth rate for chinook salmon during the first two years of life. The proportion of the mean maximum ration consumed by all fish, PCNT, is dependent upon the total amount of food available (Fig. 45). This functional relationship is based on a relationship adapted (Walters et al., 1978) from data published by Parsons and LeBrasseur (1970) and verified in the Walters model for ocean

Figure 44. The functional relationship between mean body weight of juvenile salmon and the mean maximum ration expressed as percent body weight per week.

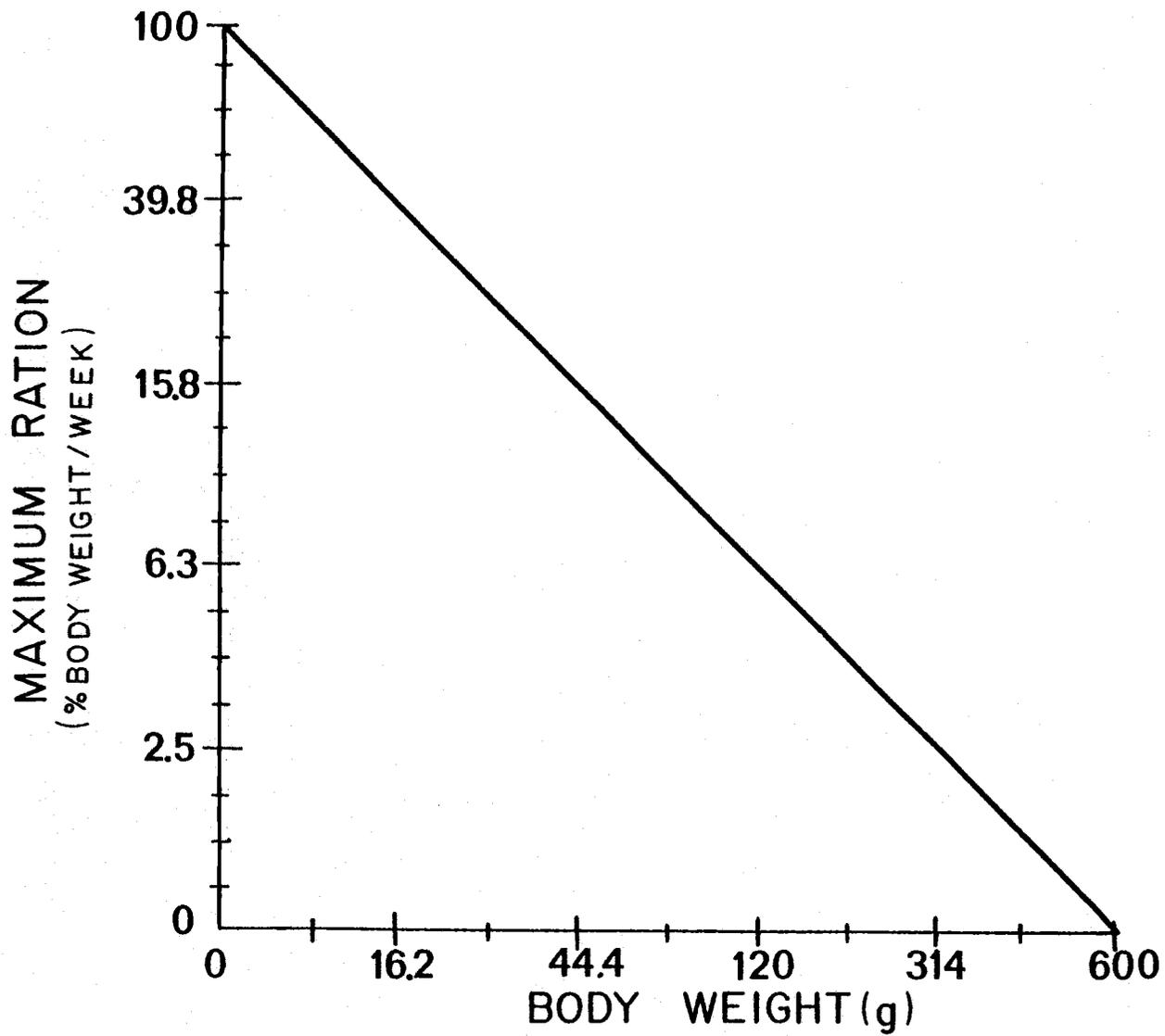


Figure 44.

Figure 45. The percentage of the total maximum ration consumed by juvenile salmon at selected densities of prey biomass.

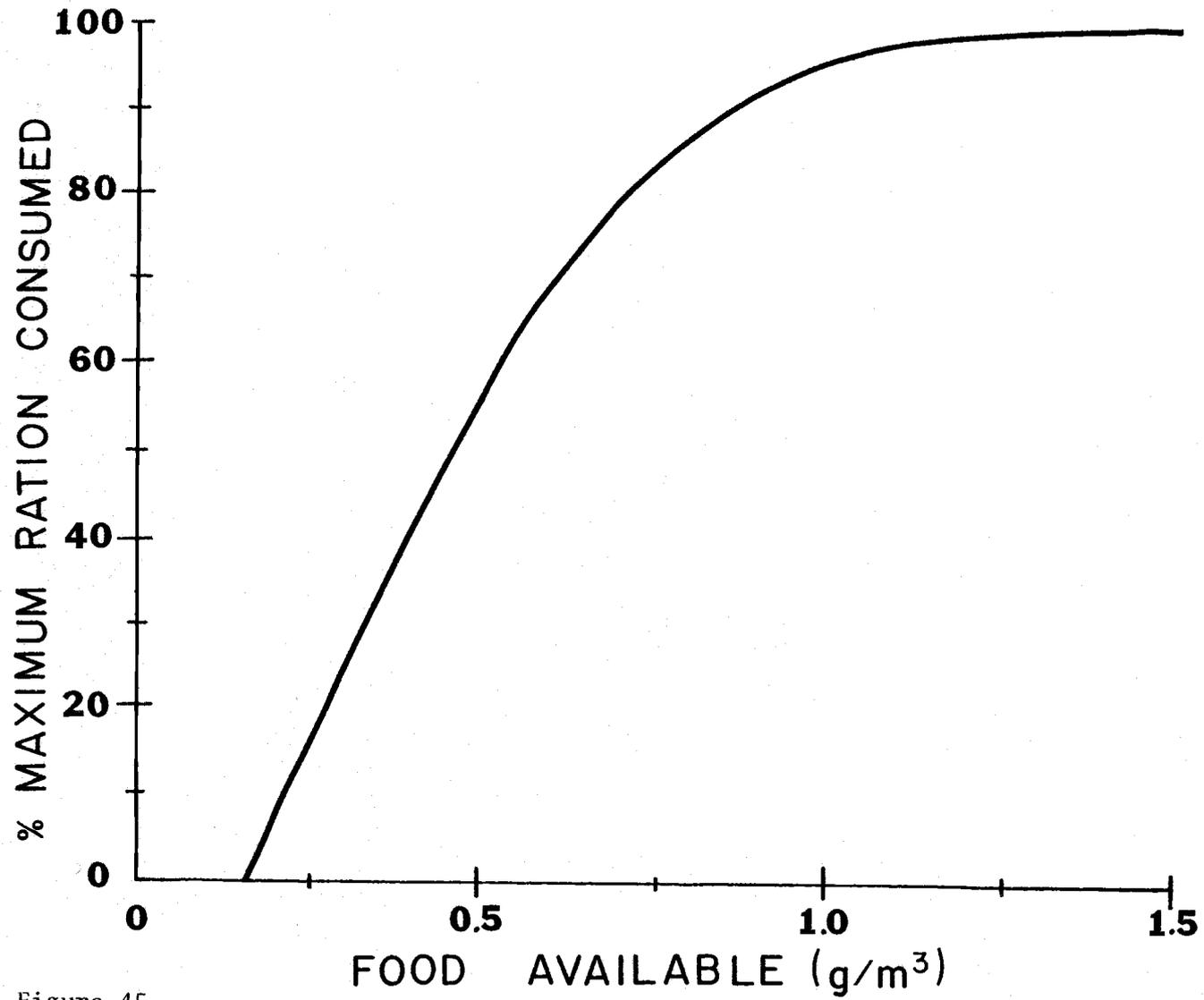


Figure 45.

smolts. The range of food densities reflects the density of insect larvae available for consumption by juvenile chinook salmon in selected Idaho streams (Sekulich and Bjornn, 1977). The total maximum ration consumed by all individuals is calculated and stored in the variable MAXRAT:

$$\text{MAXRAT} = \text{PCNT} * \text{MAXEAT}$$

Since MAXEAT may represent more food than is available for consumption by the stock, the actual amount of food consumed is modelled as a depletion-attack process (Griffiths and Holling, 1969, as cited by Walters et al., 1978). The actual amount of food consumed, FOOD, is calculated:

$$\text{FOOD} = \text{PREY} - \text{PREY} \left(1 - \frac{\text{MAXRAT}}{\text{PREY} * k}\right)^{-k}$$

where PREY is the total amount of food available for consumption and  $k$  is a constant with a value close to 1.0 (Walters et al., 1978).

To calculate the amount of food that can be converted to growth, the mean maintenance ration is determined. Relying primarily upon experimental studies (Brett, 1974; Brett, 1976) with sockeye salmon, the mean maintenance ration is calculated as a function of mean body weight (Fig. 46). The total mean maintenance ration, MAINRAT, is calculated by multiplying the mean maintenance ration times the number of individuals. If the amount of food consumed, FOOD, is greater

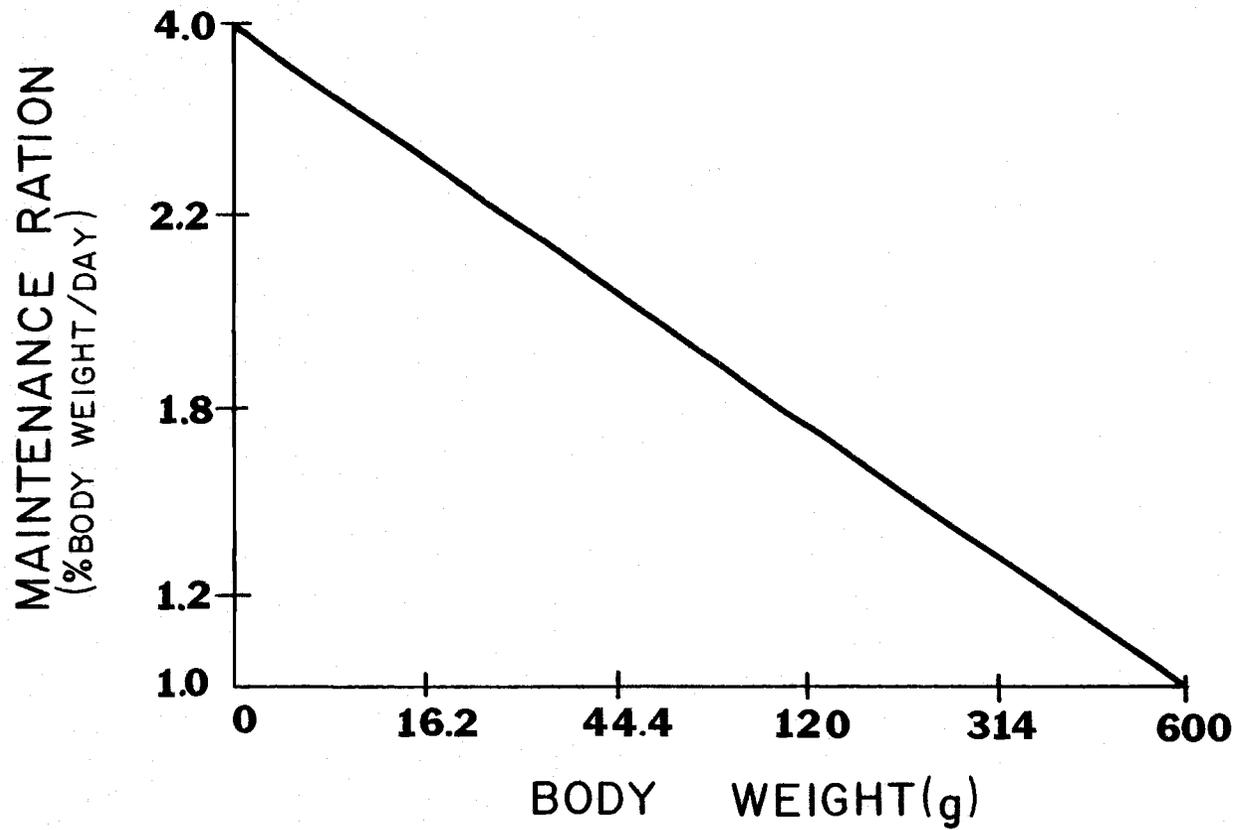


Figure 46. The functional relationship between body weight and the maintenance ration expressed as percent body weight per day.

than the total mean maintenance ration, the growth rate is calculated as a function of ration level (Fig. 47). The numerical values of the ration levels are determined from the previous relationships (Figs. 44 and 46) since the absolute ration level depends on the mean individual body weight. The weekly growth rates calculated from the ration levels are those suggested experimentally for sockeye salmon (Brett et al., 1969).

At the end of each weekly iteration of the JGROWTH subroutine, the natural mortality rate is determined. Some studies (Hager and Noble, 1976; Foerster, 1954) indicate that the natural mortality rate decreases with increased body size. Based on these data, a size-dependent natural mortality (Fig. 48) was assumed for the freshwater life history of the juvenile fish. When the amount of food potentially consumed is less than the total maintenance ration, no growth occurs and a portion of the juvenile fish die. This juvenile mortality, MORT, is dependent on the ratio of the total mean maintenance ration to the total prey abundance ( $MORT = FOOD/MAINRAT$ ). The number of fish dying from starvation is calculated; these fish are removed from the smallest individuals in the population. Based on the assumption that the largest juveniles have a competitive advantage, the smallest fish die in a food-limiting environment. The mean body weights and associated variances of all fish that have survived are updated. The

Figure 47. The functional relationship between the individual growth rate expressed as the percentage increase in body weight per week and the relative ration level consumed.

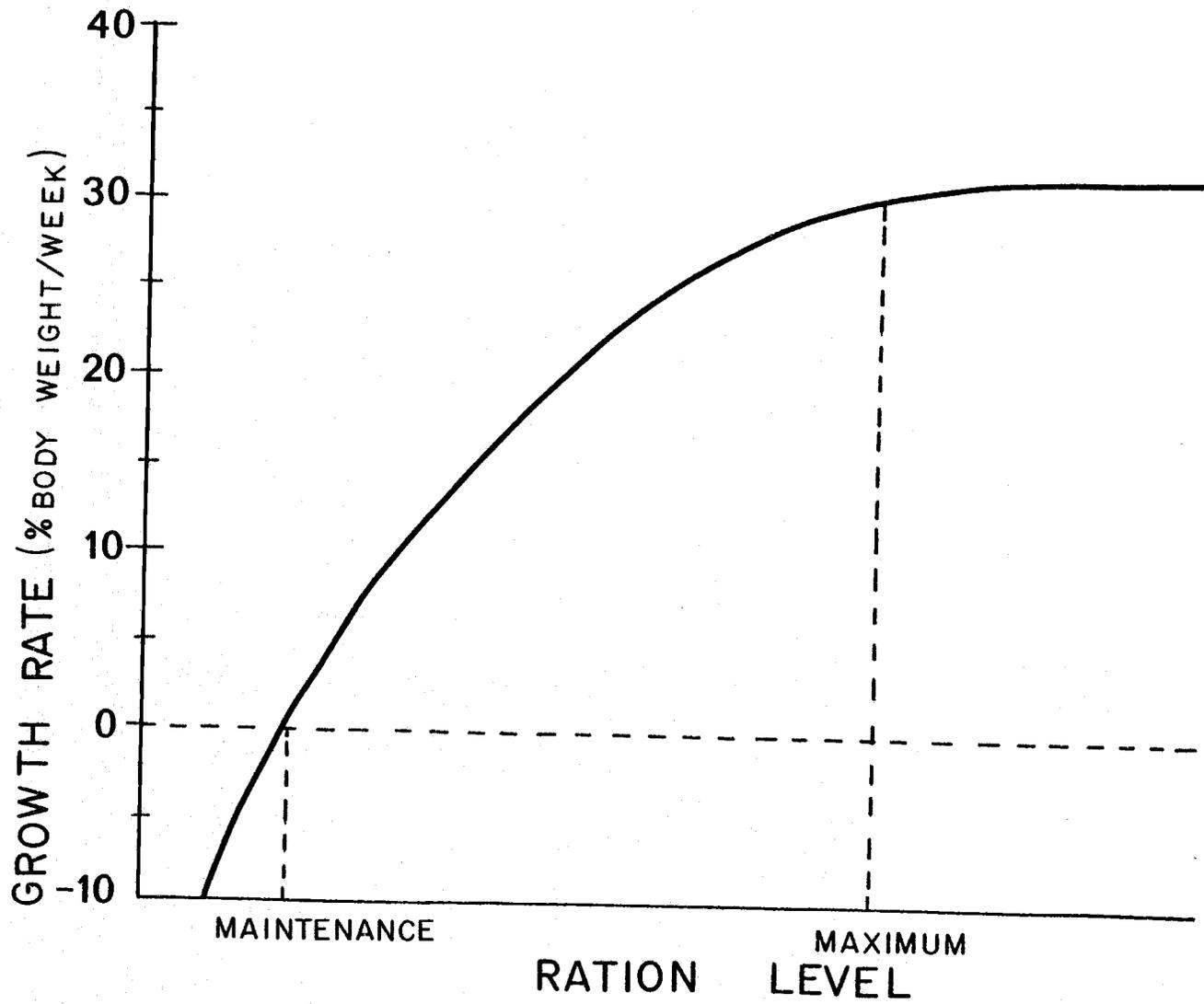


Figure 47.

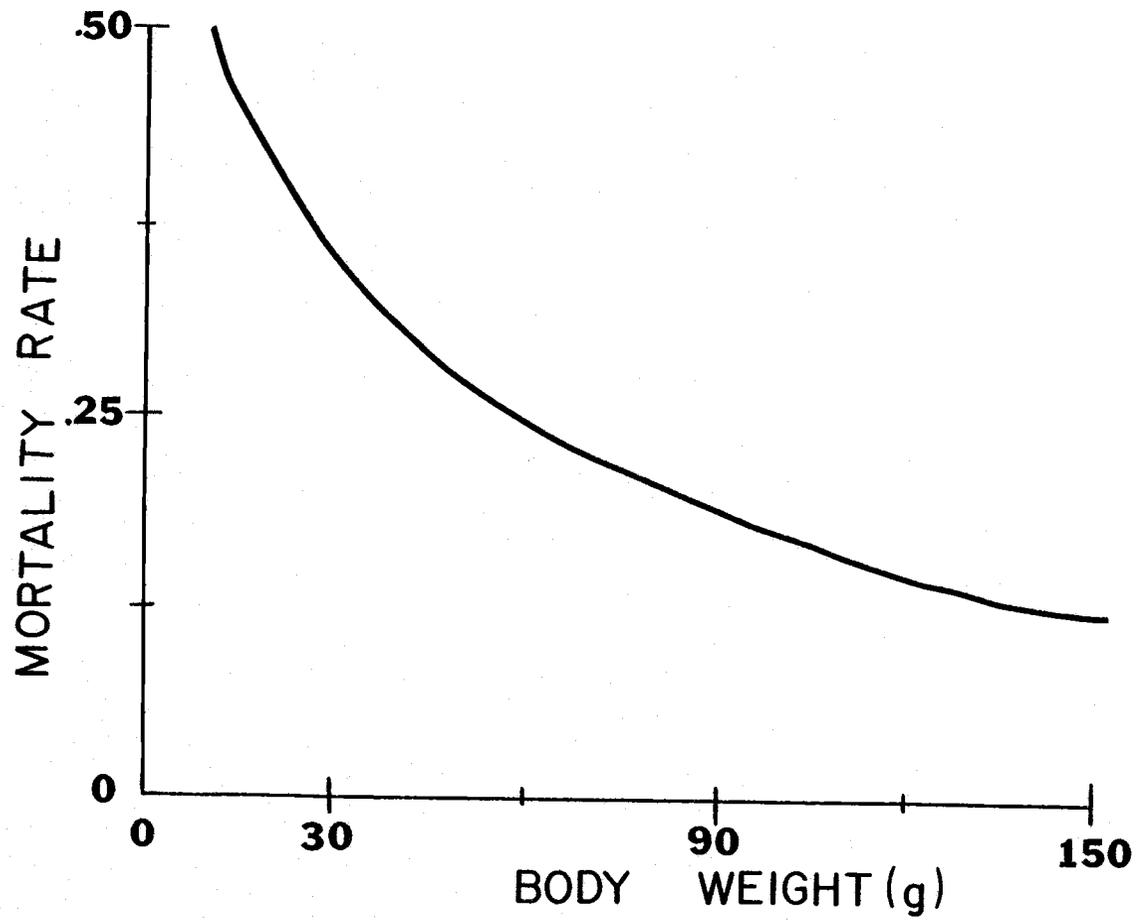


Figure 48. The mortality rate of juvenile salmon expressed as a function of body weight.

surviving fish continue to feed until the indicated number of iterations have occurred. At this time, all calculations in the SPAWNER submodel have been completed.

#### AGE(1) Submodel

The AGE(1) submodel (Appendix III-4) calculates 1) the survival and growth rates of freshwater juveniles from the fall of their first birthday until downstream migration as smolts, 2) the survival rate during outmigration, and 3) the growth and survival rates of ocean smolts until the fish reach their second birthday. Both prey abundance and environmental conditions, primarily flow, are driving variables in this submodel.

Some studies (Bjornn, 1978) have indicated that some pre-smolt fish migrate out of the native stream before their second spring. It is not clear, however, what proportion if any of these fish actually migrate to the ocean prior to their second spring. Two hypotheses, internal to the AGE(1) submodel, are presented to deal with the outmigration of pre-smolt fish. The first hypothesis considers the outmigration of pre-smolt fish as negligible and the modelled stock migrates downstream as a single unit. An alternative hypothesis considers outmigration of pre-smolt fish as a significant event. The proportion of the total population that migrates as pre-smolt fish is dependent upon both the population density and the river flows (Figs. 49 and 50).

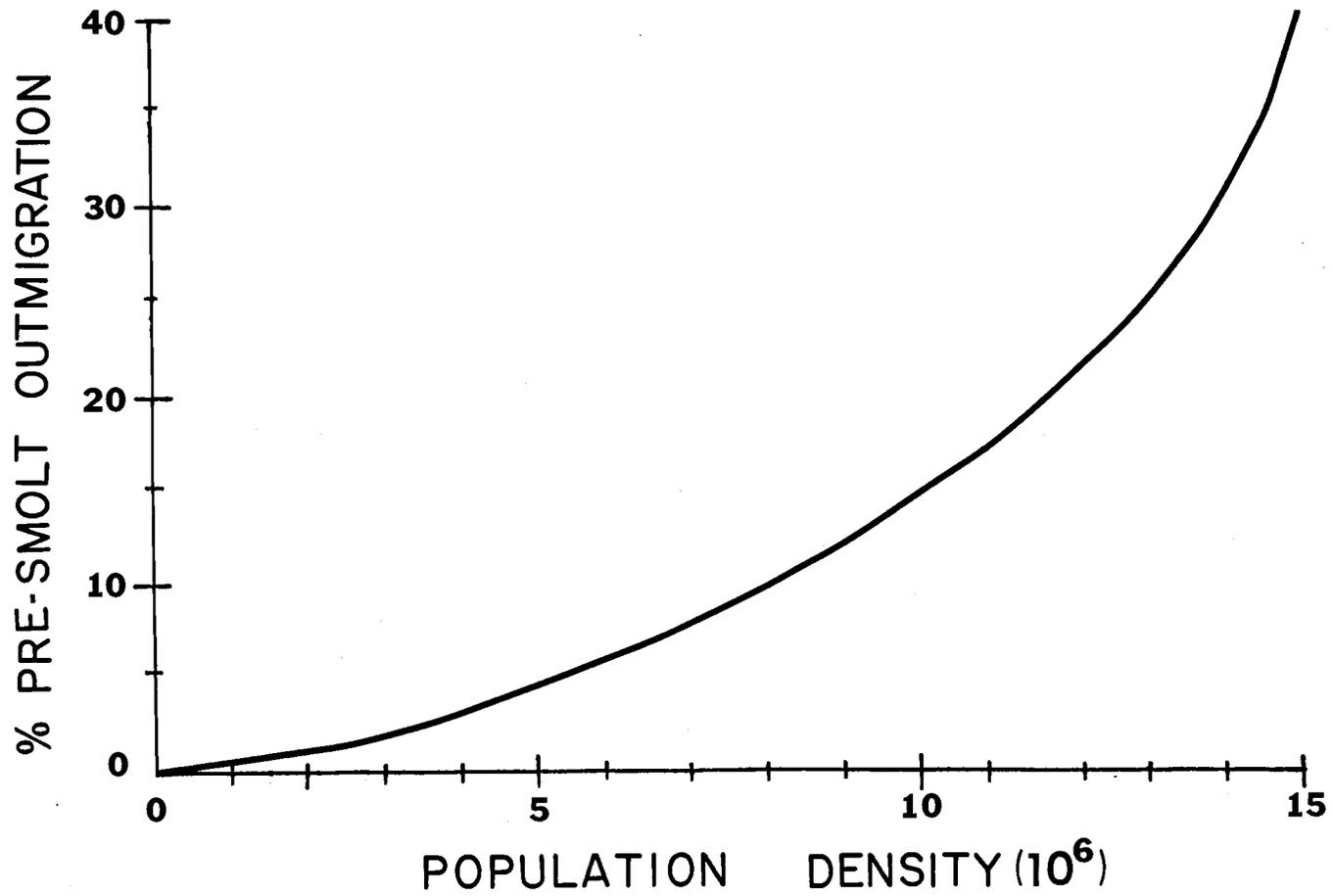


Figure 49. The percentage of fish migrating downstream as pre-smolts expressed as a function of the population density of juvenile fish in the native stream.

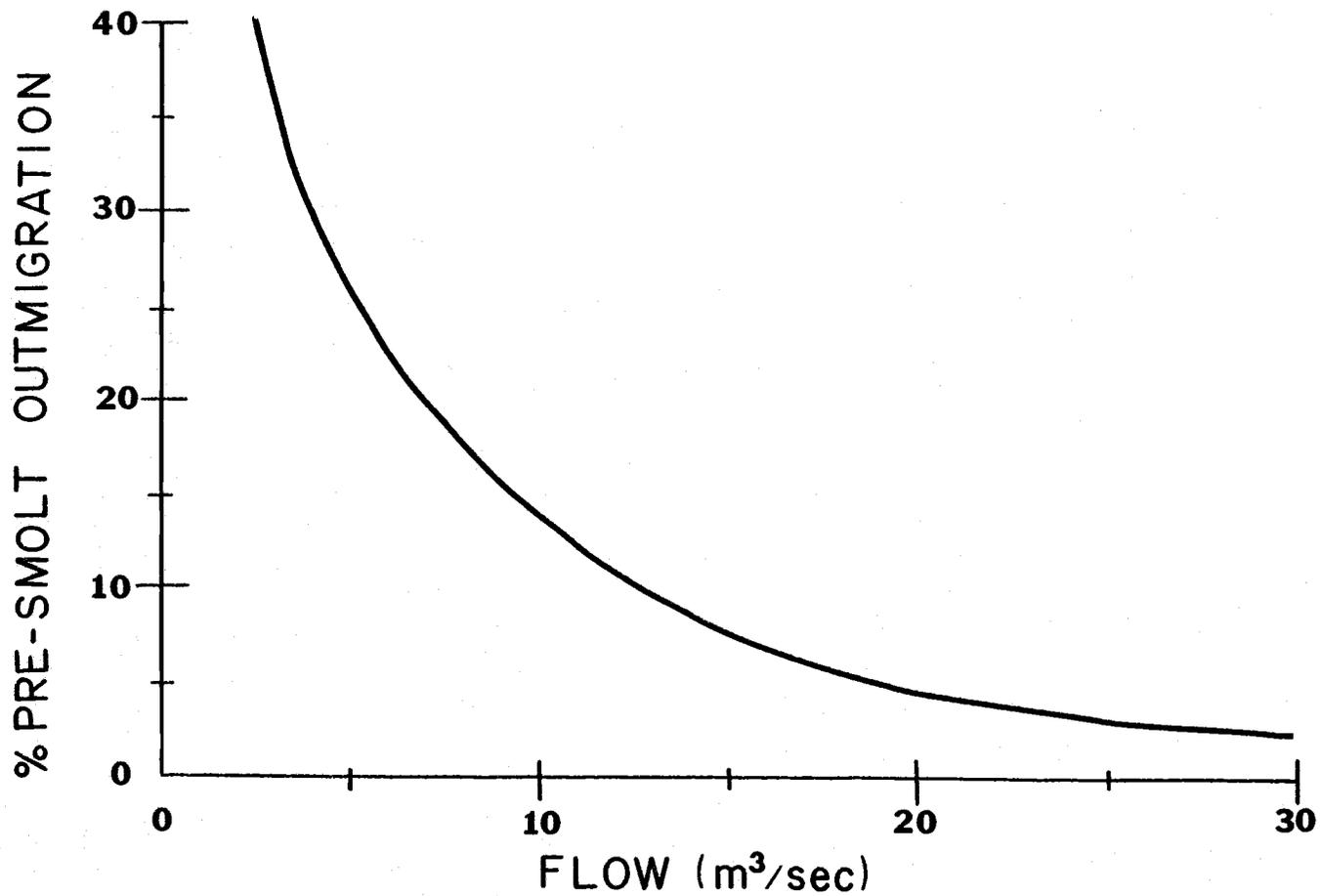


Figure 50. The percentage of fish migrating downstream as pre-smolts expressed as a function of the stream flow in the native stream.

The outmigrating fish, which presumably die, are removed from the juvenile population.

From October until March, the juvenile fish in the AGE(1) submodel continue to be influenced by growth and mortality processes in freshwater. The AGE(1) submodel initially calls the JGROWTH sub-routine. The growth and survival rates calculated for the first six months in the AGE(1) submodel are identical to those previously described for the latter months in the SPAWNER submodel.

In the spring, the surviving fish migrate downstream to the estuary. Since outmigration occurs over a relatively short time span, growth during this stage is considered negligible. Based upon the results of the statistical analyses in this study, the amount of water flowing through each dam is considered as the single most important factor influencing juvenile mortality during outmigration. Since changes in flow influence changes in other environmental variables, such as nitrogen gas supersaturation, temperature, and turbidity, this assumption appears justified.

For the conceptual model, the parabolic relationship between flow and survival rate, suggested by the statistical analyses, (Figs. 18 and 22) is separated into two independent relationships (Figs. 51 and 52). The mortality attributed to high flow levels in either the Columbia or the Snake River is assumed related to the effects of

Figure 51. The functional relationship between the flow of water through any Columbia or Snake River dam and the survival rate of juvenile downstream migrants related to nitrogen supersaturation effects.

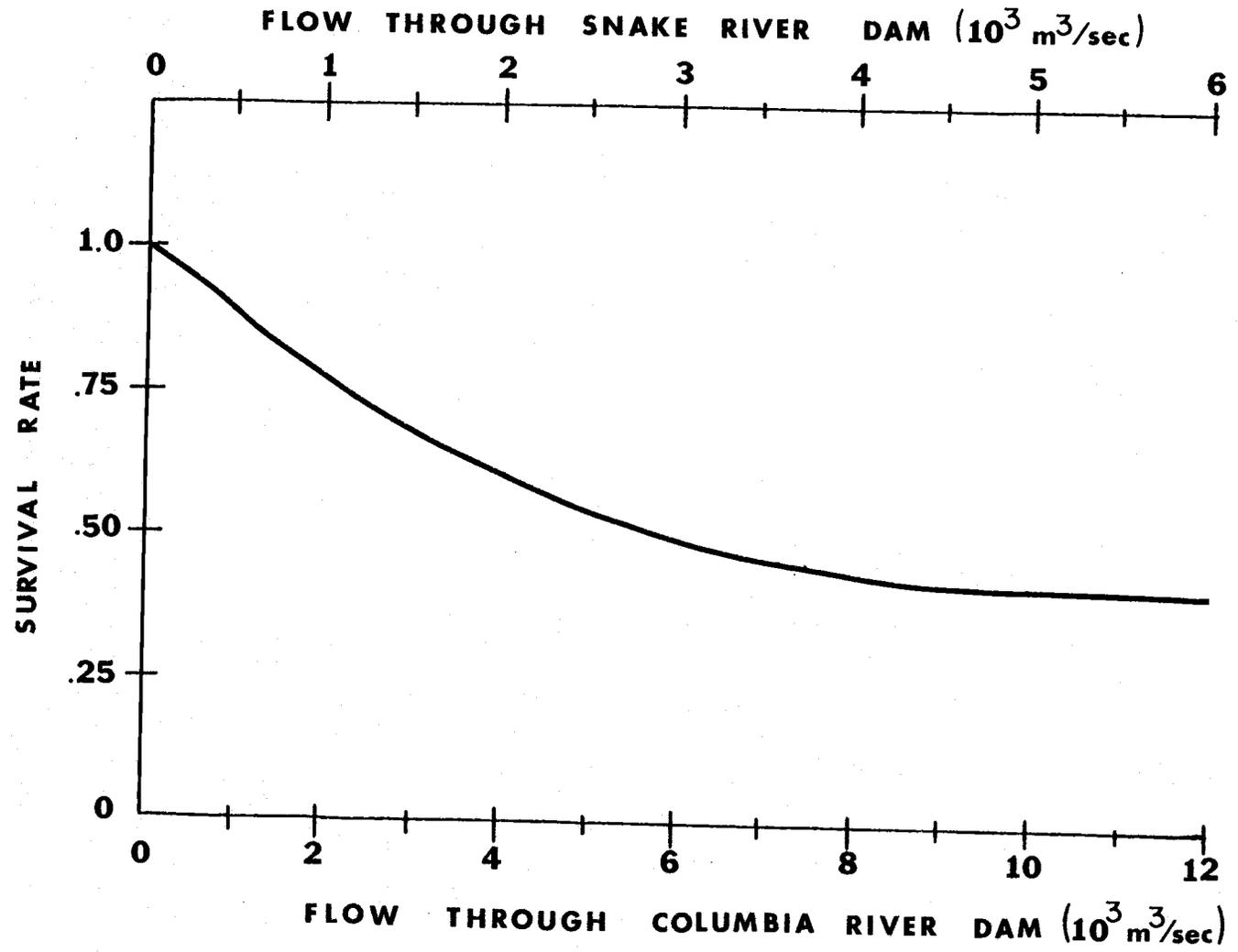


Figure 51.

Figure 52. The functional relationship between the flow of water through any Columbia or Snake River dam and the survival rate of juvenile downstream migrants related to the effects of outmigration through power turbines.

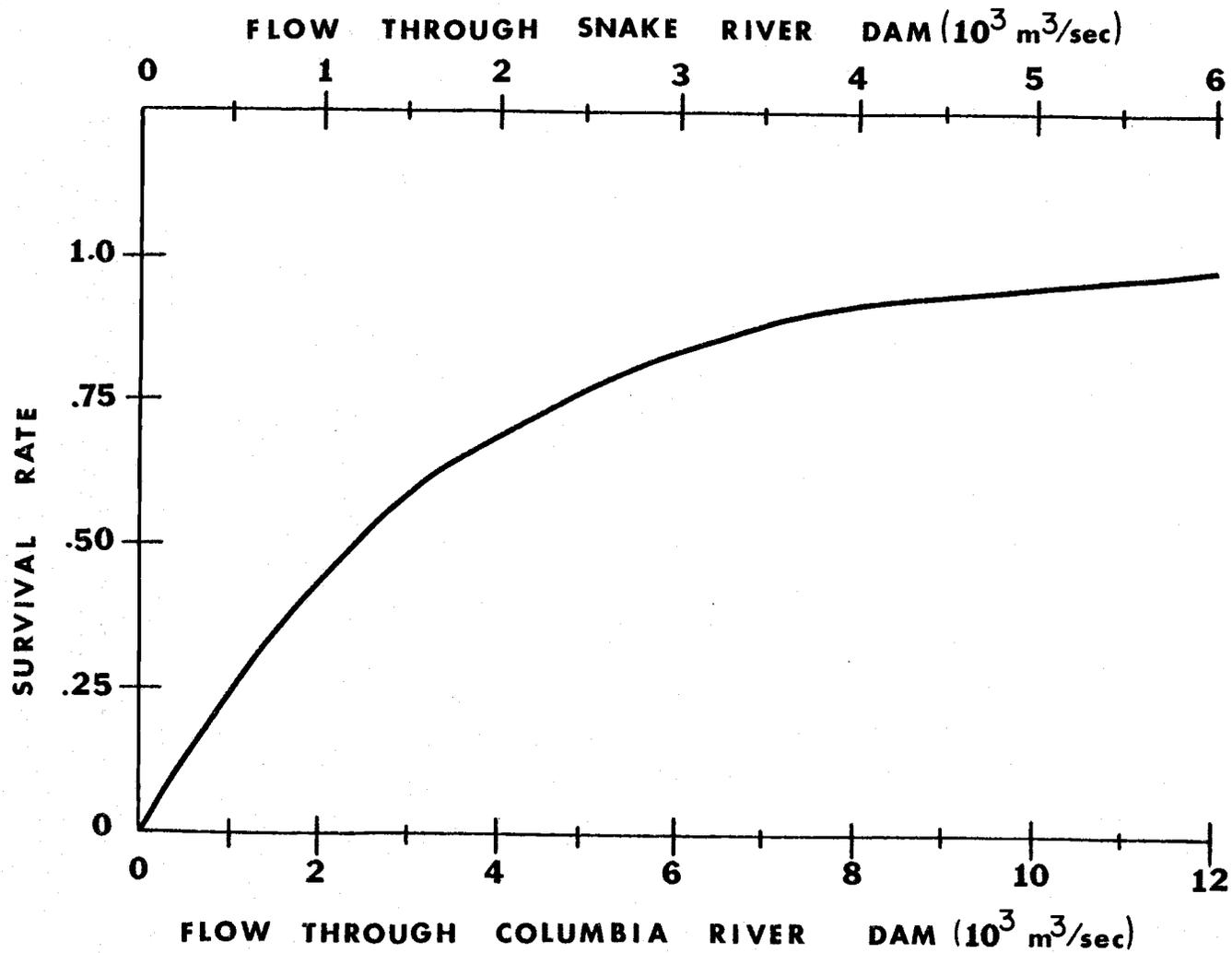


Figure 52.

nitrogen supersaturation (cf. Ebel et al., 1975). The survival of outmigrants is low during low flows due to the migration of juvenile fish through the power turbines (Fig. 52) and also low during high flows due to the highly saturated water at dam sites (Fig. 51). Since the flow regimes in the Snake River differ markedly in magnitude from those in the Columbia River, the model distinguishes between passage over Snake River and Columbia River dams. The flow associated with each dam during juvenile outmigration is internally simulated based on actual data for the months of peak juvenile outmigration, April and May (Mains and Smith, 1964; Bjornn, 1978).

Once the juvenile fish enter the estuarine environment as smolts, the major processes considered in the submodel are growth, survival, and coastal migration. To facilitate the internal bookkeeping, the coastal migration route extending from the mouth of the Columbia River northward and westward to the Aleutian Islands is divided into one hundred blocks. Each large block is subdivided into 25 sub-blocks which represent one-km strips within the large block. The ocean sub-blocks are consecutively numbered from two to 2500 starting at the Columbia River mouth and extending to the Aleutian Islands. The first sub-block represents the Columbia River estuary. The number of fish of age I found in any sub-block JK is stored in the matrix NUMB(I, JK). Thus, NUMB(1, 1) represents the number of

downstream migrants residualizing in the estuary. Since the model assumes that none of the fish spend more than six months in the estuary, NUMB(I, 1) is zero for I = 3, 4, or 5. The mean body weights and the related variances associated with each sub-block are stored in the matrices MBDWT(I, JK) and VBDWT(I, JK) respectively. The NUMB, MBDWT, and VBDWT matrices are all updated with respect to the age designations each fall in the UPDATE subroutine.

To consider the alternative migratory strategies of the out-migrating smolts in the estuary, two hypotheses are incorporated in the AGE(1) submodel. Under one hypothesis, the proportion of fish residualizing for any period of time in the estuary is assumed to be density dependent (Fig. 53). That is, when a large brood year migrates downstream, some of the smolts remain temporarily in the estuary. Limited data from recent studies (Healey, 1978; Reimers, 1973) suggest that estuarine rearing may be important to chinook salmon. The rapid growth rate associated with the relatively sheltered estuarine environment may be of particular benefit to the smallest individuals that might be at a competitive disadvantage in the ocean environment. Thus, given this hypothesis, it is assumed that the fish temporarily residualizing in the estuary are the smallest individuals of the brood. The numbers, mean body weight, and associated variance of fish residualizing in the estuary are stored in

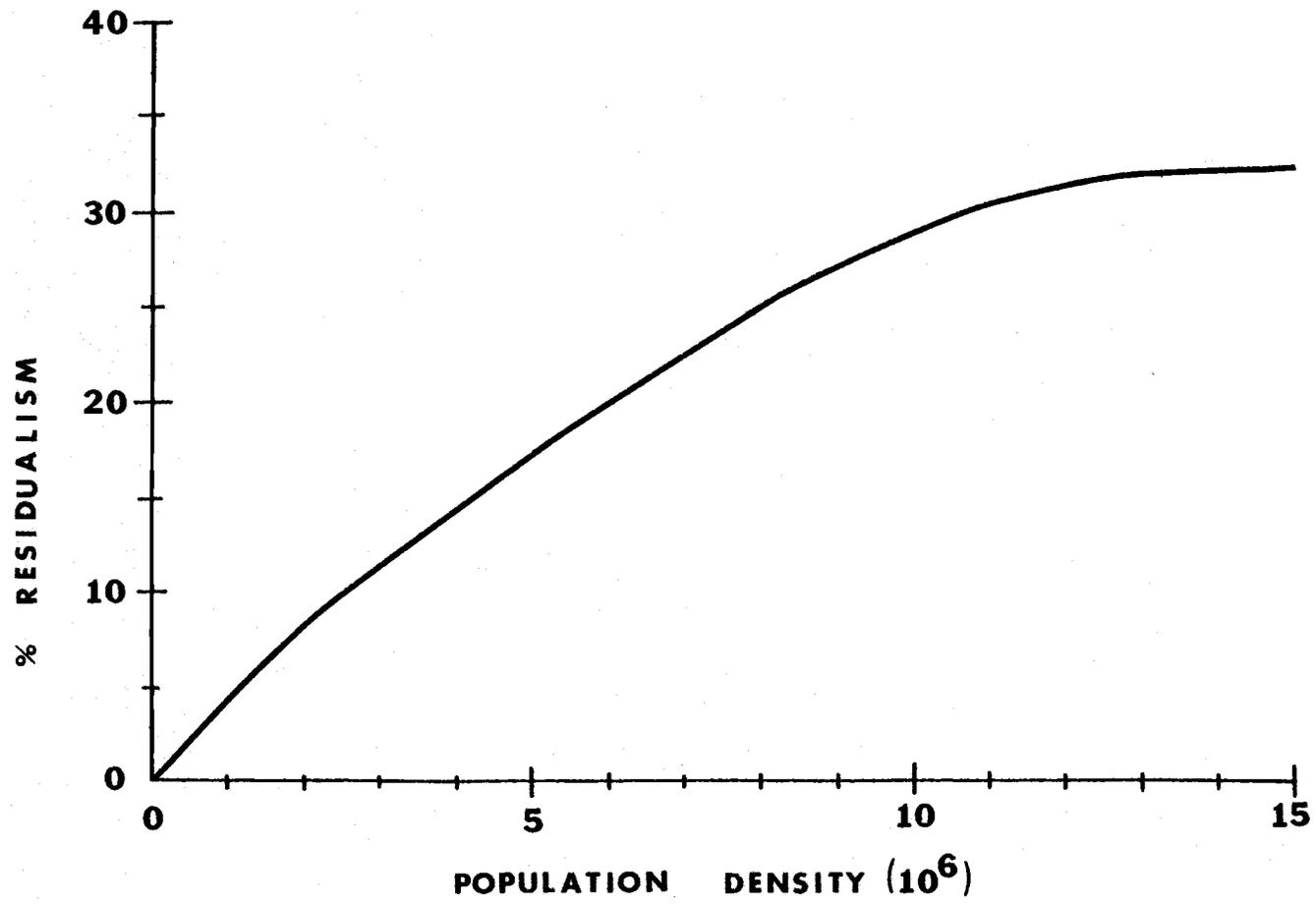


Figure 53. The percentage of outmigrating smolts residualizing in the estuary expressed as a function of the population density of the modelled stock in the estuary.

NUMB(1, 1), MBDWT(1, 1), and VBDWT(1, 1) respectively. These statistics for fish migrating directly to the ocean are stored in NUMB(1, 2), MBDWT(1, 2), and VBDWT(1, 2). The alternative hypothesis presented in the AGE(1) submodel is based on the assumption that the incidence of estuarine residualism is negligible. Under this alternative hypothesis, all fish move directly to the ocean and NUMB(1, 1), MBDWT(1, 1), and VBDWT(1, 1) are all set equal to zero.

Smolt Growth Subroutine. The SGROWTH subroutine is called from the AGE(1) submodel to calculate the growth and mortality rates of estuarine and ocean smolts in each sub-block until the fish become two years of age. In addition, the subroutine updates the total numbers and individual sizes of fish surviving each weekly iteration. The temporal resolution of the SGROWTH subroutine is weekly.

The growth and mortality processes influencing both the estuarine and the ocean smolts are conceptually modelled in the same manner although the growth and mortality rates are smallest for the estuarine fish. The major difference between these two groups of fish is the food availability. The total biomass available for consumption by the modelled stock is simulated for each spatial block and each temporal iteration in the SGROWTH subroutine. The simulation of the ocean prey biomass is that developed by Walters et al. (1978) for Canadian salmon but the magnitude of the net prey

abundance is scaled to reflect a single stock. It is assumed that the estuarine net prey abundance is less than that in the ocean. In addition, of the two size-particles of food types considered by Walters et al. (1978), only the largest food particle is considered in this study since all outmigrants should weigh at least 8 g (Bjornn, 1978).

To model the growth of post-smolts during the first months at sea, two alternative hypotheses are presented in the SGROWTH subroutine. Basic to the first hypothesis is the assumption that zooplankton abundance is not a limiting factor in fish growth and survival. Verification of this assumption is presented in Walters et al. (1978) for Canadian salmon. The alternative hypothesis developed to describe the growth of post-smolts during the first months at sea is partially based upon a recent study with Oregon coastal coho salmon (Gunsolus, 1978). This study suggested that poor fish production is associated with poor coastal upwelling during the first summer at sea. Production in the Gunsolus study is determined as an index reflecting the brood year contributions to the coastal fisheries, to the wild spawning ground, and to the hatcheries. The results of the statistical analyses in the study described herein also suggested that a high survival rate is related to a strong upwelling index (Figs. 29-30). Given the assumption that the Bakun (1973) upwelling

index is related to zooplankton productivity in the coastal waters, food may be a limiting factor with respect to growth rate for the modelled chinook salmon stock. Based on this information, an alternative hypothesis was developed in the current model to reflect a food-limiting environment for ocean post-smolt fish. The strength of the coastal upwelling index is internally simulated based on actual values over the months of June and July at  $48^{\circ}\text{N}$   $125^{\circ}\text{W}$ . Given the first hypothesis, the prey biomass potentially available for consumption is unaffected by the strength of the upwelling event. Alternately, the proportion of the total prey biomass available as food to the modelled stock is dependent upon the strength of the upwelling event (Fig. 54). During years of strong upwelling, nearly 100 percent of the prey individuals are potentially available for consumption. It is assumed that the food supply available to individuals in the estuary is not affected by the upwelling event.

The growth rate of ocean smolts is calculated in a manner similar to that used in the JGROWTH subroutine. The maximum ration (Fig. 44) and the maintenance ration (Fig. 46) are determined from the mean individual body weights. The percent of the maximum ration potentially consumed is calculated from the total available zooplankton biomass (Fig. 55). Based on the model developed by Walters et al. (1978), the actual amount of food consumed is modelled

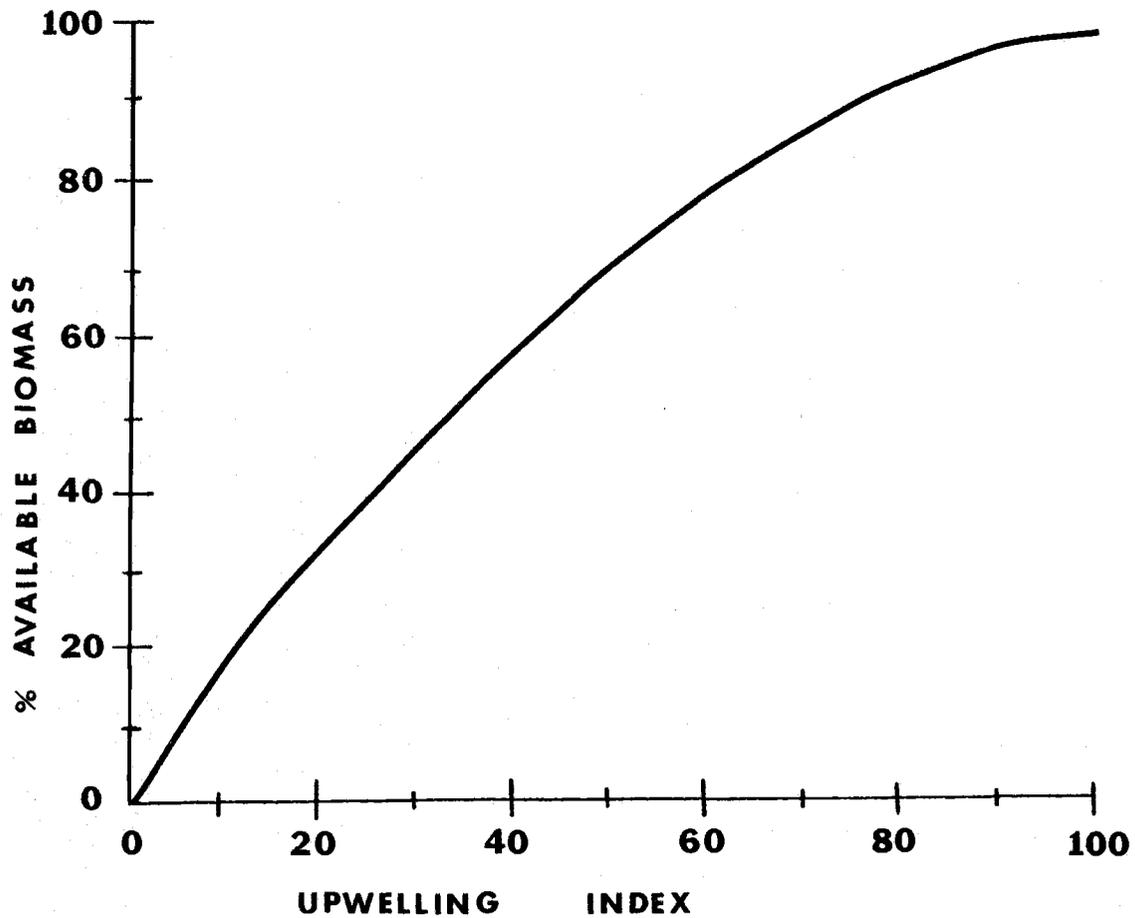


Figure 54. The proportion of the total prey biomass potentially available to the modelled stock expressed as a function of the mean June-July upwelling index for 48°N 125°W.

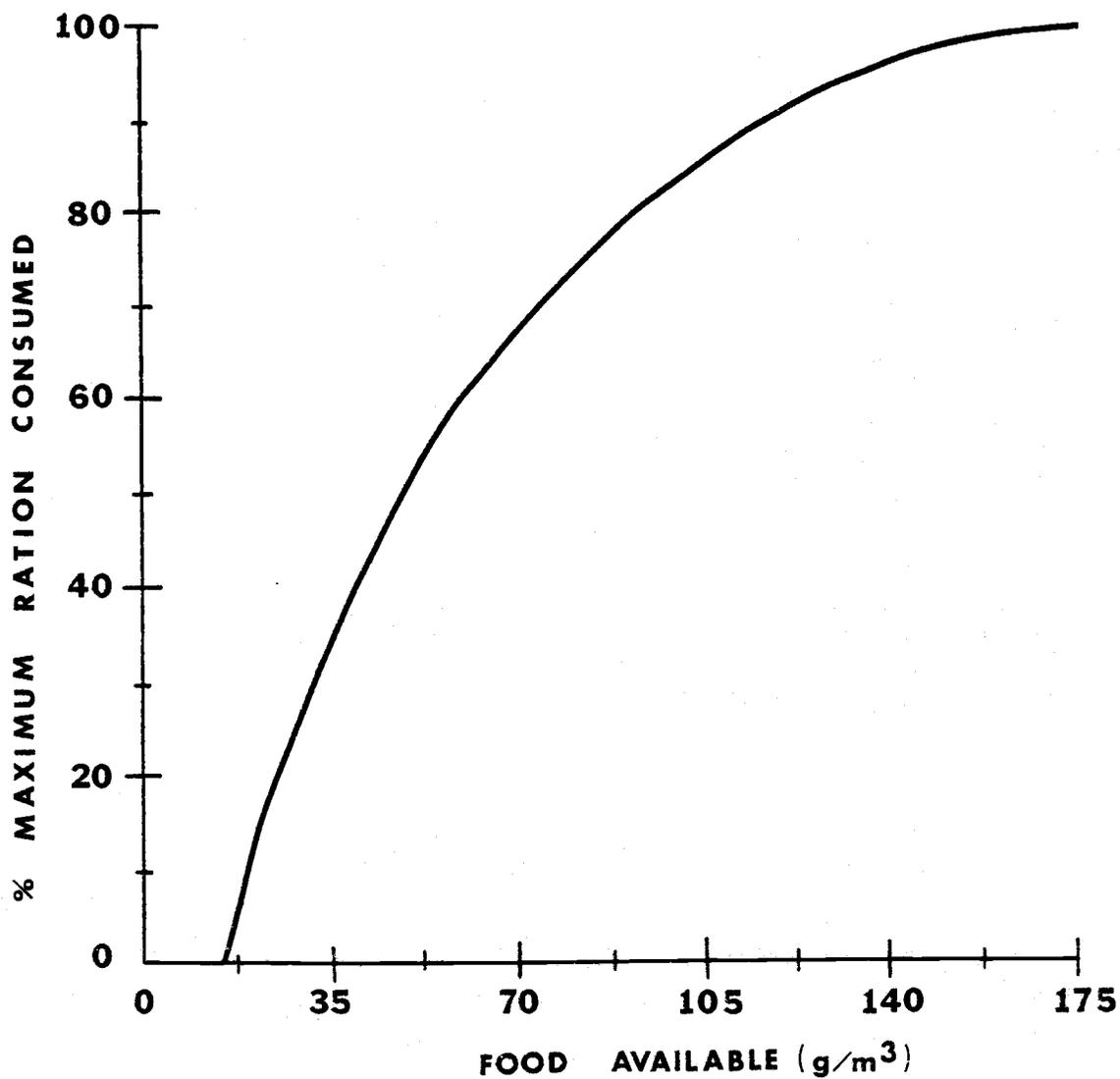


Figure 55. The percent of the maximum ration consumed by the modelled stock expressed as a function of the prey biomass density (adapted from Walters et al., 1978).

as a depletion-attack process. The growth rate is then calculated as a function of the ration level (Fig. 47). If the ration level is high enough to permit growth to occur, mean individual body weights and the associated variances are updated.

Smolt Coastal Migration Subroutine. The SMOVE subroutine is called from the SGROWTH subroutine 1) to determine the coastal migration rate of all ocean and estuarine fish, 2) to determine the natural mortality rate of all ocean and estuarine fish, and 3) to update the location, mean body weights, and number of fish surviving at age (Appendix III-6). Downstream migrants can residualize in the estuary for a maximum of six months. After six months, any fish remaining in the estuary are automatically moved to the first ocean sub-block. During these six months, movement from the estuary is size-dependent (Fig. 56). As the estuarine fish grow, they presumably become competitive in the ocean environment and emigration from the estuary is favored.

Two strategies are developed in the SMOVE subroutine to describe the coastal migration rate of the ocean fish. The first strategy relies on the assumption that this migration rate is directly related to body weight. Thus, the large fish will migrate northward along the coast at a faster rate than the small fish. Two different functional relationships are developed to describe the relationship between

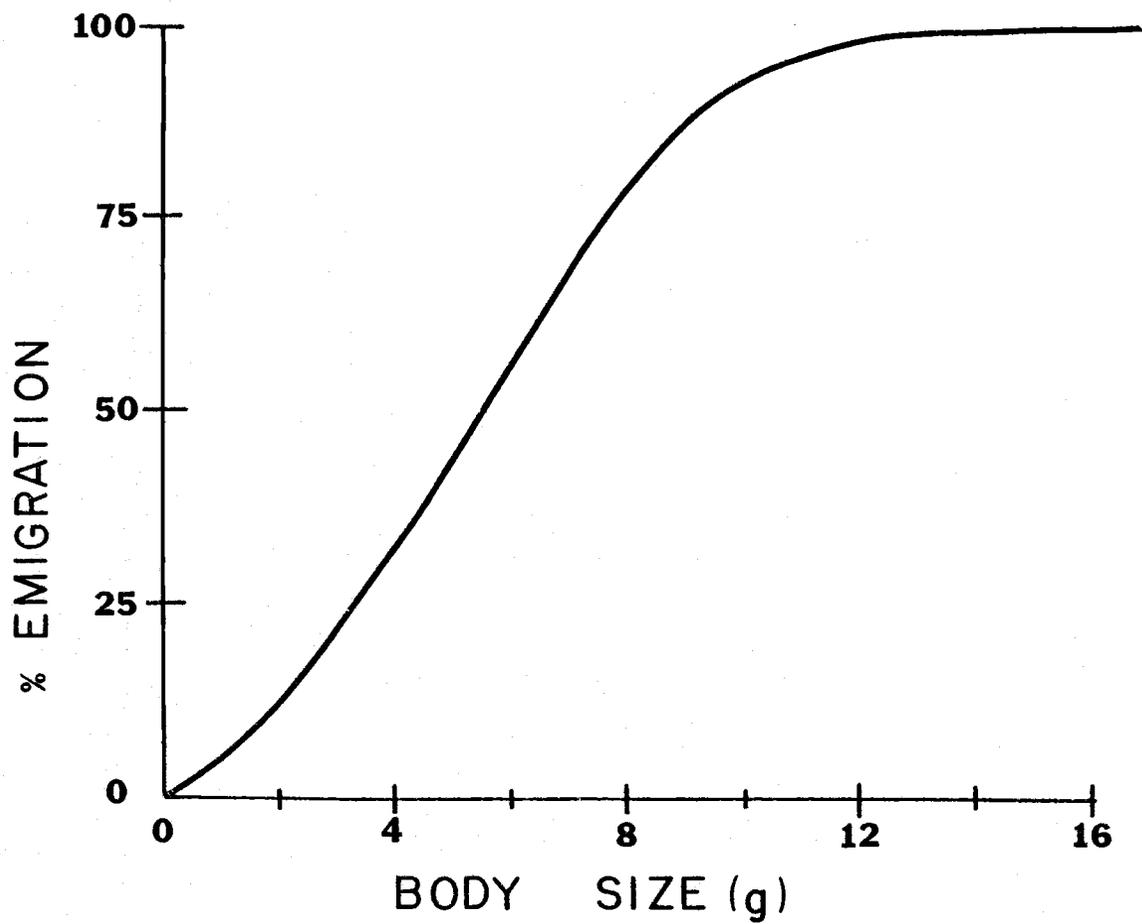


Figure 56. The proportion of smolts emigrating from the estuary to the ocean expressed as a function of the mean body size of the estuarine fish.

migration rate and body weight. In the first relationship, the migration rate is linearly related to mean body weight (Fig. 57). This type of functional relationship was incorporated in the model of Walters et al. (1978). Subsequent verification of the model produced a reasonable coastal distribution of the modelled stocks. The range of body weights and migration rates used to describe this relationship reflect the expansion of the current model to include all age classes of ocean fish. On the other hand, the relationship between the coastal migration rate can be curvilinear (Fig. 58). This relationship is based on the assumption that once fish have reached a particular body weight, the rate of migration is constant. Since the Walters et al. (1978) model only considered a body weight-migration rate relationship for small post-smolt fish, the curvilinear relationship suggested in this model assumes that this functional relationship is not linear for the large ocean fish.

The alternative strategy developed to describe coastal migration was based on the population density in each spatial block. Based on limited data, Barber (1979) hypothesized that the extension of ocean range for Pacific salmon is related to the ocean density of these fish. Given this hypothesis, the coastal migration rate of ocean fish was related to the population density (Fig. 59). The results (Healey, 1978) of length-frequency studies for chinook salmon indicated that the

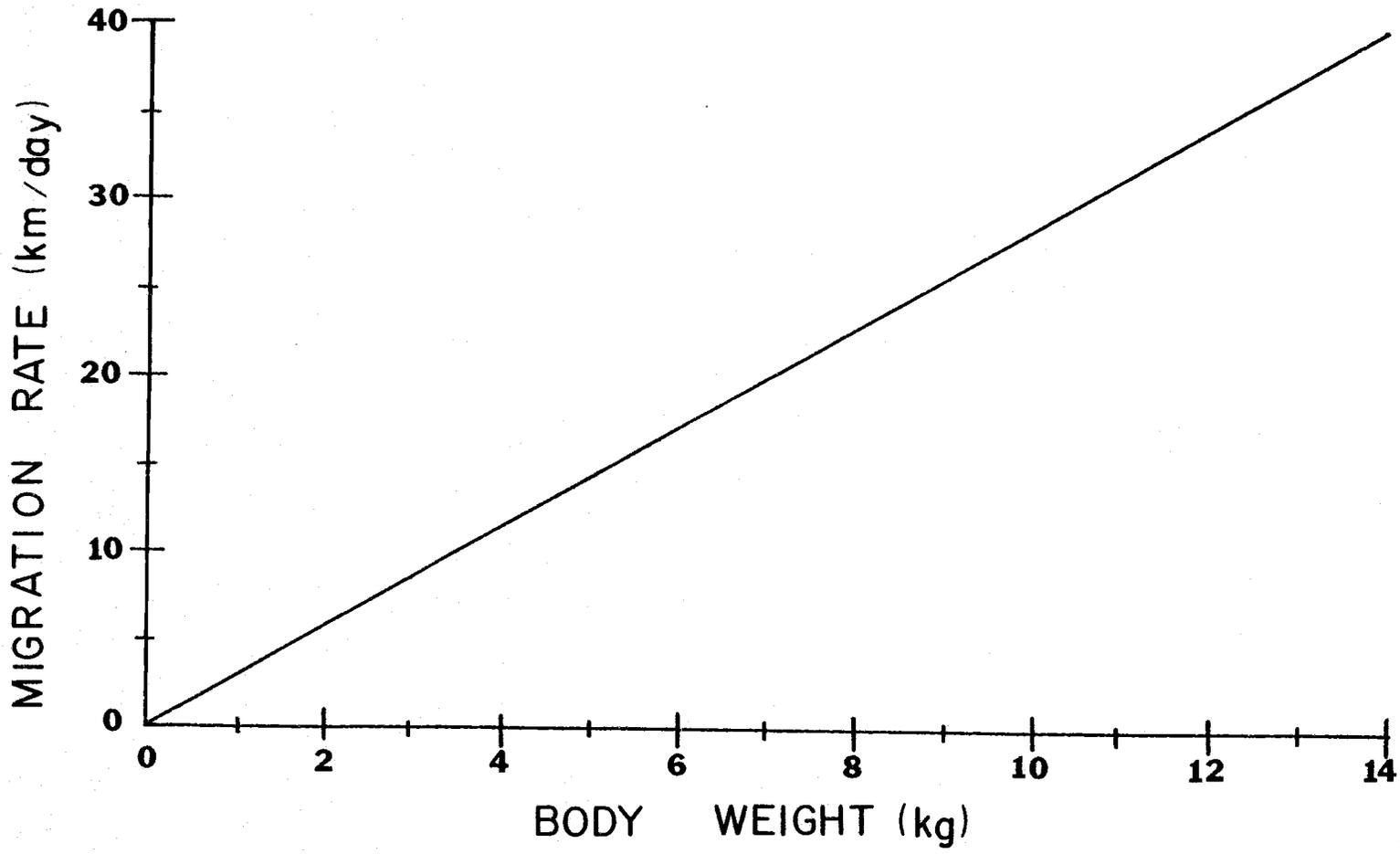


Figure 57. The functional relationship between coastal migration rate and the mean body weight per individual for immature ocean fish assuming a linear relationship between the two variables.

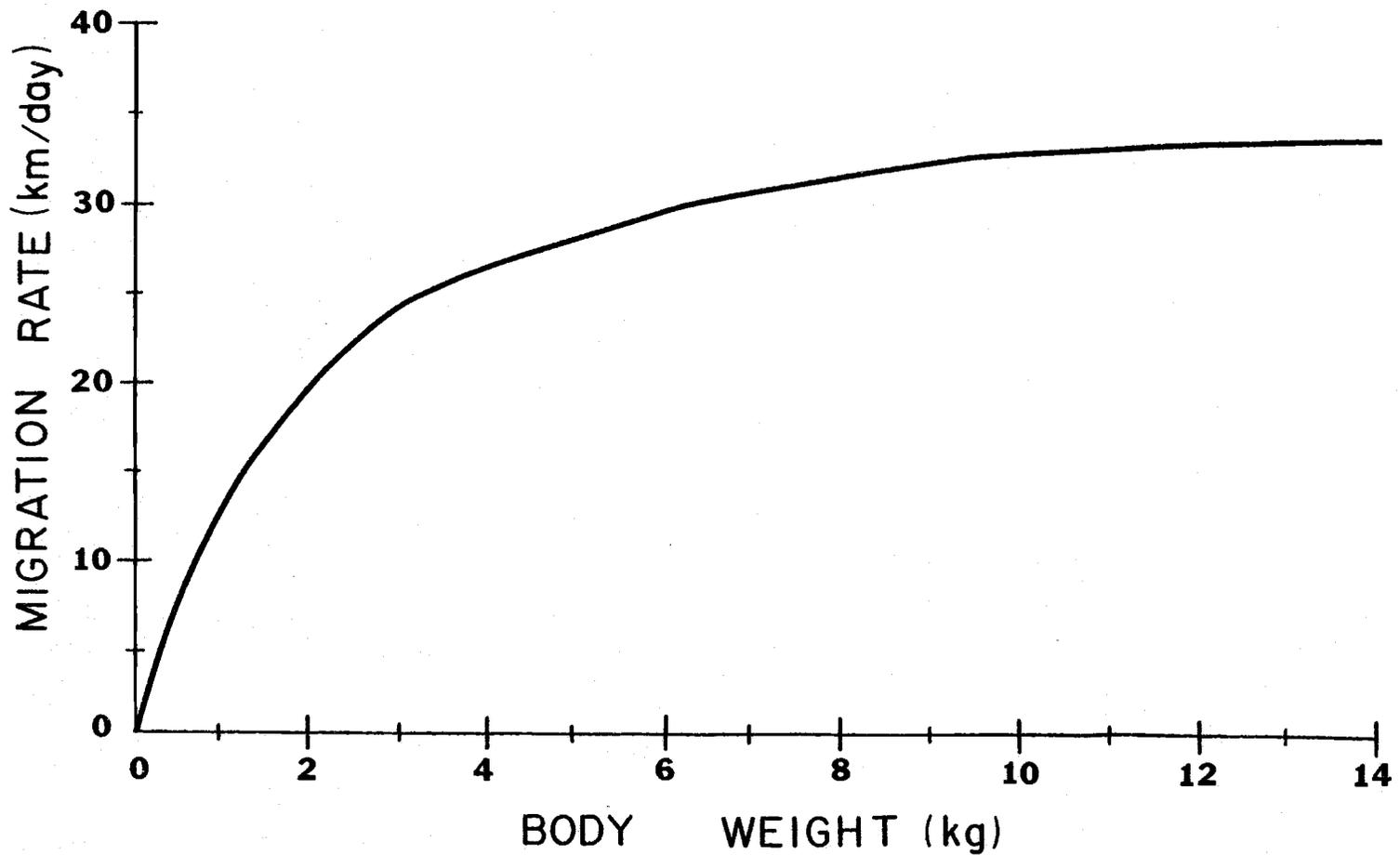


Figure 58. The functional relationship between the coastal migration rate and the mean individual body weights for immature ocean fish assuming a curvilinear relationship between the two variables.

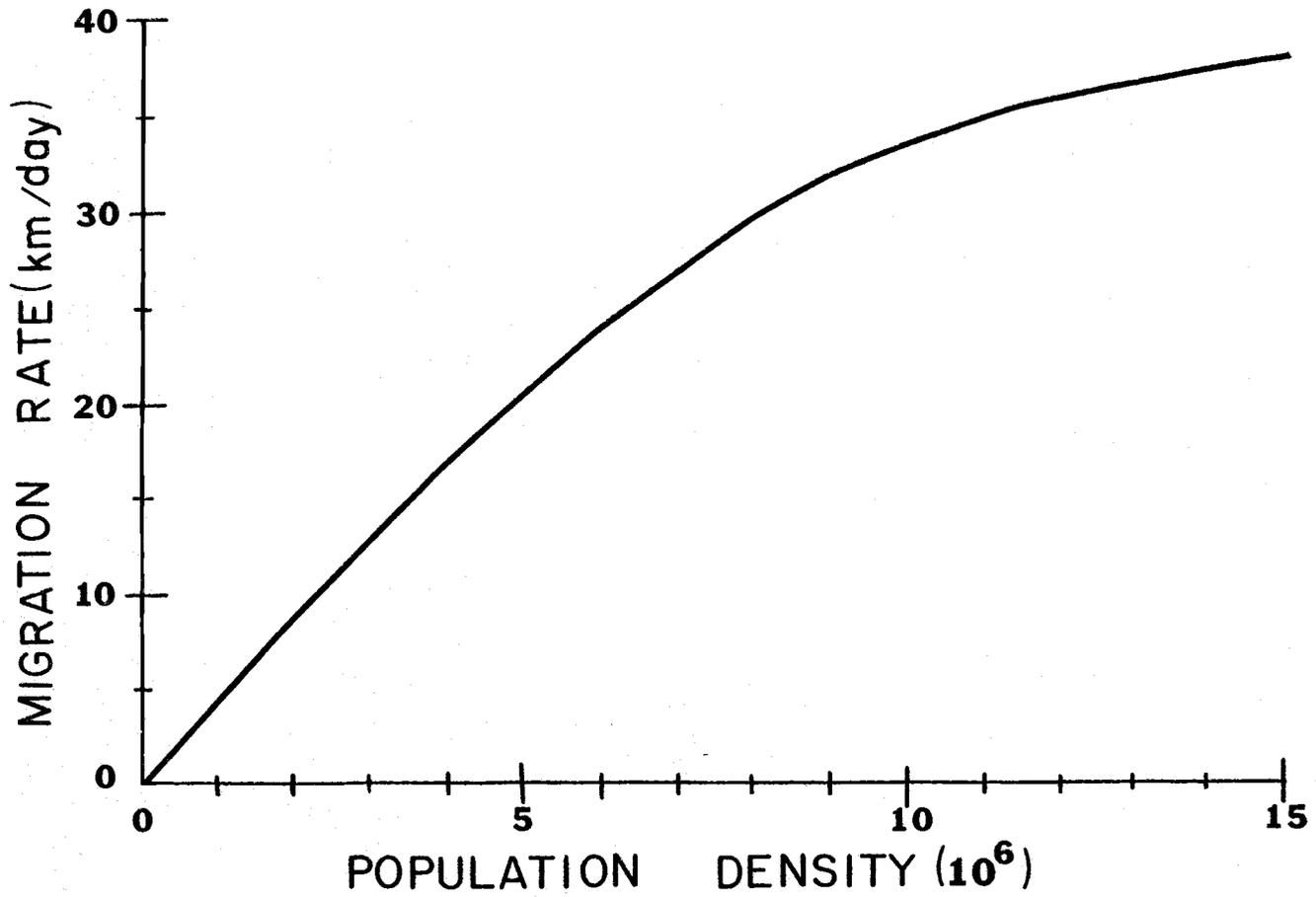


Figure 59. The functional relationship between the population density associated with any spatial block in the ocean and the coastal migration rate.

largest individuals had migrated farther northward than the smallest fish. Based upon these results, the largest fish in each spatial block move northward when coastal migration occurs. After each temporal iteration, the mean body size and variance associated with fish in each block are updated.

The natural mortality rate of ocean smolts is size-dependent (Fig. 60). Presumably, the largest individuals are most likely to escape mortality associated with predation. Since the prey biomass available for consumption determines the growth rate of the salmon, the natural mortality rate can be indirectly associated with the strength of the upwelling event. That is, if a functional relationship between prey density and upwelling exists, strong upwelling years will be characterized by a high ocean smolt growth rate. These fish will subsequently escape predation pressures in fewer weeks than fish entering the ocean during a poor upwelling event.

All calculations in the SGROWTH and SMOVE submodels are reiterated until these fish have spent six months at sea. At this time, as noted by Walters et al. (1978), the growth predictions become unrealistic. The fish have reached their second birthday and the model progresses to the ocean fish submodel.

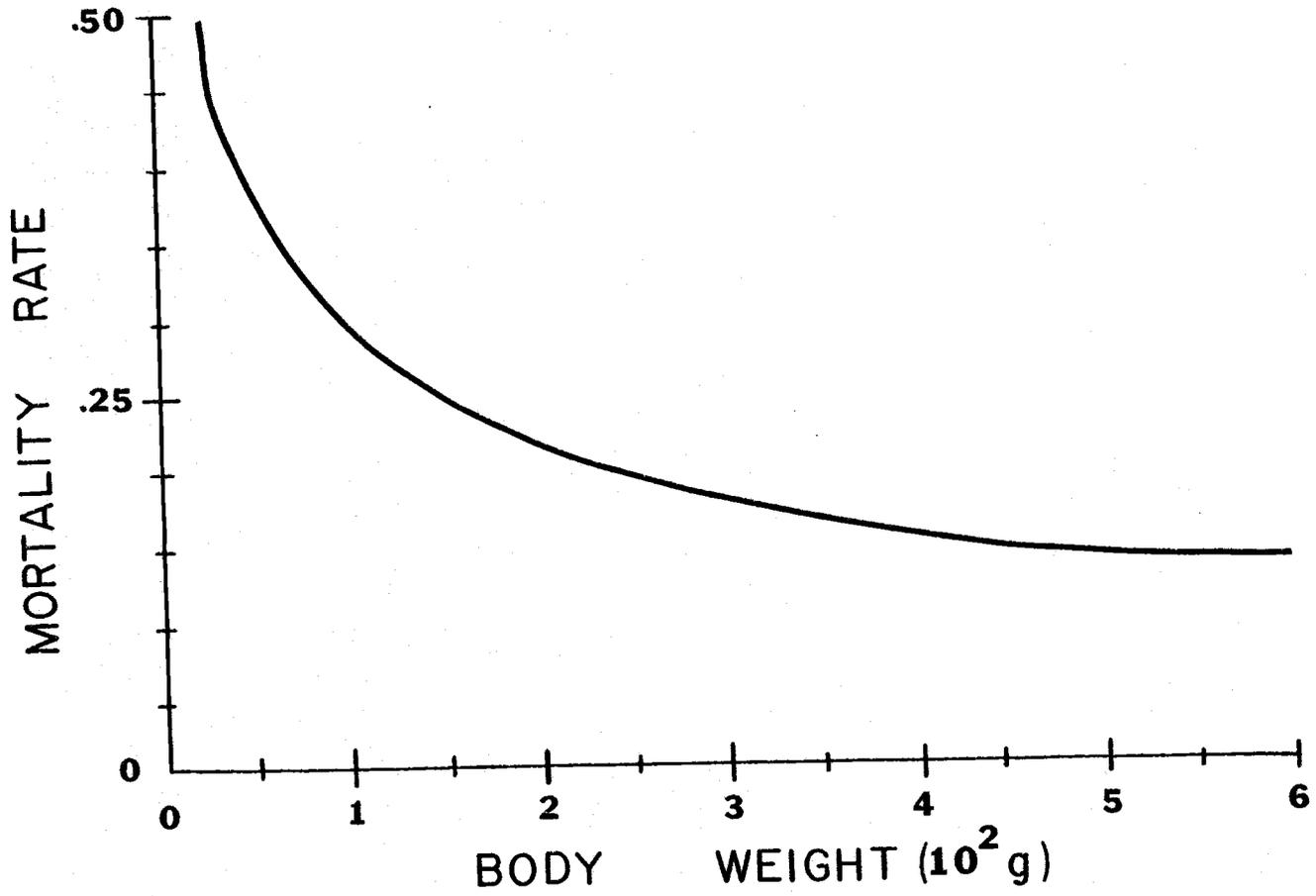


Figure 60. The functional relationship between the mean body weight and the natural mortality rate for ocean smolts (based on Walters et al., 1978).

### Ocean Fish Submodel

Since the factors influencing AGE(2), AGE(3), and AGE(4) ocean fish are similar, the OCEAN submodel makes the necessary calculations for all three age groups (Appendix III-7). The OCEAN submodel calculates 1) the growth and survival of immature two- and three-year-old fish in the ocean, 2) the total landings in the ocean troll fishery, 3) the growth and survival of maturing two-, three-, and four-year-old jack and adult salmon in the ocean, and 4) the number and mean weights of adult fish ready to spawn.

Currently, the mechanisms responsible for determining the age at which a spring chinook salmon matures and returns to freshwater are unknown. To model the ocean maturation of chinook salmon, it is assumed that the age at return is a function of growth rate the year prior to return. Scale studies (Wright and Bernhardt, 1972) have indicated that the earliest maturing fall chinook jack and adult salmon have a faster growth rate the year prior to return than the late maturing fish. Based on these data, the percentage of an entire brood year returning as three- or four-year-old fish is determined from the growth rate of these fish as two- and three-year-old fish respectively (Fig. 61). In the model, it is assumed that mature fish return as three-year-old jack salmon and four- and five-year-old adult spawners. The return of fish older than five years is

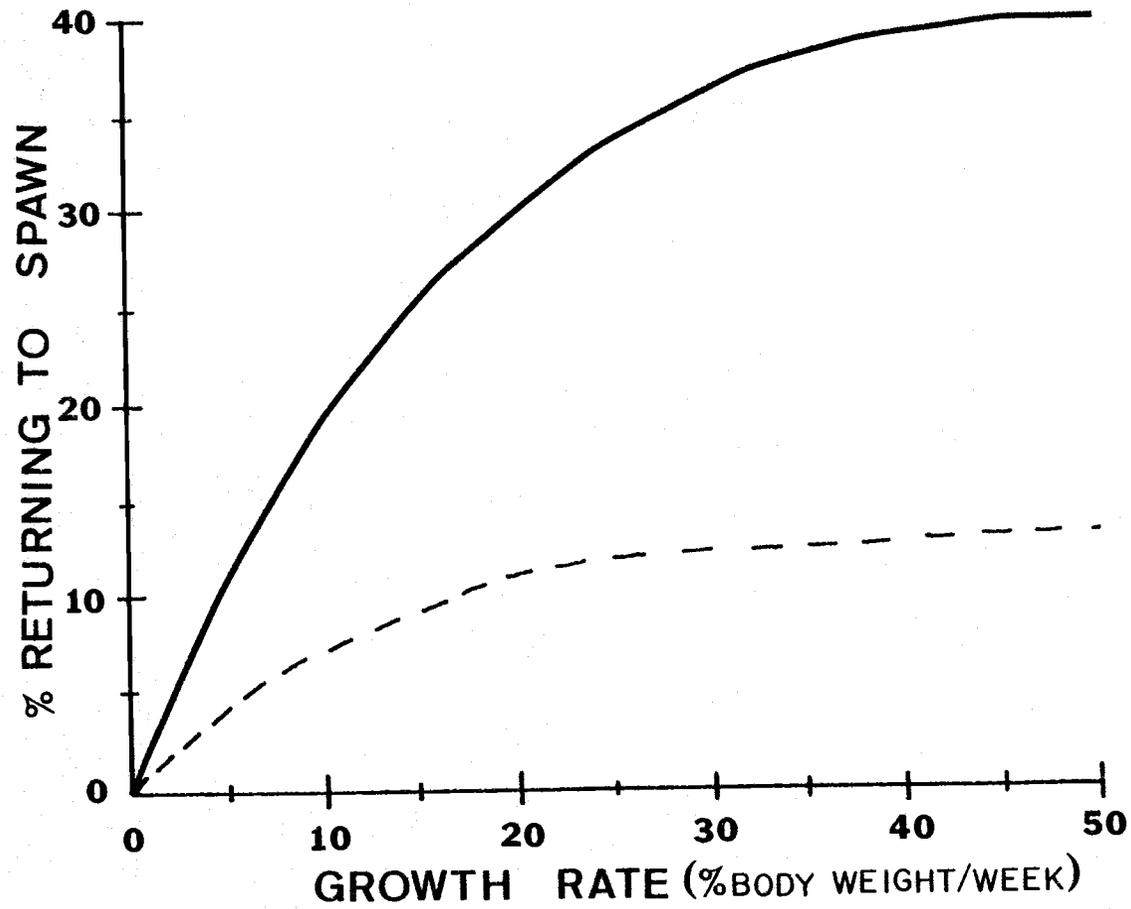


Figure 61. The percentage of three- (---) and four- (—) year old fish returning to spawn expressed as a function of the growth rate and three-year old fish respectively.

considered negligible.

Essentially nothing is known about the ocean life history of upriver spring chinook salmon. Limited tagging studies (French et al., 1975) suggest that these fish migrate northward parallel to the Canadian and Alaskan coastlines. The annual growth rates and survival rates of these fish have not been accurately determined (Ricker, 1976). In addition, the contribution of these fish to any troll fishery is unclear. As a result of the large gaps in data for the ocean life history of these fish, numerous assumptions must be made in the simulation model.

Each of the three age classes (AGE(2), AGE(3), AGE(4)) is treated as a unit in the OCEAN submodel. Initially, the number of maturing fish in each age class is calculated:

$$\text{MATURE}(I+1) = \text{AGE}(I) * \text{RCNT}(I)$$

where RCNT(I) is an array designating the percentage of fish in age class I destined to mature the following year. For the fish maturing as three- or four-year-old fish, the percentage of fish destined to mature the following year is related to the growth rate (Fig. 61). Since no fish return as two-year-old fish, RCNT(1) = 0. Also, RCNT(4) = 1.0 since all immature four-year-old fish potentially return to spawn the following year. Based on the assumed

relationship between maturity and growth rate, the largest individuals of each age group in the SIZE array are designated as maturing fish. The sizes of maturing fish are subsequently stored in the array SPSIZE(I). For each age class, the numbers, mean sizes, associated variances, and locations of both maturing and immature individuals are updated. The calculations internal to each ocean submodel for all immature individuals of each age group are determined for the entire year. After these calculations have been performed, the growth and survival rates for maturing fish of all age groups are determined as a unit in the PRESNAWner subroutines. In all subroutines, the temporal resolution level is weekly.

Ocean Growth Subroutine. The OGROWTH subroutine (Appendix III-8) calculates 1) the ocean growth and survival rates and 2) the coastal migration rates for immature two- and three-year-old ocean fish. The growth rates are dependent upon body weight and ration. Mortality rates, attributed to either natural causes or a fishery, are calculated in the OSURV subroutine. The rate of coastal migration is dependent upon either mean individual body weight or population density within a spatial block. The alternative hypotheses derived in the SMOVE subroutine (Figs. 57-59) are also incorporated in the OCEAN submodel to describe the coastal migration rates of ocean fish.

Controlled studies on the ocean growth rates and ration levels

for immature and maturing spring chinook salmon have not been performed. Essentially no information exists to suggest reasonable ration levels and the species composition of prey items for spring chinook salmon. It is assumed that fish species comprise the bulk of the food items for spring chinook salmon that have spent at least six months at sea. Although the feeding strategies of freshwater and ocean salmon may differ, it is assumed that the types of functional relationships used to describe juvenile salmon growth also describe the growth of ocean salmon. Different growth rates and prey biomass densities are used to describe the growth of ocean fish.

In the absence of extensive data on the species composition of prey items, the food available to the salmon is classified only as net biomass. The ration levels for each spatial block are simulated for each weekly time interval within the OGGROWTH subroutine. The mean maximum ration level (Fig. 62) and the mean maintenance ration level (Fig. 63) and associated variances per individual at age are determined from the mean body weight of the fish at age in each block. The total maintenance and maximum ration levels are determined for each spatial block. The percent of the maximum ration level potentially consumed is based on the available food biomass in each block (Fig. 64). The amount of food actually consumed in each block is modelled as a depletion attack process. If the ration level in

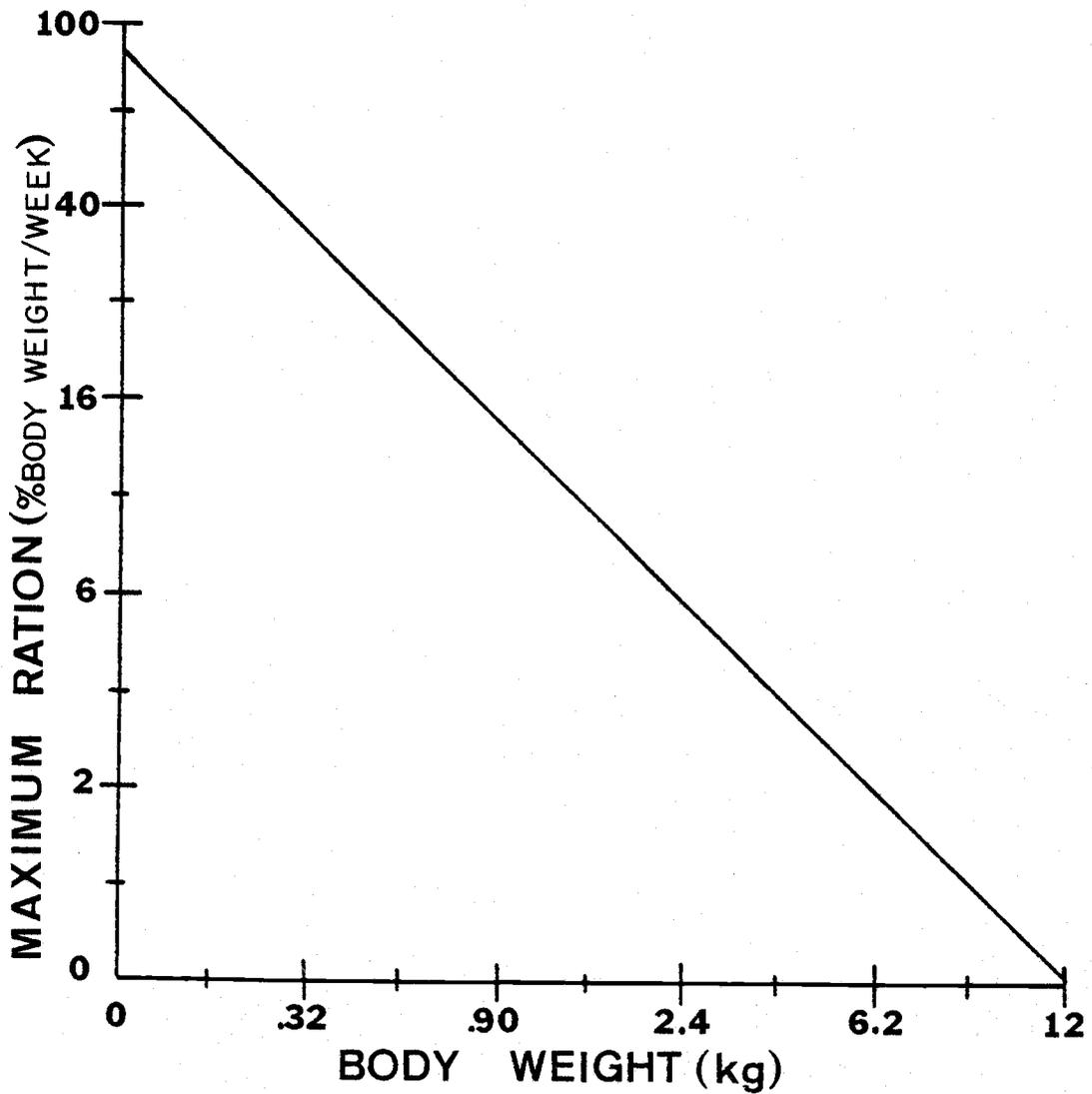


Figure 62. The relationship between the mean individual body weight and the mean maximum ration for immature ocean fish (based on Brett, 1974; Brett, 1976).

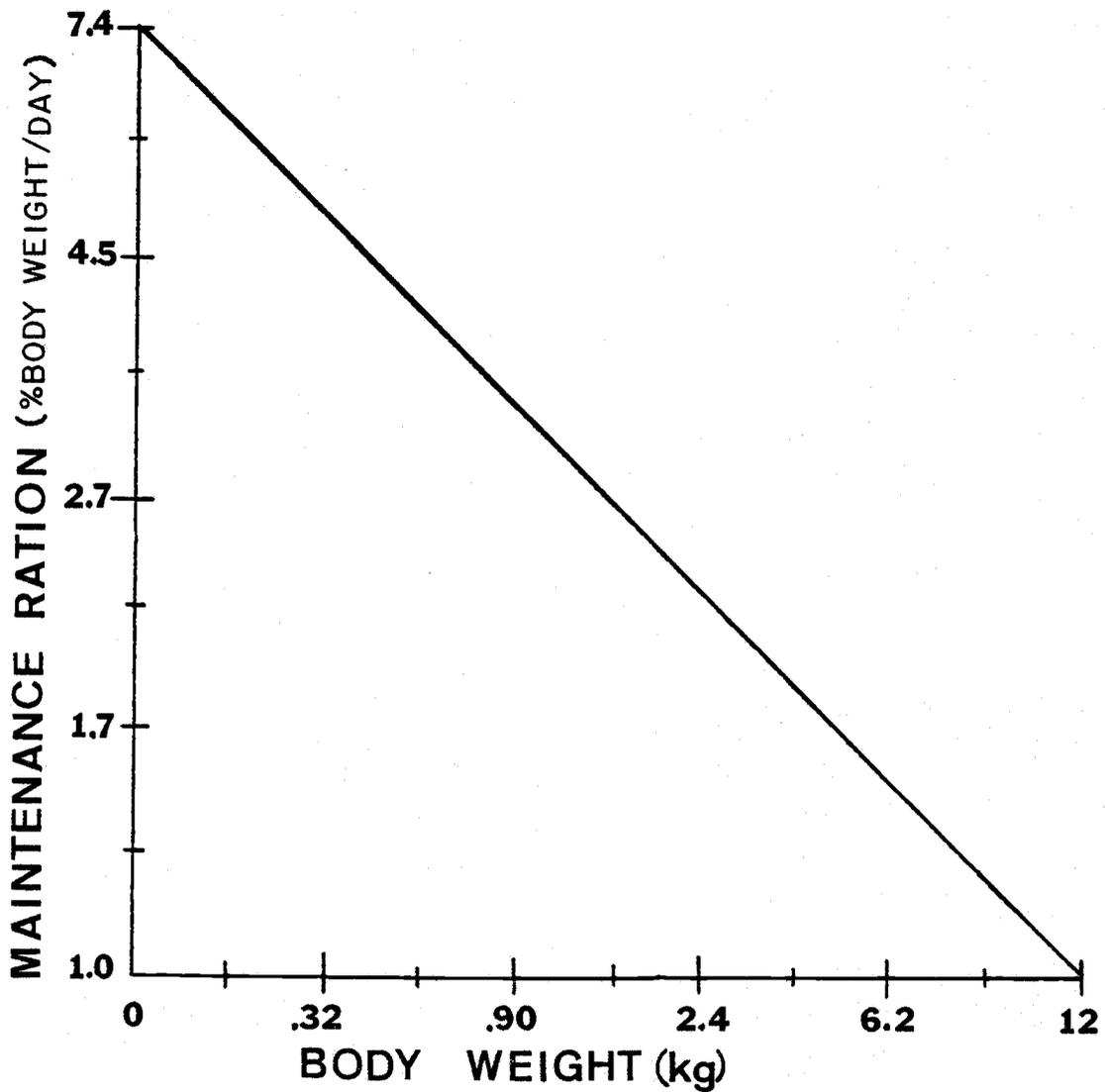


Figure 63. The relationship between the mean individual body weight and the mean maintenance ration for immature ocean fish (based on Brett, 1974; Brett, 1976).

Figure 64. The percent maximum ration actually consumed as a function of the total food density.

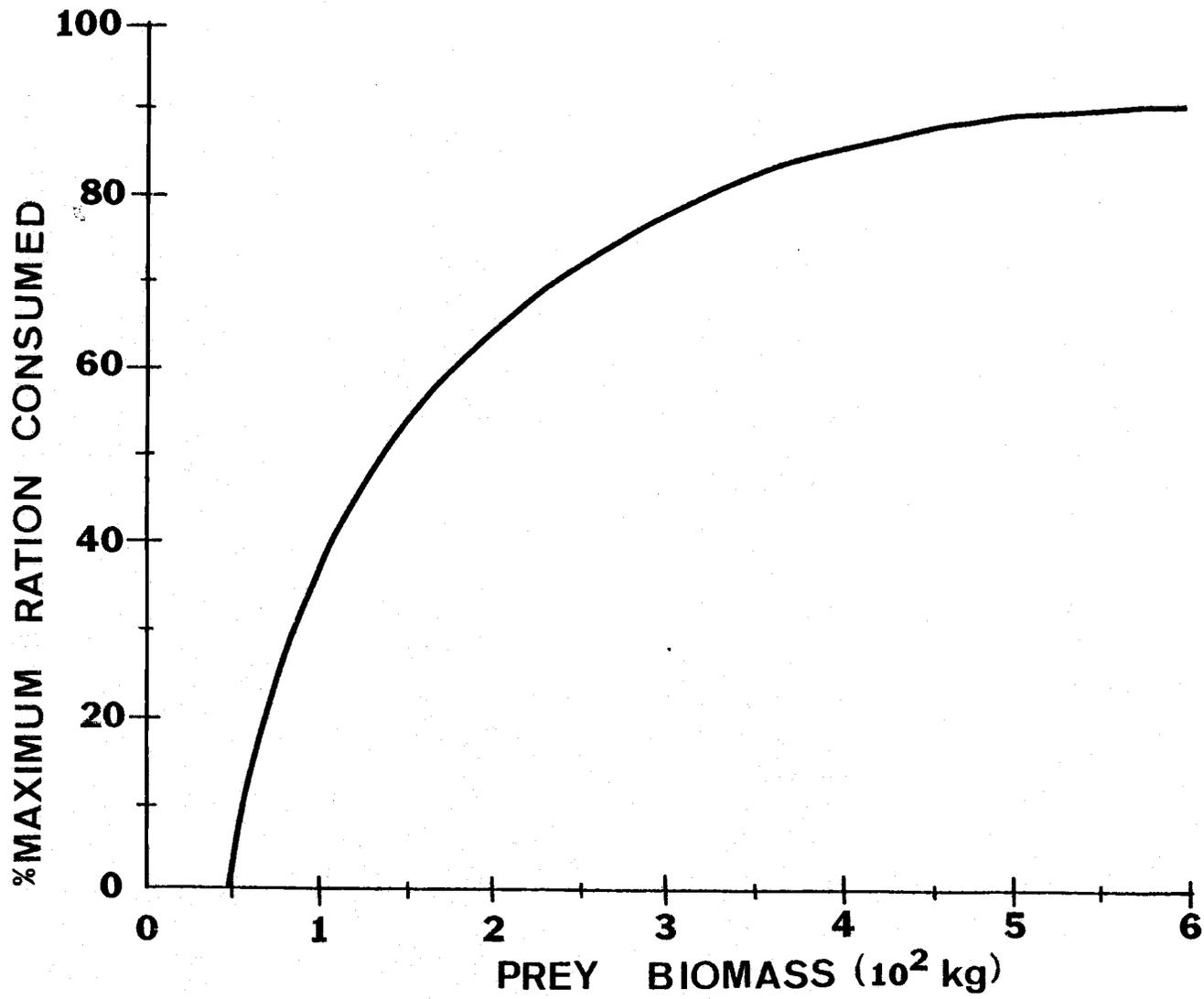


Figure 64.

a spatial block is greater than the total maintenance requirement for the block, the weekly growth rate is determined. Since growth rates of Pacific salmon decrease with an increase in age (Ricker, 1976), the growth rate of ocean fish is dependent upon age (Fig. 65). The mean weights of fish in the block are updated.

No data exist to determine the types of factors responsible for the coastal migration of any species of Pacific salmon. To deal with the coastal migration of the ocean fish in the current model, two alternative hypotheses were developed. The first hypothesis is based on the assumption that food is the driving mechanism for coastal migration. A curvilinear relationship is suggested (Fig. 66) between the total ration actually available as food and the proportion of the population that will migrate. This relationship is based on the assumption that individuals will leave a block when food is limiting in search of a new feeding ground. Given that the largest fish have a greater demand for food than the smallest fish due to the food ration-body size relationship, the largest fish in the block migrate. The rate of coastal migration is related to either body size (Figs. 57 and 58) or to population density (Fig. 59). When coastal migration occurs, it is assumed that all fish consume a maintenance ration and no growth occurs. Based on very limited data, only four- and five-year-old spring chinook salmon originating from the Columbia River

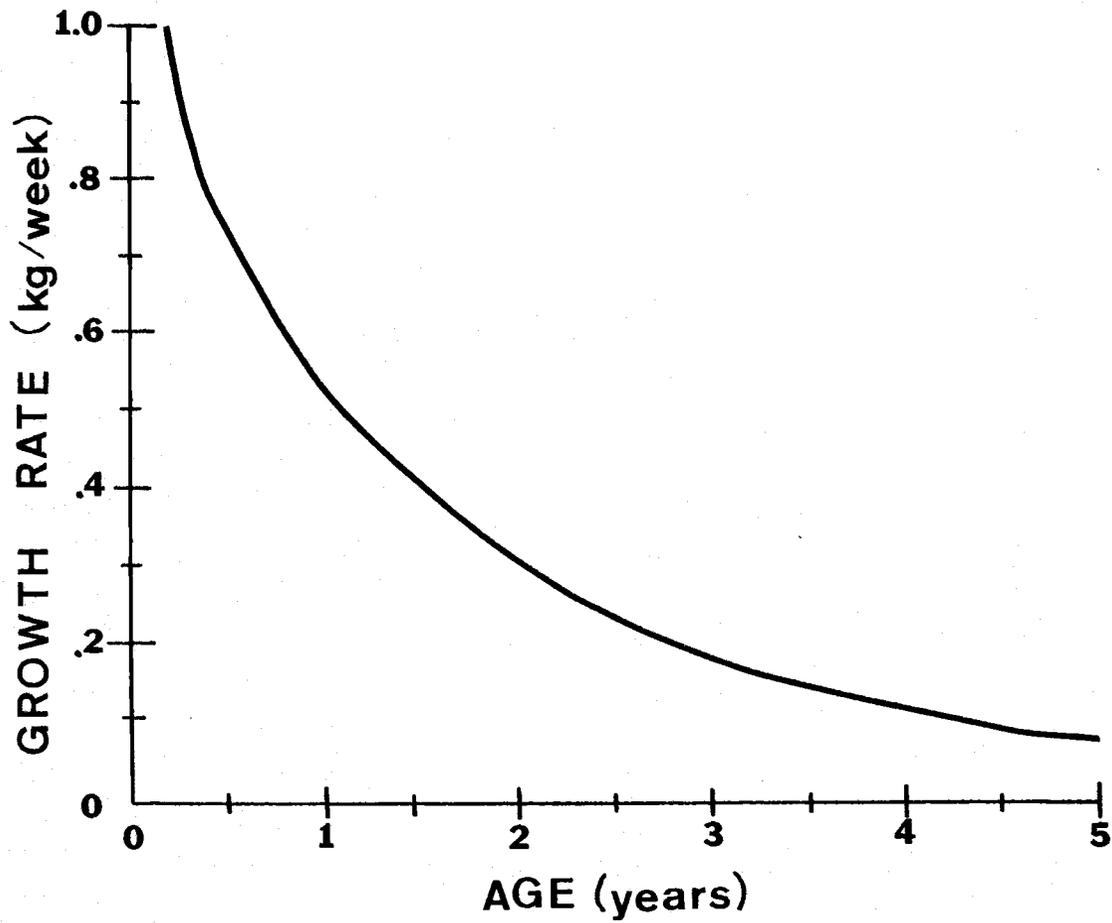


Figure 65. The growth rate of immature ocean fish expressed as a function of age.

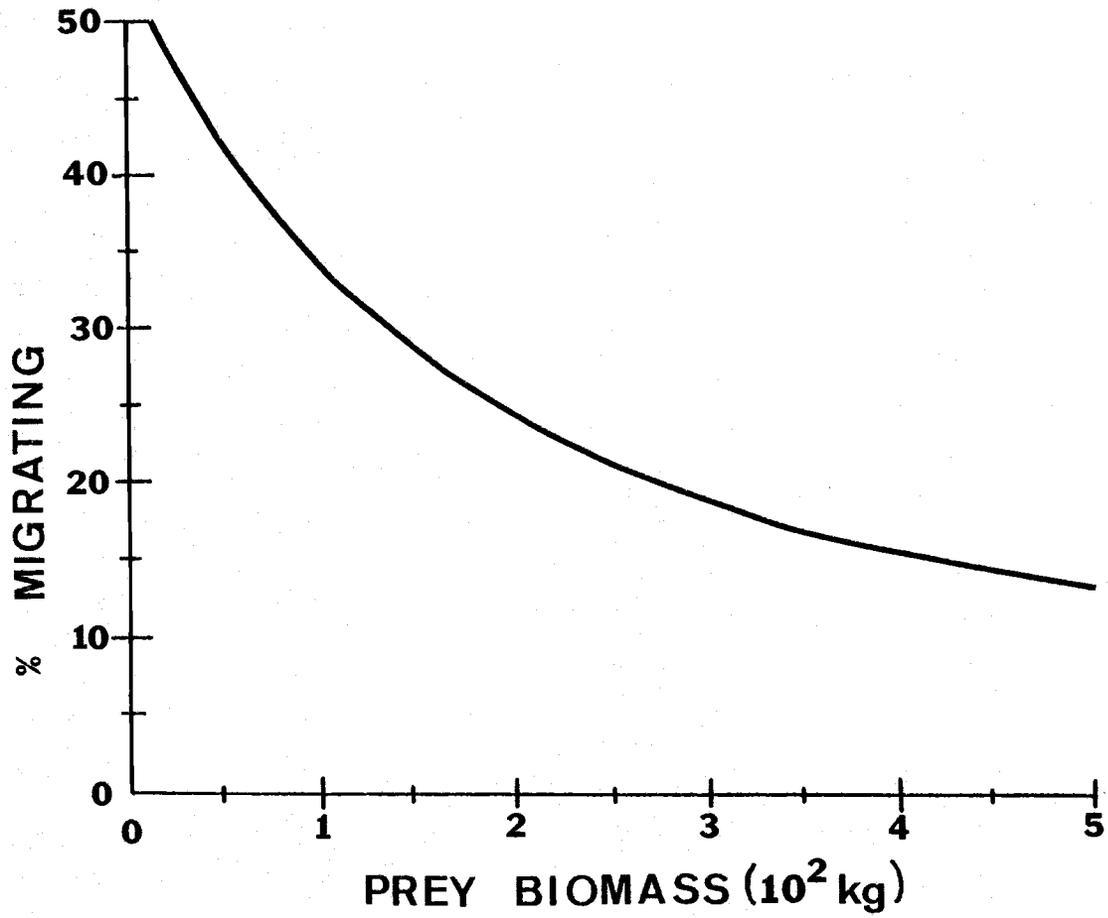


Figure 66. The proportion of the ocean spatial block population that migrates expressed as a function of the ration level available to the modelled fish in the spatial block.

have been recovered in the Aleutian Islands. The mechanism responsible for coastal migration should predict that the oldest fish will migrate the farthest from the Columbia River.

The alternative hypothesis to a food related migratory mechanism is a density related migration. Obviously, the two hypotheses are not mutually exclusive. The second hypothesis is based on a curvilinear relationship between the population density of the block and the proportion of the block population that migrates (Fig. 67). Migrating individuals are randomly selected among all individuals of the block. After the coastal migration is calculated for the fish in all spatial blocks, the mean weights, associated variances, and location of fish are updated. After these calculations have been performed, the OSURV subroutine is called.

Ocean Survival Subroutine. The OSURV subroutine (Appendix III-9) calculates 1) the weekly natural ocean mortality and 2) the weekly troll fishing mortality for immature ocean fish. Natural mortality due to predation, diseases, and other causes is assumed to be size-dependent (Fig. 68). The largest fish have a higher survival than the smallest individuals. The mortality rates associated with the vertical axis are based on limited scale analyses (reviewed by Ricker, 1976). The largest weights in the SIZE(I) array are associated with the surviving fish.

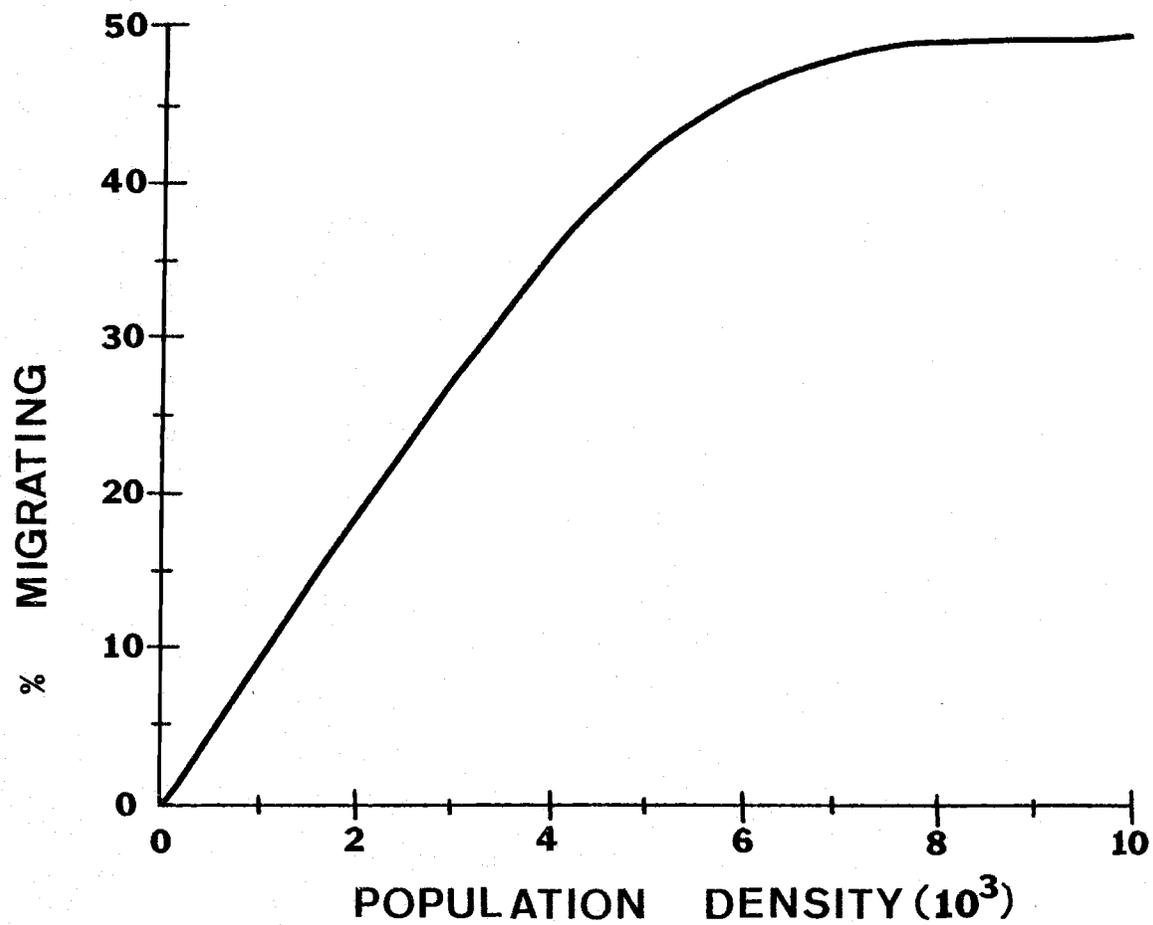


Figure 67. The proportion of any ocean spatial block population that migrates expressed as a function of the population density associated with the spatial block.

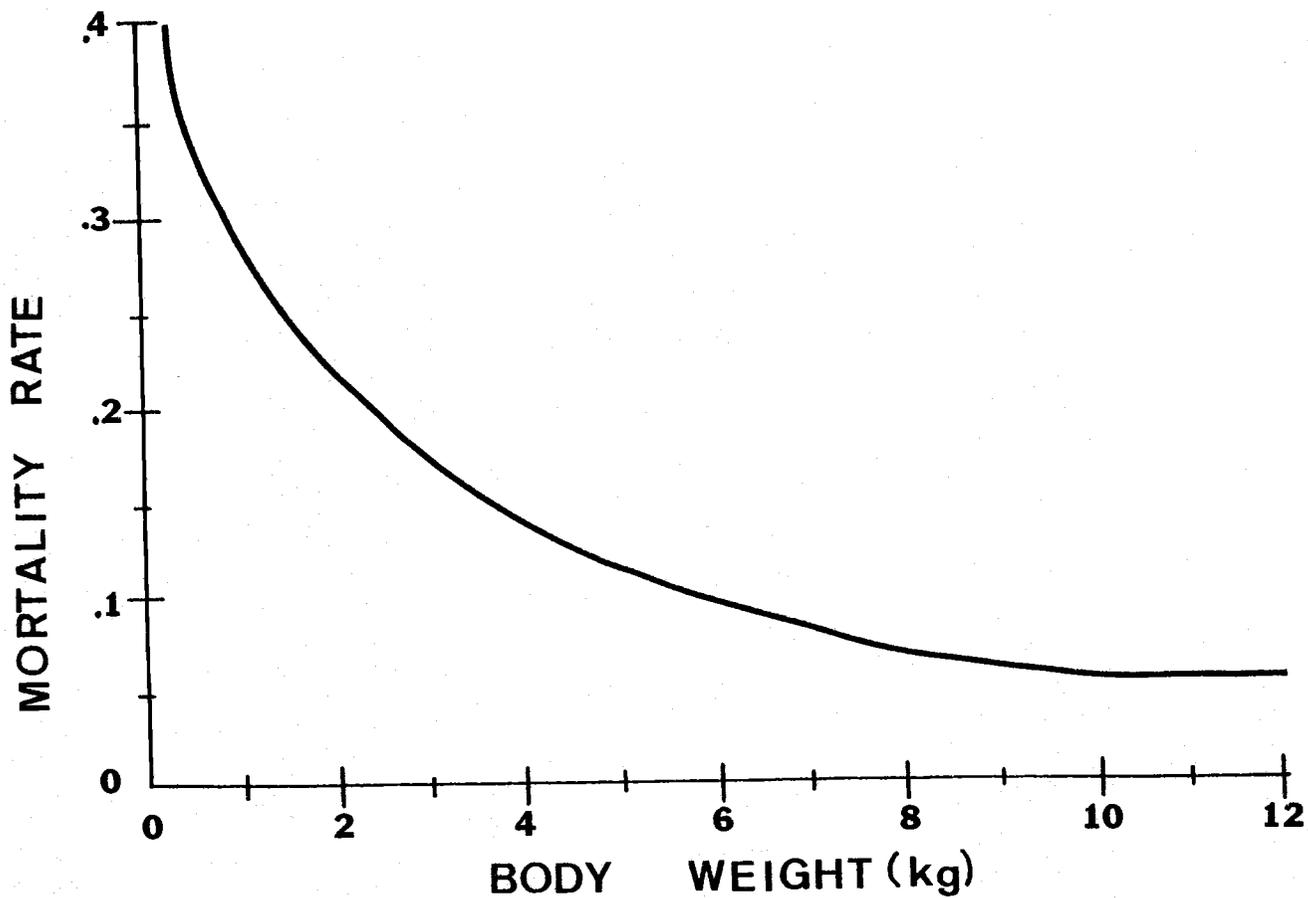


Figure 68. The functional relationship between the natural mortality rate and the mean body weight associated with ocean fish.

Although no data exist to suggest that upriver spring chinook salmon contribute to a domestic troll fishery, the results of the statistical analyses in this study suggest that these fish may be landed in the Canadian troll fishery. To account for this possibility, a size-limited fishery is included in the blocks corresponding to Canadian waters. For all fish in the designated blocks, the individual body weights (kg) are converted to fork length (cm) (Ricker, 1971). The model determines the number of fish in each block that are large enough to be landed in the troll fishery. The weekly fishing mortality rate for each block is input by the modeller. In addition, the size of entry to the fishery is input for each fishery by the modeller. In this way, the user controls the length of the fishing season each year. Thus, it is possible to account for no fishing mortality during season closures and to incorporate some management regulations into the model. For those blocks outside Canadian waters, the user should designate an unreasonably large (i. e. 10 m) size limit for entry to the fishery. In this way, no fish will ever enter the fishery and fishing mortality in these waters will be zero. The total number of fish surviving all mortality processes is determined for each block. The calculations internal to the OGWOTH and OSURV subroutines are repeated for all spatial blocks, all age classes, and all temporal iterations until the ocean fish reach their next birthday.

### Pre-Spawner Submodel

The processes influencing fish of all age classes designated to return as mature fish the following year are calculated in the submodel PRSPAWN (Appendix III-10). This submodel calculates 1) the ocean growth and survival during the last six months at sea, 2) the mortality in the Columbia River gill net fishery, 3) the mortality related to Columbia River environmental conditions during upstream migration, 4) the mortality attributed to the sport fishery, and 5) the natural mortality in the native stream prior to spawning. It is assumed that these fish do not migrate northward once they have been designated as maturing fish. Since the arrival of these fish in the Columbia River coincides with the opening of the troll fishery season, it is also assumed that these maturing fish are not landed in the coastal fishery during the last six months at sea. Initially, the PRSPAWN submodel determines the ocean growth and survival of the maturing fish by calling the PGROWTH subroutine.

The PGROWTH subroutine (Appendix III-11) calculates 1) the ocean growth rate and 2) the ocean survival rate of the maturing fish. The method for calculating ocean growth is identical to that previously described for the OGROWTH subroutine. The maximum ration (Fig. 62) and the maintenance ration (Fig. 63) are calculated from individual body weights. The total ration level for each block, which is

internally simulated, is adjusted (Fig. 69) to reflect the proportion of the ration required for the maturation and development of the reproductive organs. The growth rate of maturing fish is assumed to be less than that of immature fish of the same age modelled in the OGROWTH subroutine. The relationship between growth rate and age (Fig. 70) is similar to that for immature fish but the vertical axis is rescaled to reflect the energy required for maturation and reproductive development. The weights of fish in each block are updated. The natural mortality rate for the maturing ocean fish depends on body size (Fig. 68). The ocean growth and mortality calculations are performed for each block for five months. At this time, the fish have returned to the mouth of the Columbia River.

As soon as the maturing fish enter the Columbia River, all three-year-old spawners (MATURE(3)) are eliminated. Since the number of eggs potentially deposited by the current brood is controlled only by the number of female spawners, male fish are no longer of interest in the model. In addition, all three-year-old spawners are precocious males and do not contribute significantly to the gill net fishery. It is assumed that a sufficiently large number of males exists on the spawning ground to insure fertilization of all eggs. Since one male can fertilize several redds, this assumption appears justified. The escapement of adult spawners from the

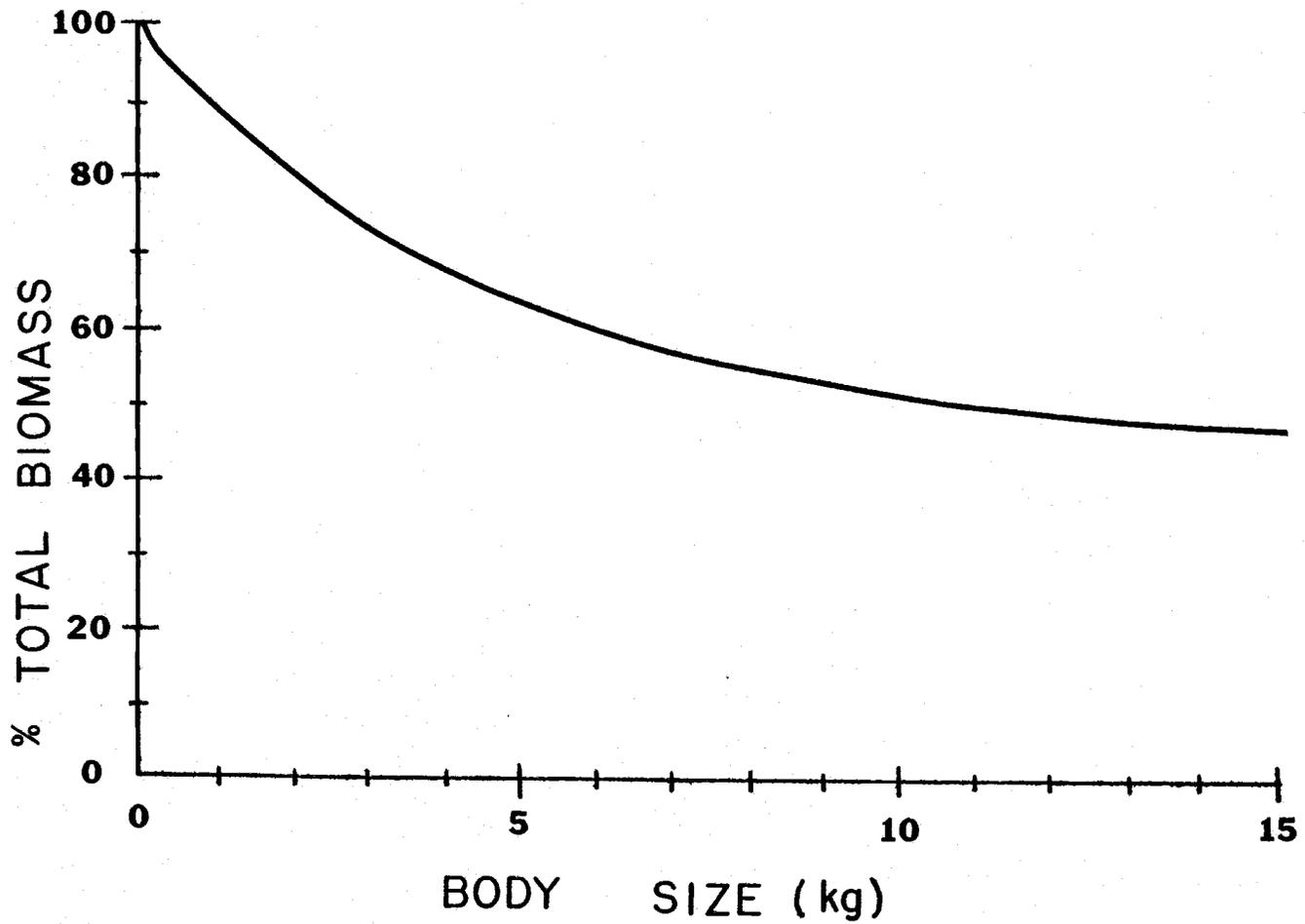


Figure 69. The percentage of the total prey biomass actually available to maturing ocean fish for growth expressed as a function of mean body size of these fish.

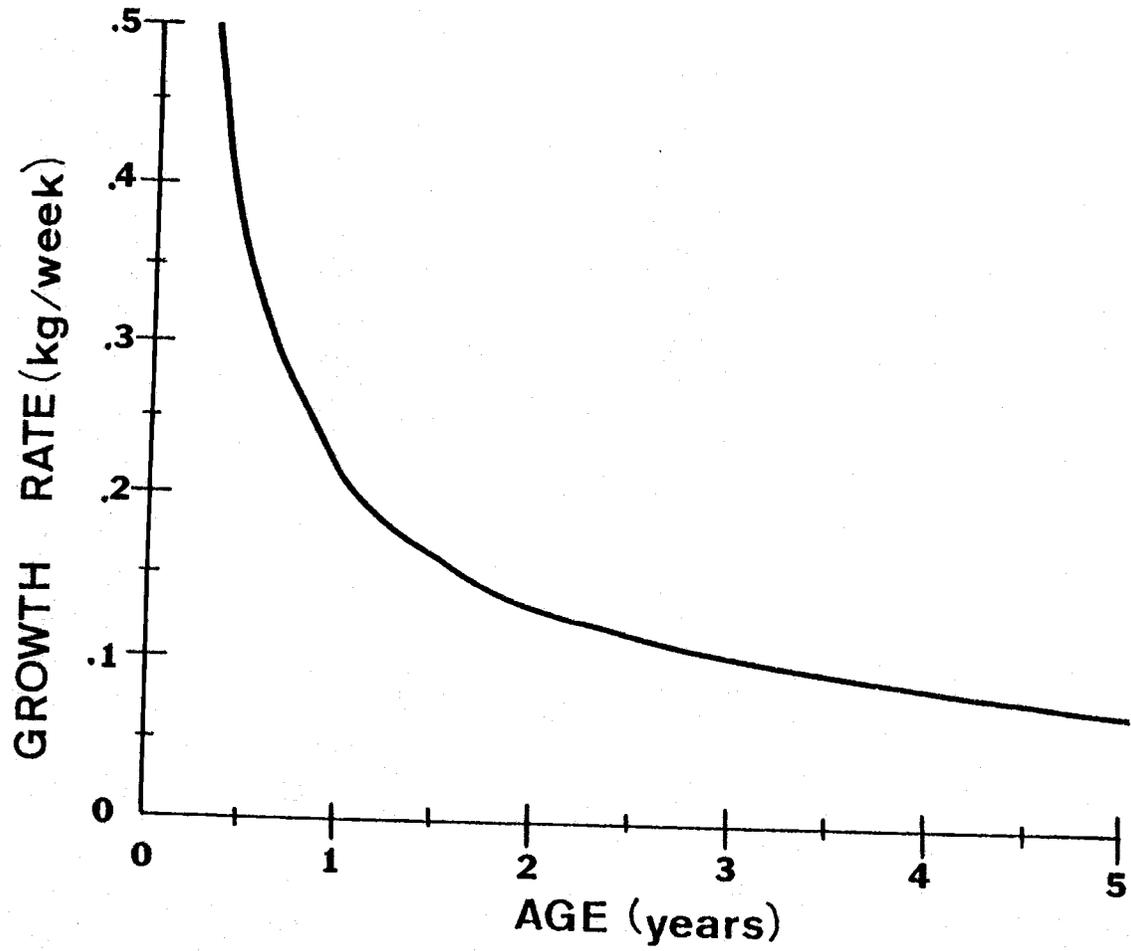


Figure 70. The growth rate of maturing ocean fish expressed as a function of age.

Columbia River gill net fishery is related to the population density of returning fish (Fig. 71) (ODFW and WDF, 1977). This relationship, based on data for all stocks of upriver fish, is scaled to reflect the range of run sizes anticipated for one upriver stock. The number of survivors is calculated and the mean weight and variance associated with the survivors is determined.

The adult spawners must migrate upstream across a series of dams before reaching the native stream. At each dam, fish may "fall back" over the dam thus delaying the rate of upstream migration (Junge and Carnegie, 1976). The rate of fall back (% FB) may be related to the amount of water spilling over the dam (Johnson, 1965). The spill at each dam is internally simulated based upon actual data for the months of upstream migration. In this model, the rate of fallback is calculated as a function of spill for either a Snake River or a Columbia River dam (Fig. 72). The data used to develop the functional relationship are from Johnson (1965). Johnson also determined that fifty percent of the spawners falling back over each dam subsequently die. The mortality attributed to fallback is calculated:

$$\text{MORT} = 0.5 * (\text{MATURE}(4) + \text{MATURE}(5)) * \% \text{ FB}$$

where % FB is the percent fallback calculated from the spill. The incidence of fallback may actually be related to the proportion of spawners that have migrated past their stream of origin. Verification

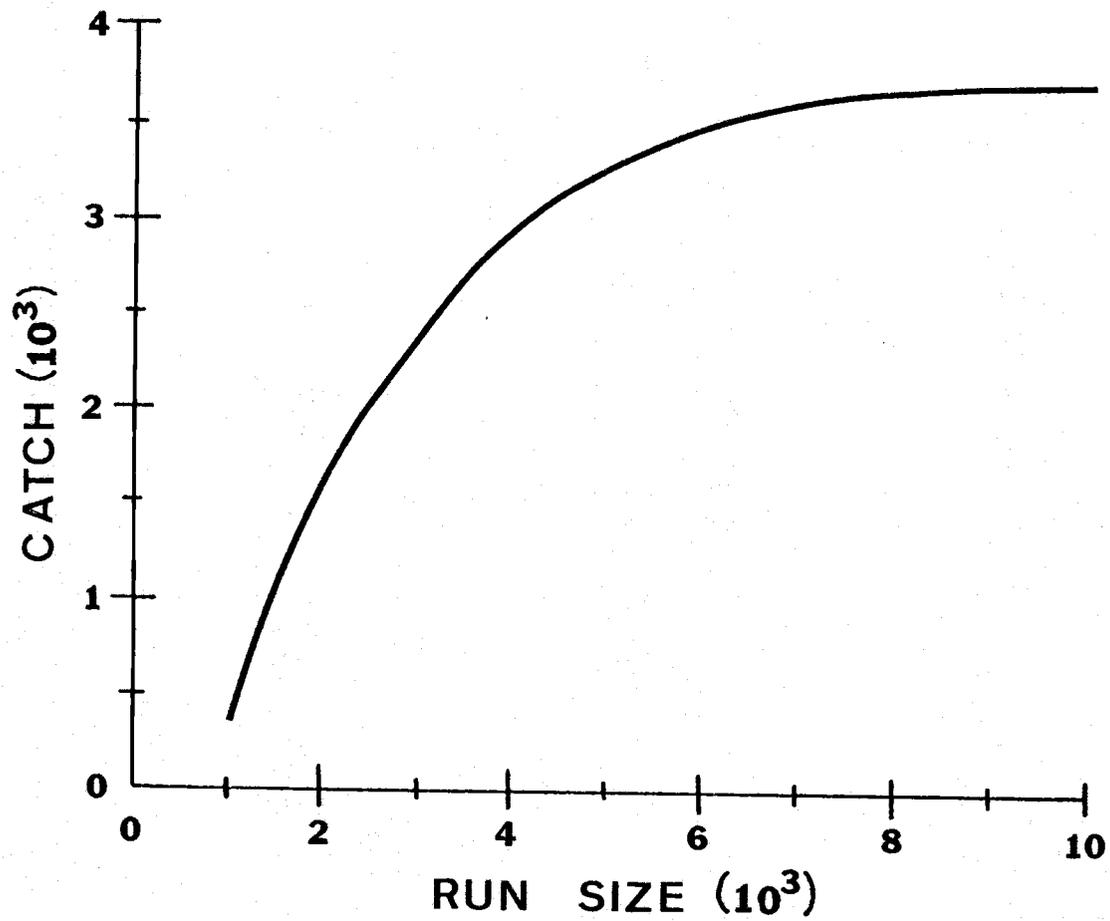


Figure 71. The density dependent relationship between the numbers of upriver fish captured in the gill net fishery and the total number of upriver fish returning to the Columbia River.

Figure 72. The percentage of adult spawners falling back across Columbia and Snake River dams expressed as a function of the spill of water over each dam.

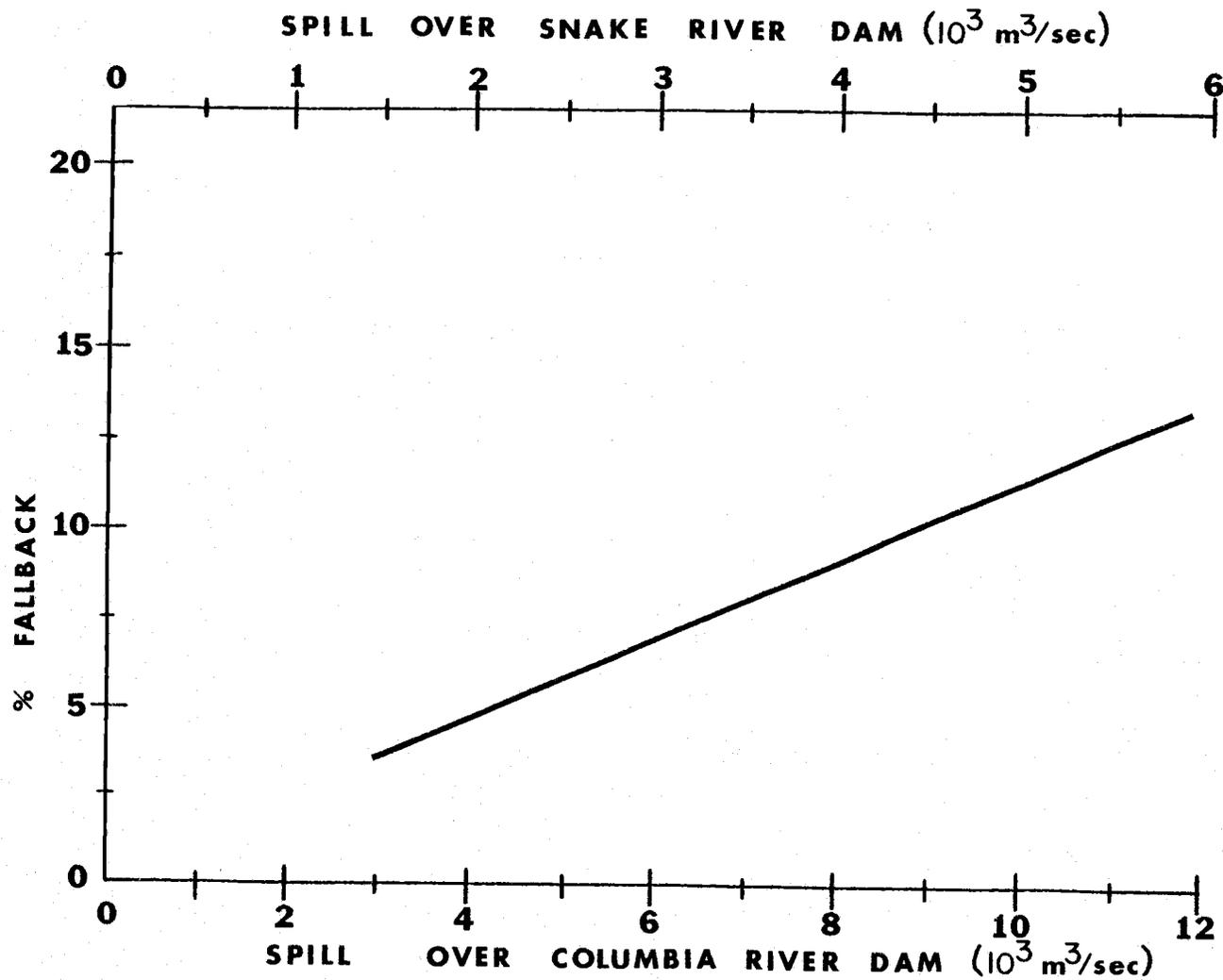


Figure 72.

of the model would permit the testing of this hypothesis.

Laboratory and field studies (Nebeker et al., 1976; Merrell et al., 1971) indicated that 16 to 40 percent of the adult chinook salmon died when exposed to water with high levels of air supersaturation. In the Columbia and Snake Rivers, a strong correlation exists between the amount of water spilling over a dam and the supersaturation level in the adjacent water. To model this mortality process, the mortality rate during upstream migration is calculated as a function of the spill over the dam (Fig. 73). A distinction is made between Columbia and Snake River dams due to the different flow regimes in the two rivers. After the fish have crossed each dam, the total number of surviving fish is calculated:

$$N_t = N_o e^{-(MORT + NMORT)}$$

where MORT is the mortality attributed to fallback and NMORT is the mortality attributed to nitrogen supersaturation. These calculations are repeated for each dam until the fish reach the stream of origin.

In the native stream, the fish reside in deep pools throughout the summer months until spawning occurs in the fall. During this time, the fish are subjected to mortality from natural causes and from the sport fishery. Surveys from Idaho streams (Ortmann, 1976) suggest that the survival rate in the Idaho sport fishery is related to the population density (Fig. 74). In addition, it is assumed that the

Figure 73. The natural mortality rate of adult fish expressed as a function of the spill over Columbia and Snake River dams during the upstream migration of spawning adult salmon.

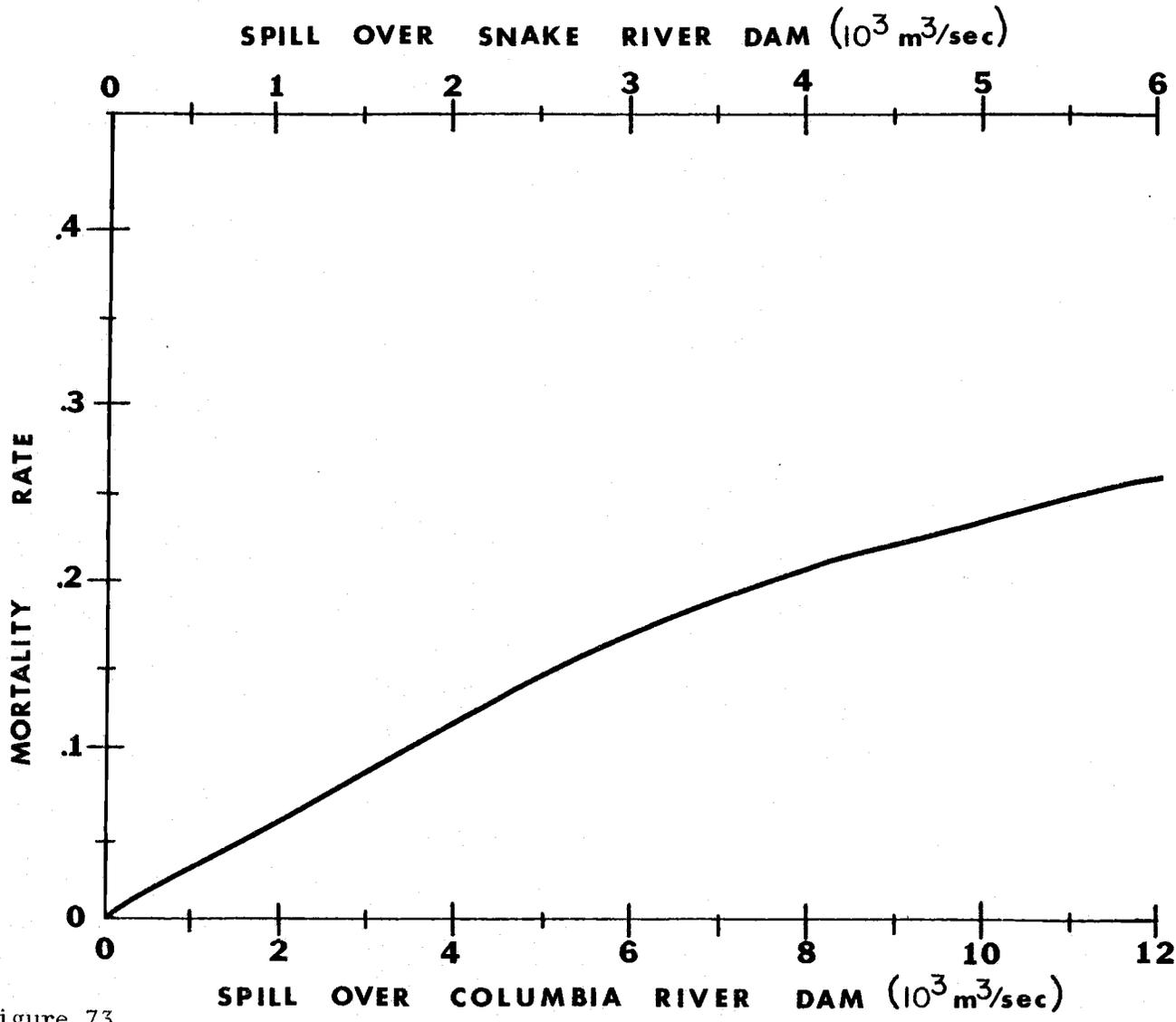


Figure 73.

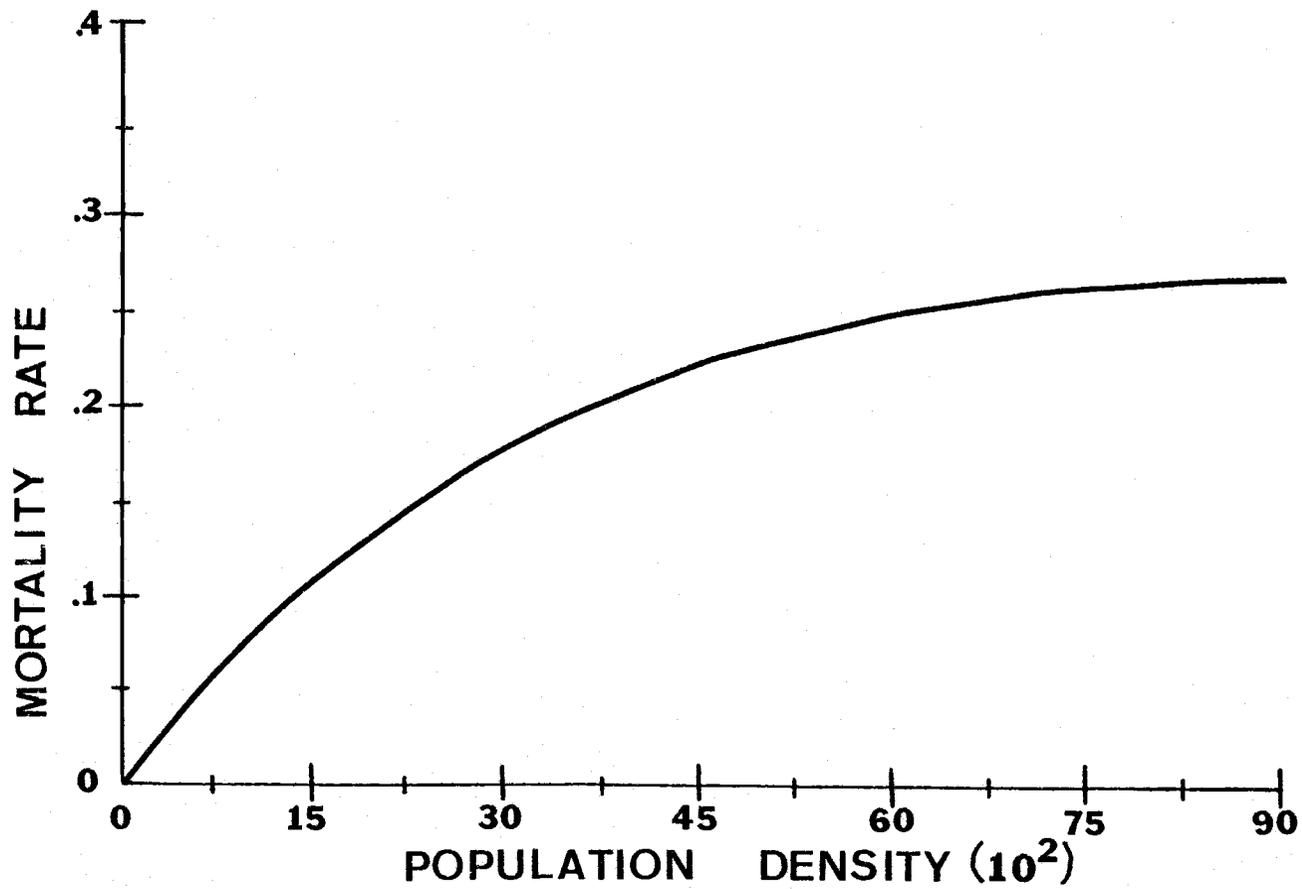


Figure 74. The sport fishing mortality associated with the modelled stock calculated as a function of the adult spawning density.

natural survival rate of these fish is density-dependent (Fig. 75). The total mortality in the native stream is calculated and the sizes of the surviving fish are selected from the largest individuals in the SPSIZE(I) array. It is assumed that the contribution of straying fish (cf. Ricker, 1972) from other streams to the modelled spawning stock is not significant. At this time, the fish are ready to spawn and the calculations in the PRSPAWN submodel are completed. Annual iterations through the model proceed for the desired number of years. On the last iteration, the UPDATE subroutine is called for the print-out of the last annual iteration.

The conceptual biological model presented in this study is an attempt to describe the types of relationships that significantly influence upriver spring chinook salmon. Where insufficient data exist to concretely suggest the nature of these functional relationships, alternative explanations are proposed. The model is not presented as a definitive description of the life history of these salmon; rather, it should be viewed as an initial attempt to understand in depth the events influencing the life cycle of these fish.

#### Management Model Applications

A significant problem facing fisheries agencies in the Pacific Northwest is the wise management of all species of salmon. Due to

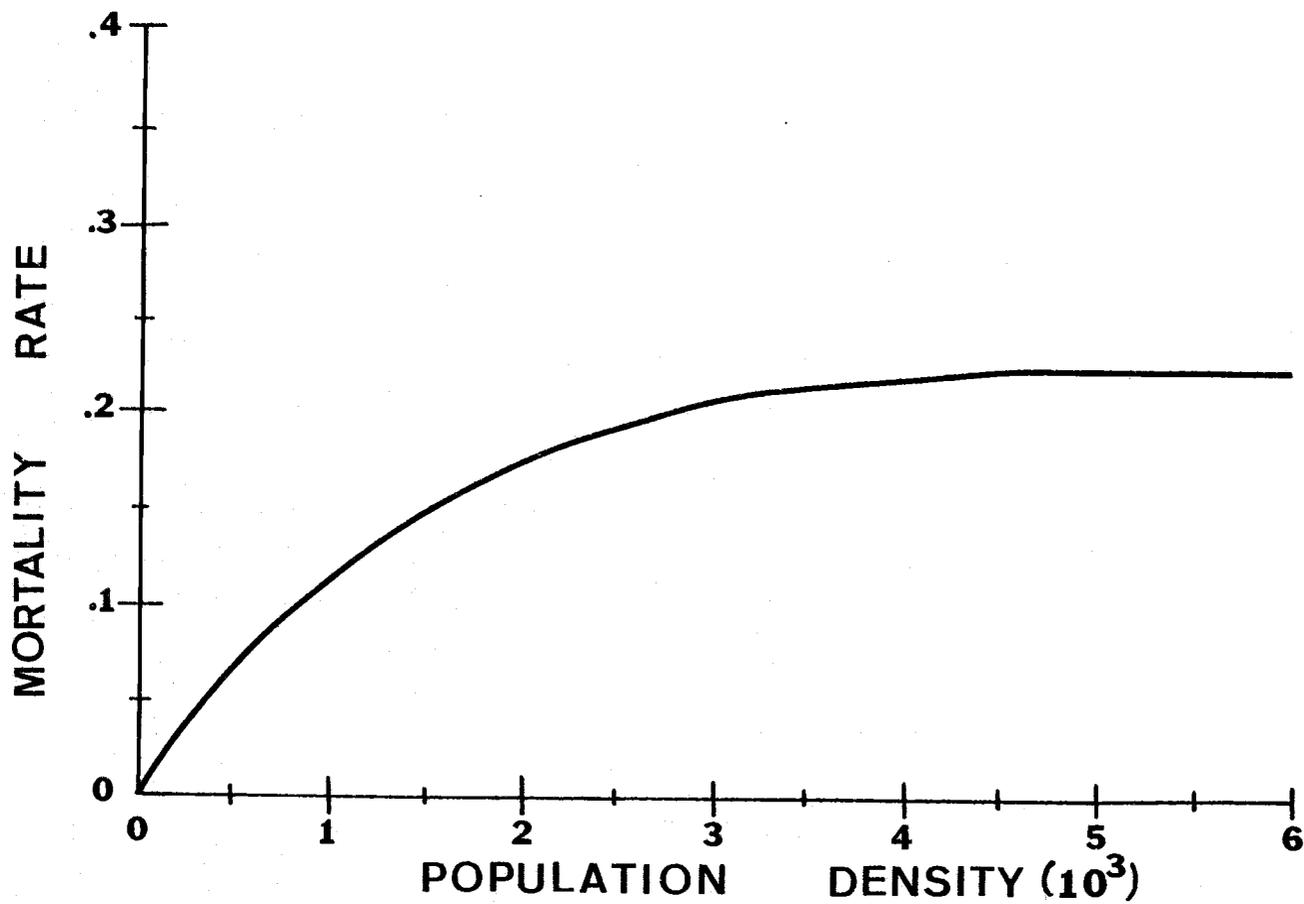


Figure 75. The functional relationship between the adult spawning density and the natural mortality in the native stream prior to spawning.

the paucity of data relevant to upriver spring chinook salmon, the management of these fish has been particularly difficult. The biological model presented herein may potentially enhance the current understanding of the life history of upriver spring chinook salmon; however, the complex functional relationships used in the model limit its usefulness as a management tool. Within the framework of the biological model, however, it is possible to suggest a simplified model potentially of more immediate use to fisheries agencies. That is, a management model can be suggested to describe the life history of an upriver spring chinook salmon stock using input data potentially available to fisheries agencies. In this context, the main objective of such a management model would be to point out specific areas for future data collection.

The following discussion of a management model which can be derived from both the biological model and the results of the statistical analyses is presented primarily to illustrate the types of functional relationships integral to such a model. It is not within the realm of this study to present a detailed model as was done for the biological model; instead, the presentation is an illustration of the potential application of a theoretical biological model to management problems.

The major components of the management model are similar

to those of the biological model (Fig. 37). The nature of the functional relationships are, however, simplified. As in the biological model, the functional relationships are based upon available data for upriver spring chinook salmon. Where such data is lacking, data relevant to other Pacific salmon species is incorporated.

The number of outmigrating fish generated by the spawning stock is determined from data collected on the Lemhi River (Bjornn, 1978). A Ricker-type reproduction curve is fit to the relationship between the outmigrating fish and female spawners (Fig. 76). From these data, the Ricker curve is described by the equation:

$$R = Pe^{7.55(1-P/10886)}$$

The maximum progeny abundance of 1,008,000 fish occurs at a spawner abundance of 1442 fish. The replacement abundance occurs at 10,886 fish. In the Lemhi River, the density of female spawners from 1965 to 1971 has never been great enough to surpass the carrying capacity of the stream. Additional stream studies measuring spawner and progeny abundances could shift the maximum progeny abundance to the left in the Ricker relationship.

From the hatching of the eggs until outmigration, the juvenile fish are most strongly influenced by growth and survival processes. The types of growth relationships incorporated in the biological model can not be considered in the management model since these

Figure 76. The number of juvenile fish migrating downstream expressed as a function of the female spawner escapement in the Lemhi River. The solid curve represents the Ricker reproduction curve calculated from the data points. The year associated with each data point refers to the brood year.

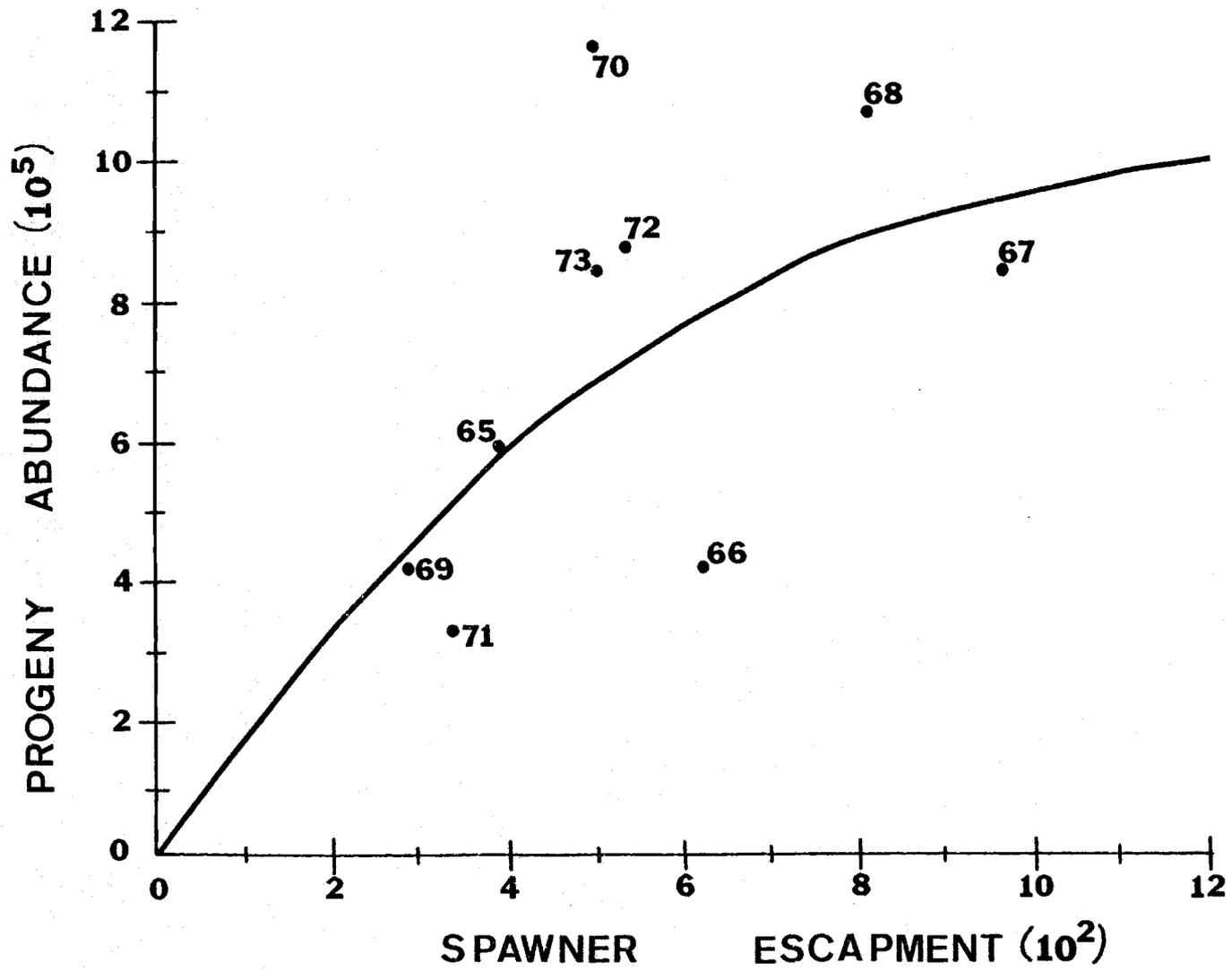


Figure 76.

relationships rely on input data not readily collected. The mean body size of the outmigrating fish is determined from the mean body size of the female spawners (Fig. 77). Fowler (1972) described a positive relationship between female spawner body size and the size of eggs produced by these fish. Fowler's studies with fall chinook salmon further suggested that the largest eggs also produced the largest juveniles released from the hatchery. The natural mortality rate of juvenile fish in freshwater is size-dependent (Fig. 48).

During outmigration, flow appears most important in controlling juvenile mortality. The parabolic relationships suggested by the results of the statistical analyses (Figs. 18 and 22) are incorporated in the management model. Thus, the greatest mortality during outmigration occurs during years of very low or high flows.

Once the fish reach the ocean, growth and mortality become the major processes influencing the fish. For the first six months at sea, the post-smolt growth rate is assumed to be related to the strength of the upwelling event (Fig. 78). Presumably, a strong upwelling event results in an abundance of food which results in a high growth rate. In the model, it is assumed that beyond a specified upwelling strength, no increase in the growth rate occurs and it may decrease (Fig. 78). The mortality rate during the first months at sea is assumed to be negatively related to both body size (Fig. 79)

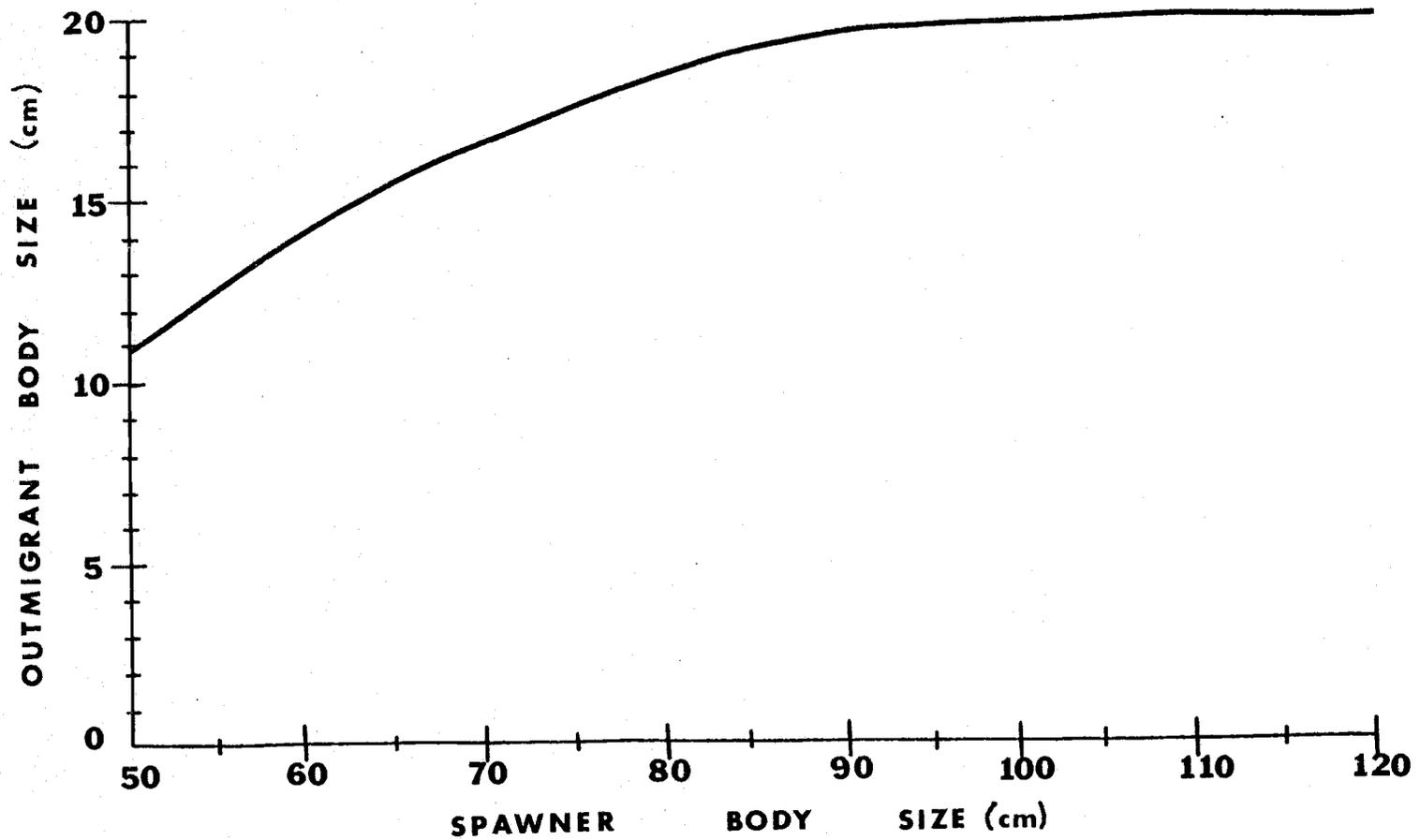


Figure 77. The mean body size of juvenile downstream migrants expressed as a function of the mean body size of the female spawners.

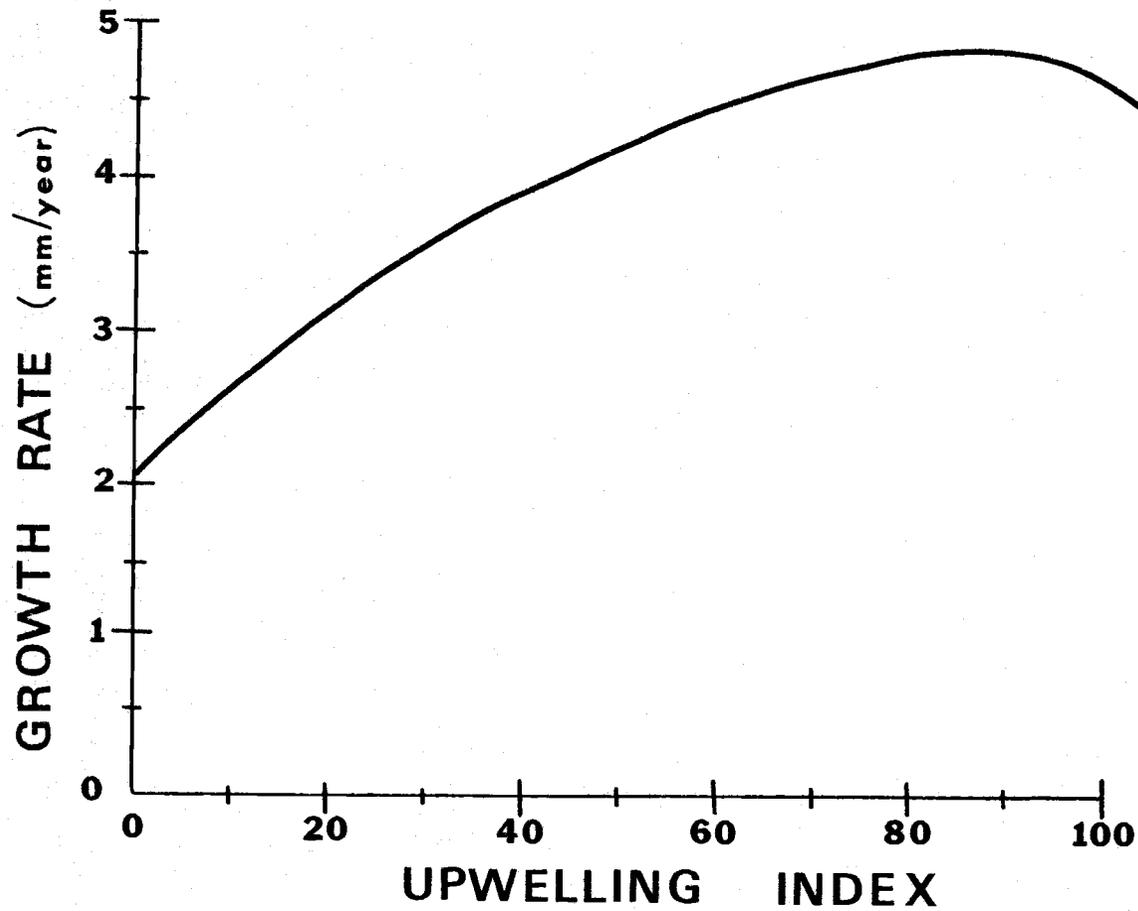


Figure 78. The growth rate of ocean post-smolt fish expressed as a function of the mean June-July upwelling index for 48°N 125°W.

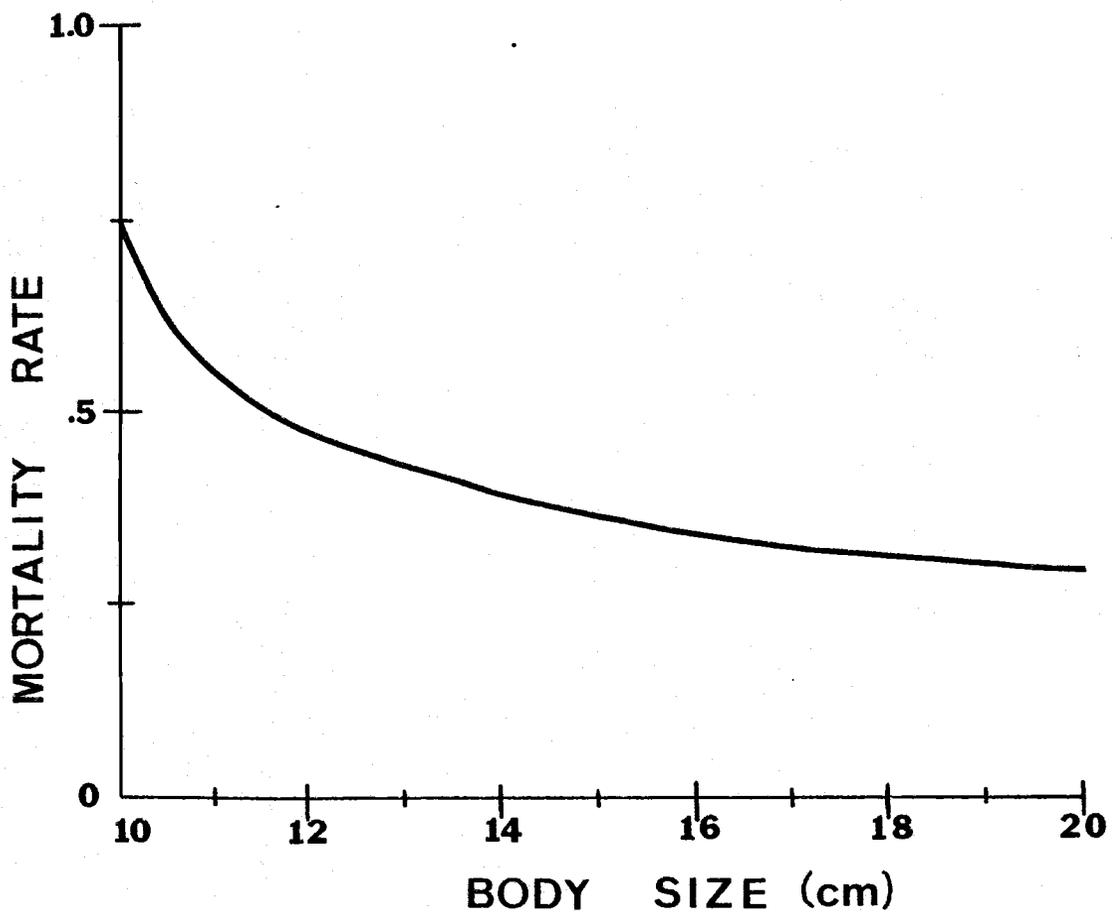


Figure 79. The natural mortality rate of ocean post-smolt fish during the first months at sea expressed as a function of the mean body size.

and the strength of the upwelling event (Fig. 80).

For the two-, three-, and four-year-old fish in the ocean, the growth and mortality rates most significantly influence the abundance of these fish. Conceptually, the management model can be designed like the biological model with a prespawner submodel to account for maturing ocean fish. In addition, the blocks used to account for ocean locations can also be incorporated in the management model. In this way, the model can predict ocean locations of the modelled fish which can be verified or refuted with collected data.

The maturation rate of upriver spring chinook salmon is unknown. Verification of the biological model may suggest the most viable explanation for factors leading to early maturation. In the absence of concrete data, the maturation rate of fish in the management model was positively related to age (Fig. 81). Few three-year-old spring chinook salmon return as jack salmon to freshwater to spawn and all fish reaching their fourth birthday in the ocean potentially return to freshwater the following spring. For immature ocean fish, both the growth and mortality rates are size-dependent. The mortality rate decreases with an increase in mean body weight (Fig. 68). The growth rate decreases curvilinearly with the increase in mean body weight associated with age (Fig. 82). The fishing mortality rate described for the biological model can be incorporated in

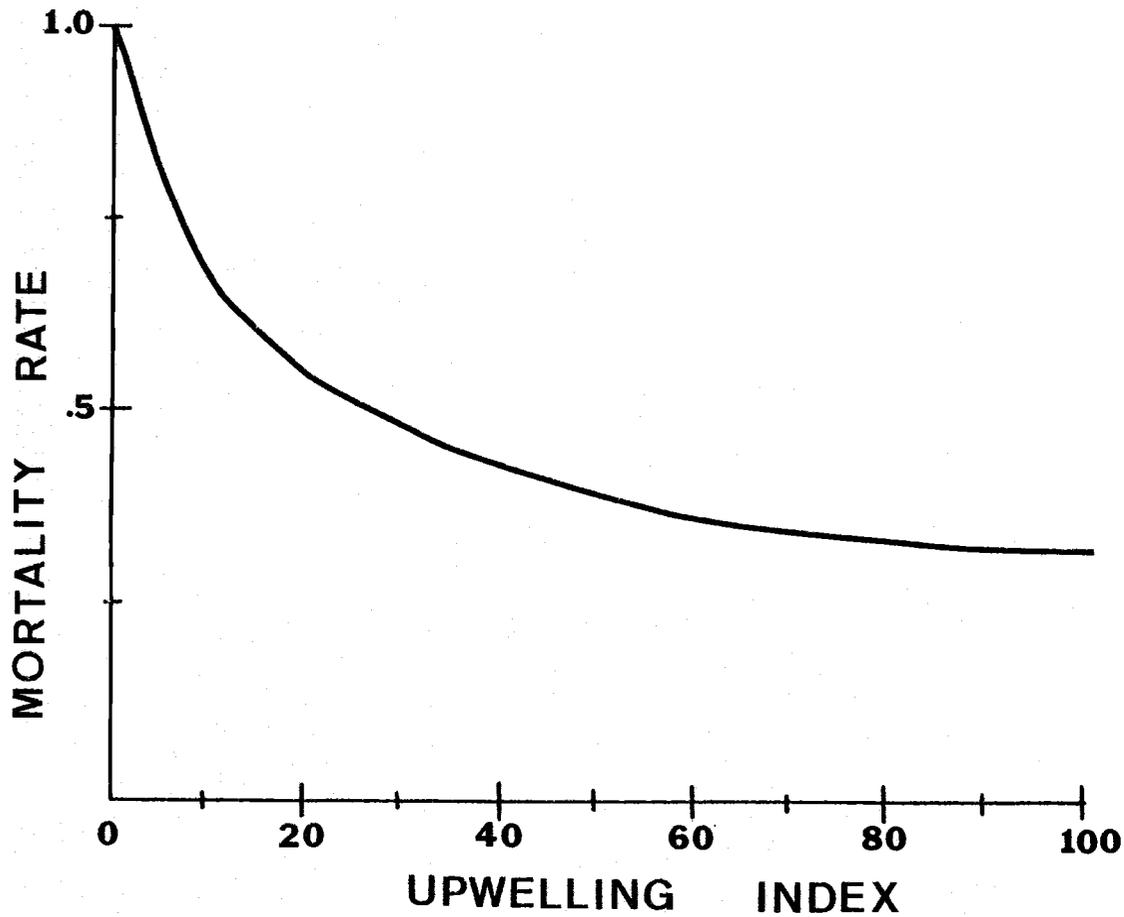


Figure 80. The influence of the mean June-July upwelling index at 48°N 125°W on the natural mortality rate of ocean post-smolt fish.

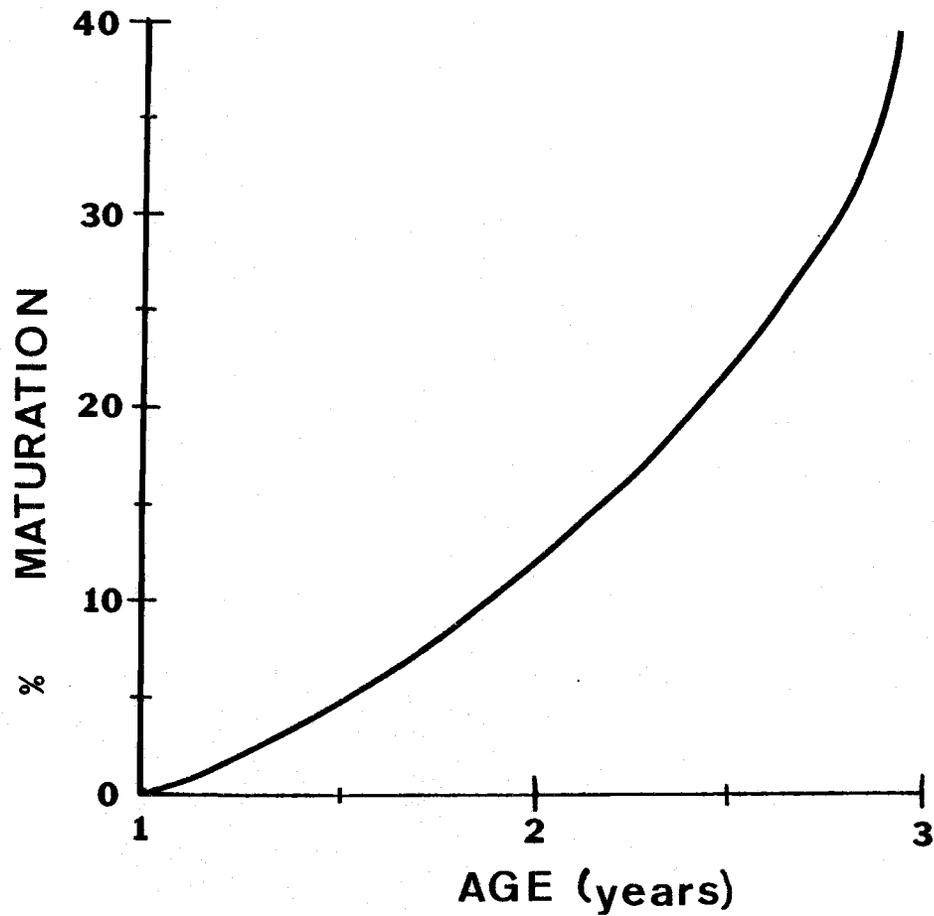


Figure 81. The rate of maturation for ocean fish expressed as a function of age. The age refers to the age of the fish one year prior to spawning.

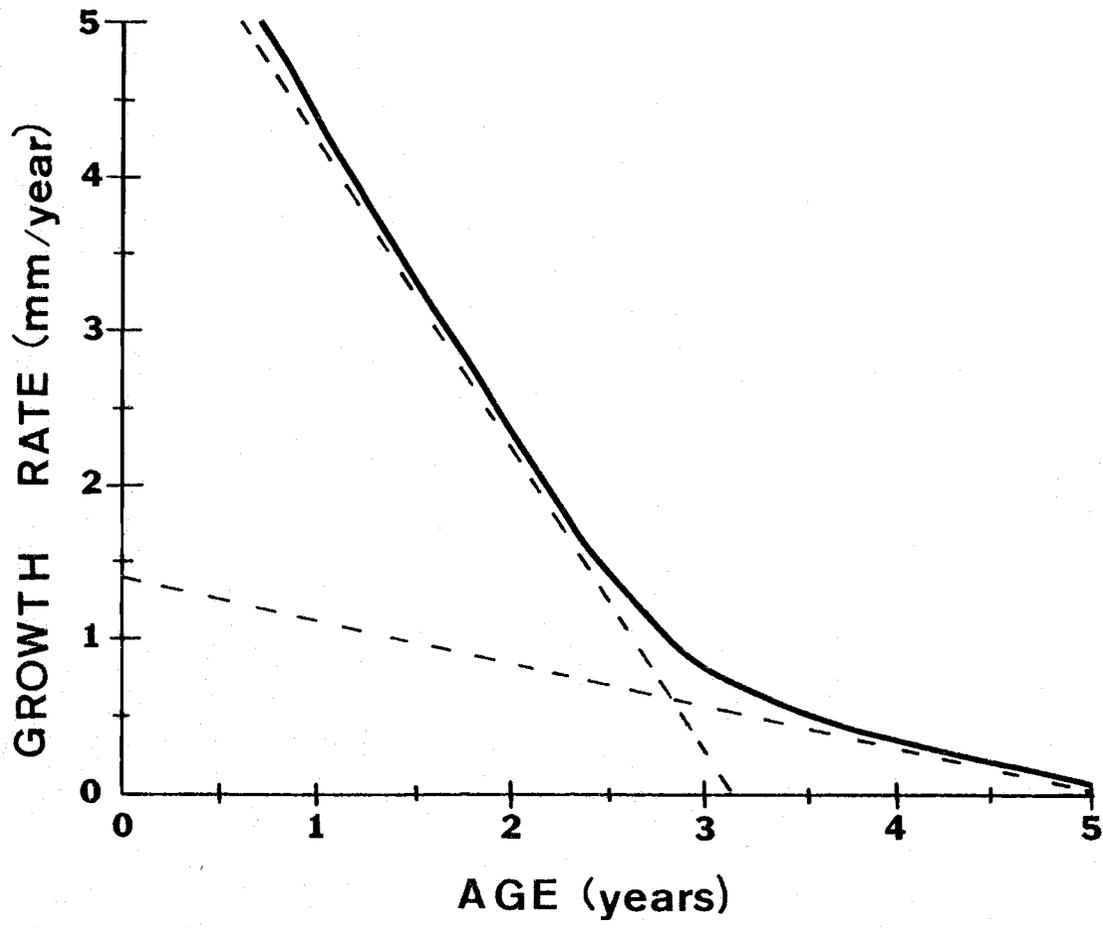


Figure 82. The decrease in growth rate for ocean fish with a corresponding increase in age.

the management model. In this manner, the latter model becomes potentially useful as a management tool.

The curvilinear relationship between growth rate and age (Fig. 82) is derived from data collected for Lemhi River spring chinook salmon (Bjornn, 1978). The growth rate of fish at age 1 could be determined from the mean size of these fish relative to the mean size of fish at the button-up stage. Since fish return to the Lemhi River as three-, four-, and five-year-old fish, the growth rates associated with fish at each of these ages could be determined. The mean size at age was determined for spawners returning to the spawning ground during the ten year study. It was assumed that the growth rate of immature ocean fish was comparable to that of maturing fish. Additional length at age studies for ocean fish may suggest differential growth rates for mature and immature fish due to the energy expended for the maturation of the reproductive organs. The curvilinear relationship between growth rate and age (Fig. 82) determined from these data is described by two linear relationships. For fish less than 3.25 years of age, the growth rate (Y) in mm/year is described as:

$$Y = 6.25 - 1.95 X$$

where X is the age of the fish in years. For fish older than 3.25 years, the growth rate (mm/year) is described as:

$$Y = 1.40 - 0.27 X$$

The types of calculations incorporated in the PRSPAWNer submodel of the biological model are similar to those that could be used in a management model. The natural mortality rate at age is determined as for the immature fish (Fig. 68). No troll fishing mortality occurs since the return of these fish to freshwater is coincident with the opening of the troll season.

In freshwater, the maturing spawners are most greatly influenced by natural mortality and fishing mortality. The precocious male spawners, jack salmon, can be eliminated in the freshwater submodel since they do not significantly contribute to the gill net fishery or to the number of eggs produced on the spawning ground. The mortality of the adult salmon in the gill net fishery is density dependent (Fig. 71). As in the biological model, the mortality of adult spawners during the upstream migration is primarily related to the spill over dams (Figs. 72 and 73). On the spawning grounds, natural and sport fishing mortality among spawners is presumably density dependent (Figs. 74 and 75).

This description of the management model derived from the statistical results and the biological model is intentionally brief. The main purpose of this discussion is to illustrate the types of management applications potentially available from this type of study. The management model not only illustrates the framework for a

decision-making model but also demonstrates general areas for future data collection and research.

#### Areas for Future Research and Data Collection

This study has focused on isolating the types of factors significantly influencing the abundance of spring chinook salmon spawning above Bonneville Dam. Whereas the results of the statistical analyses suggested that selected environmental factors influence these fish, the modelling effort suggested major areas for future research to enhance the current understanding of the life history of these fish. Since the Columbia River spring chinook salmon are of commercial importance to the Pacific Northwest, the types of additional research suggested by this study will be enumerated as a guideline for future studies.

Additional stream studies comparable to that undertaken on the Lemhi River (Bjornn, 1978) should be initiated. The results of the statistical aspects of this study illustrated that parent spawners alone accounted for greater than 70% of the variability associated with the Ricker reproduction curve (Table 9). However, the upriver Ricker reproduction curve (Fig. 14) generated for the upriver fish may represent the mean response of several stocks spawning above Bonneville Dam. Additional stream studies, particularly for populations that reach and exceed the stream carrying capacity, should

further reduce the variability associated with this Ricker relationship.

Very little data has been collected for the determination of growth rate at age for spring chinook salmon. Scale samples in conjunction with length-frequency data from the domestic troll fishery could contribute valuable growth rate information. A comparison of growth rates at age for fish landed in the troll fishery with those landed in the Columbia River gill net fishery could provide an indication of the relative growth rates of maturing and immature fish. To determine if the growth rate of ocean post smolts is indeed related to the strength of the upwelling event, correlation coefficients could be calculated between the growth rates determined from scale analyses and the appropriate upwelling indices.

The ocean life history of upriver spring chinook salmon is virtually unknown. Ideally, an extensive tagging project could be initiated to assess the ocean location of these fish and their relative contribution to domestic and Canadian troll fisheries. However, the expense and logistic problems associated with such a project are almost prohibitive. Some tagging projects are currently underway for upriver fish; however, the emphasis of these projects is on hatchery fish. The difficulty associated with marking hundreds of thousands of wild fish has precluded extensive studies with upriver spring chinook

salmon. An alternate approach to the mapping of the ocean distribution of upriver spring chinook salmon would entail an extensive scale analysis. If the upriver spring chinook salmon could be characterized by unique scale characteristics, ocean identification of these fish would be possible in the absence of a tagging study.

Although most fisheries biologists associated with Pacific salmon have an "innate" feeling for the magnitude of the juvenile mortality rate during outmigration, few studies have been designed to empirically measure this mortality. Extensive tagging-recapture studies over a period of several years corresponding to a wide range of flow regimes could improve the current estimates.

The virtual absence of extensive estuarine studies of Pacific salmon is noted. Studies should be initiated to determine if upriver spring chinook salmon residualize extensively in the estuary. If such residualism is noted, causative factors, such as body size or food availability, should be noted. Due to the size of the Columbia River estuary, it might be advisable to initiate such a study on a small coastal river with an extensive tagging and recapture project.

Finally, little information exists concerning the food habits of ocean spring chinook salmon. Stomach analyses of fish landed in the troll fishery could indicate the species composition of the prey items. In addition, a qualitative assessment of the relative "fullness" of the

stomach could provide some initial indication of the limitations or lack thereof of the ocean environment.

## CONCLUSIONS AND SUMMARY

The results of this study illustrated the overwhelming effect of parent spawners on the survival of the offspring. Parent spawners alone accounted for 58% to 70% of the variability associated with the Ricker reproduction curves for the upriver data. Additional in-stream studies may further decrease this deviation with reliable estimates of spawner and recruit abundances for a single stock.

There appears to be little question that the upriver spring chinook salmon populations, particularly those spawning in the Snake River watershed, are declining. Conceivably, hatchery compensation of some wild streams may be necessary. Currently, a full assessment of the cost-benefit ratio associated with current upriver spring chinook salmon hatcheries should be evaluated before additional facilities can be proposed.

The presence of dams on the Columbia River continues to influence the survival of outmigrating juveniles. A parabolic relationship was noted between flow during brood-year outmigration and the survival of the brood year. As additional dam modifications become operational and juvenile mortality associated with supersaturation decreases, it is anticipated that this parabolic relationship will become asymptotic. To maximize the survival rate of outmigrating fish,

particularly during low-flow years, it may become necessary to develop minimum flow requirements for salmonids.

The survival of ocean post-smolts appears positively related to the strength of the upwelling event. It was proposed that a strong upwelling event may be related to the presence of a good food supply for post-smolt fish. Specifically, the post-smolts would escape some predation pressures more quickly during years associated with a good food supply promoting a high growth rate than in years characterized by a poor food supply and weak upwelling.

The mapping of the ocean distribution of the upriver spring chinook salmon may suggest additional areas for ocean exploitation. Expansion of the fishery in the river is difficult to foresee due to the current problems associated with the allocation of the resource. In fact, management agencies are currently faced with the immediate necessity of a reliable means for the prediction of spring chinook salmon abundance. Although the management problems prevalent for spring chinook salmon are significant, a thorough evaluation of previously collected data in conjunction with the development of simulation models may provide a basis for better management when years of detailed data collection are not feasible.

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## APPENDICES

Appendix I-1. Measures of the abundance of fish spawning above Bonneville Dam and the Canadian troll landings and effort recorded three years after the brood year spawning. The total returns refer to the total number of fish returning to the spawning ground from a single brood year. The four-year old returns refer only to the total number of four-year old fish returning to the spawning ground from a single brood year.

Brood Year	Spawners (S)	Total Returns (R)	4-year old Returns (RF)	Canadian Troll Fishery				
				$\ln(R/S)$	$\ln(RF/S)$	Year	Catch ( $10^3$ kg)	Effort ( $10^3$ days)
1957	135200	101600	66215	-.286	-.715			
1958	71700	243600	155844	1.223	.776			
1959	60500	134600	67758	.800	.113			
1960	69100	160800	102785	.845	.397	1963	3103	131
1961	97100	173000	119340	.577	.206	1964	3855	147
1962	87400	182200	122640	.735	.339	1965	3972	142
1963	66300	145400	93620	.786	.345	1966	5171	148
1964	80100	173800	84105	.775	.049	1967	4736	148
1965	64600	206000	132101	1.160	.715	1968	4916	155
1966	110400	167800	105079	.419	-.049	1969	4911	139
1967	73100	187900	104222	.944	.355	1970	4503	155
1968	83200	308200	193732	1.309	.845	1971	6901	156
1969	140600	188000	123812	.291	-.127	1972	6377	141
1970	97000	108200	55080	.109	-.566	1973	5769	132
1971	112800	90400	59337	-.222	-.642	1974	6123	126
1972	143300	74100	48546	-.659	-1.082	1975	5701	121

Appendix I-2. Environmental variables recorded both in the Columbia River and the Pacific Ocean during the outmigration of an upriver brood year. The mean April-May flow, temperature, turbidity, and nitrogen supersaturation were recorded at Bonneville Dam. The monthly mean Columbia River discharge was recorded at Astoria, Oregon, and the mean June-July upwelling index was determined for 48°N 125°W. The parabolically transformed flow variable ( $\Delta$  Flow) was calculated from the flow recorded at Bonneville Dam.

Year	Flow (m <sup>3</sup> /sec)	Temp. (°C)	Turb. (cm)	N2 (%)	$\Delta$ Flow (10 <sup>3</sup> m <sup>6</sup> /sec <sup>2</sup> )	Upwelling	Discharge (m <sup>3</sup> /sec)				
							Jun	Jul	Aug	Sep	Oct
1959	7970	10.7	65.0		2560	26	16	11	6	5	7
1960	8112	10.7	70.2		3034	34	12	9	5	3	4
1961	7185	11.3	68.0		664	18	18	8	4	3	3
1962	7438	10.9	62.2		1141	33	13	8	5	3	4
1963	6133	11.2	67.7		56	34	12	8	4	3	3
1964	6137	10.7	76.9		54	20	18	12	5	4	4
1965	9246	10.6	52.8		8271	60	15	9	5	4	4
1966	6015	11.7	83.9		126	33	11	8	5	3	4
1967	5687	11.2	83.6	104.4	466	78	17	11	5	4	5
1968	4667	11.2	88.8	120.0	2900	42	11	8	4	4	5
1969	10489	11.0	46.4	127.0	16966	60	11	8	4	3	4
1970	5920	10.8	86.3	110.0	202	38	11	6	4	4	4
1971	10475	10.6	52.5	111.8	16851	22	16	10	5	4	4
1972	9657	10.4	51.9	115.6	10804	21	18	10	6	5	4
1973	4160	11.9	106.1	102.6	4884	22	5	4	4	4	4
1974	9400	10.8	47.6	115.0	9181	28	16	10	6	4	4

Appendix I-3. Measures of the abundance of fish spawning in the Lemhi River and environmental variables recorded in the Snake River during the outmigration of the brood year. The mean April-May flow, temperature, and turbidity were recorded at Ice Harbor Dam. The parabolically transformed flow variable ( $\Delta$  Flow) was determined from the flow recorded at Ice Harbor Dam.

Year	Spawners (S)	Total Returns (R)	$\ln(R/S)$	Year	Flow ( $m^3/sec$ )	$\Delta$ Flow ( $10^3 m^6/sec^2$ )	Turb. (m)	Temp. ( $^{\circ}C$ )
1964	1075	1016	- .056	1966	1898	868	.558	10.8
1965	765	1074	.339	1967	2302	279	.476	10.8
1966	1473	870	- .527	1968	1674	1336	.616	11.0
1967	1844	1288	- .359	1969	3694	746	.378	10.9
1968	1943	1254	- .438	1970	2366	215	.601	10.3
1969	755	537	- .341	1971	4246	2005	.339	10.4
1970	1217	940	- .258	1972	3435	366	.363	10.1
1971	831	513	- .482	1973	1327	2259	.622	11.6

Appendix I-4. Annual landings in numbers of fish caught in the California, Oregon, Washington, and S.E. Alaskan chinook salmon troll fisheries, annual landings in kilograms of fish caught in the Canadian chinook salmon troll fishery and the mean size of of fish landed in the Canadian troll fishery.

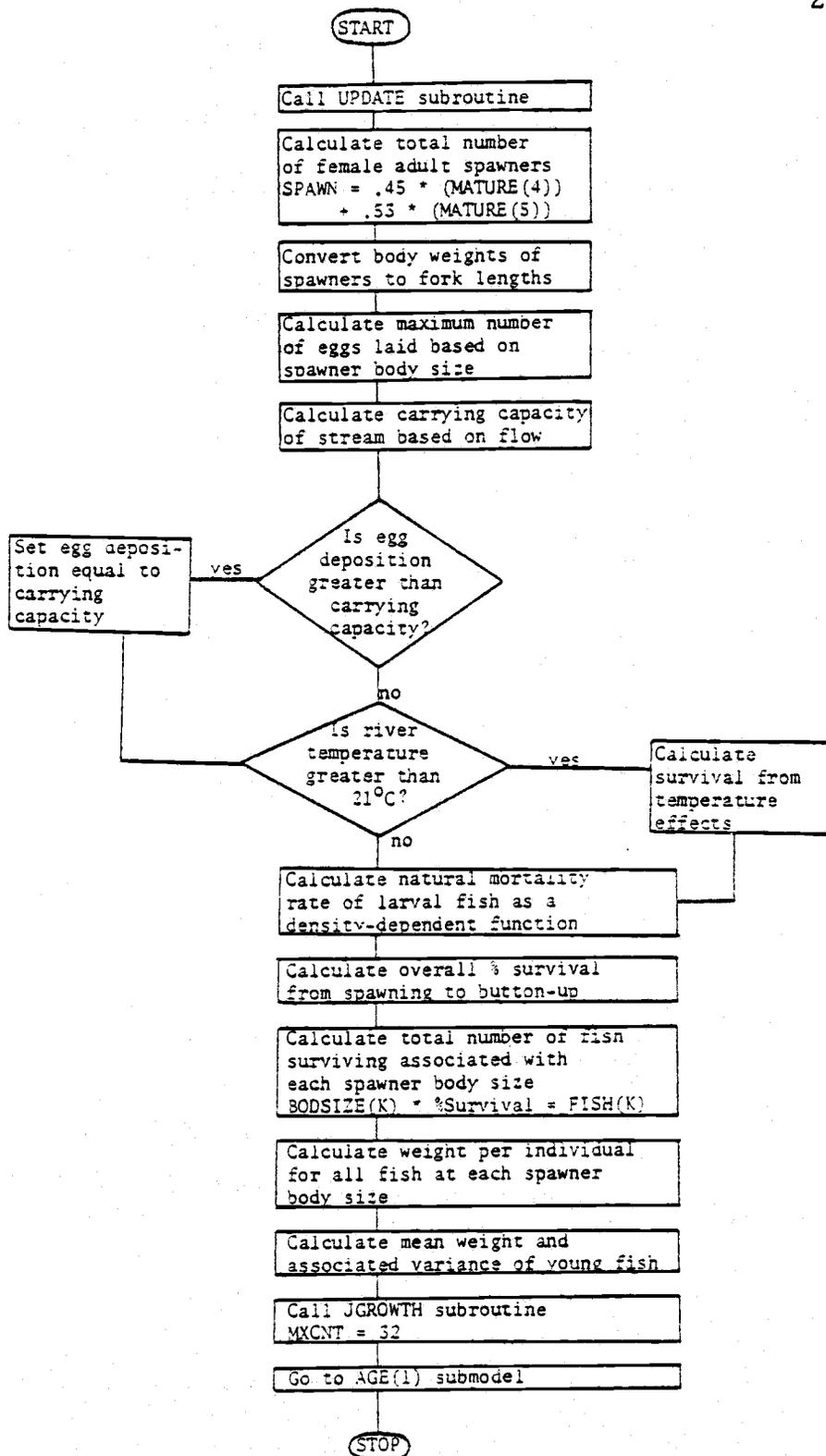
Year	California	Oregon	Washington	S.E. Alaska	Canadian Fishery	
					Catch (10 <sup>3</sup> kg)	Mean Size (kg)
1960	539702	128000	121805	282678		
1961	773660	116000	182328	204276		
1962	556219	52600	159030	173578		
1963	662432	153400	204178	243679	3103	5.76
1964	686680	52742	163618	329461	3855	6.26
1965	705260	57683	95855	258730	3972	5.85
1966	552024	116459	167192	282080	5171	5.99
1967	337884	99749	131736	274673	4736	6.17
1968	472000	110150	162787	304455	4916	6.40
1969	551423	140285	186417	289983	4911	5.90
1970	516648	163369	214298	304245	4503	5.44
1971	433927	162929	252177	311420	6901	5.49
1972	492203	127287	202868	242285	6377	5.40
1973	816968	363267	316777	307648	5769	5.31
1974	491500	224110	353056	322129	6123	5.22
1975					5701	5.17
1976					6257	5.03
1977					5467	5.03

Appendix II. Hatcheries currently releasing spring chinook salmon above Bonneville Dam in the Columbia River watershed (from Wahle et al., 1975).

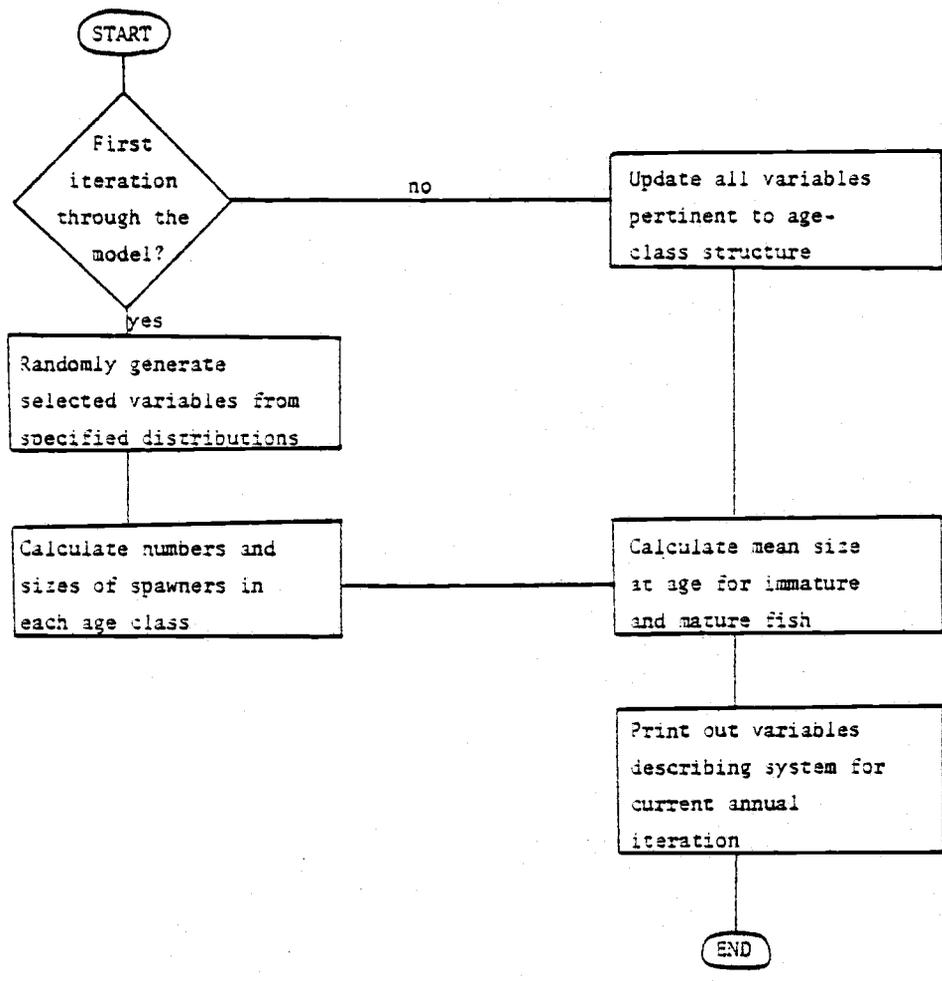
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Hatchery Name	Primary Release Site	First Year of Operation
Leavenworth	Wenatchee River, Wash.	1958
Rapid River	Rapid River, Idaho	1964
Hayden Creek	Salmon River, Idaho	1966
Little White Salmon	Little White Salmon River	1966
Kooskia	Clearwater River, Idaho	1969
Decker Pond	Salmon River, Idaho	1970
Sandpoint	Lochsa River, Idaho	1970
Ringold Pond	Columbia River	1971

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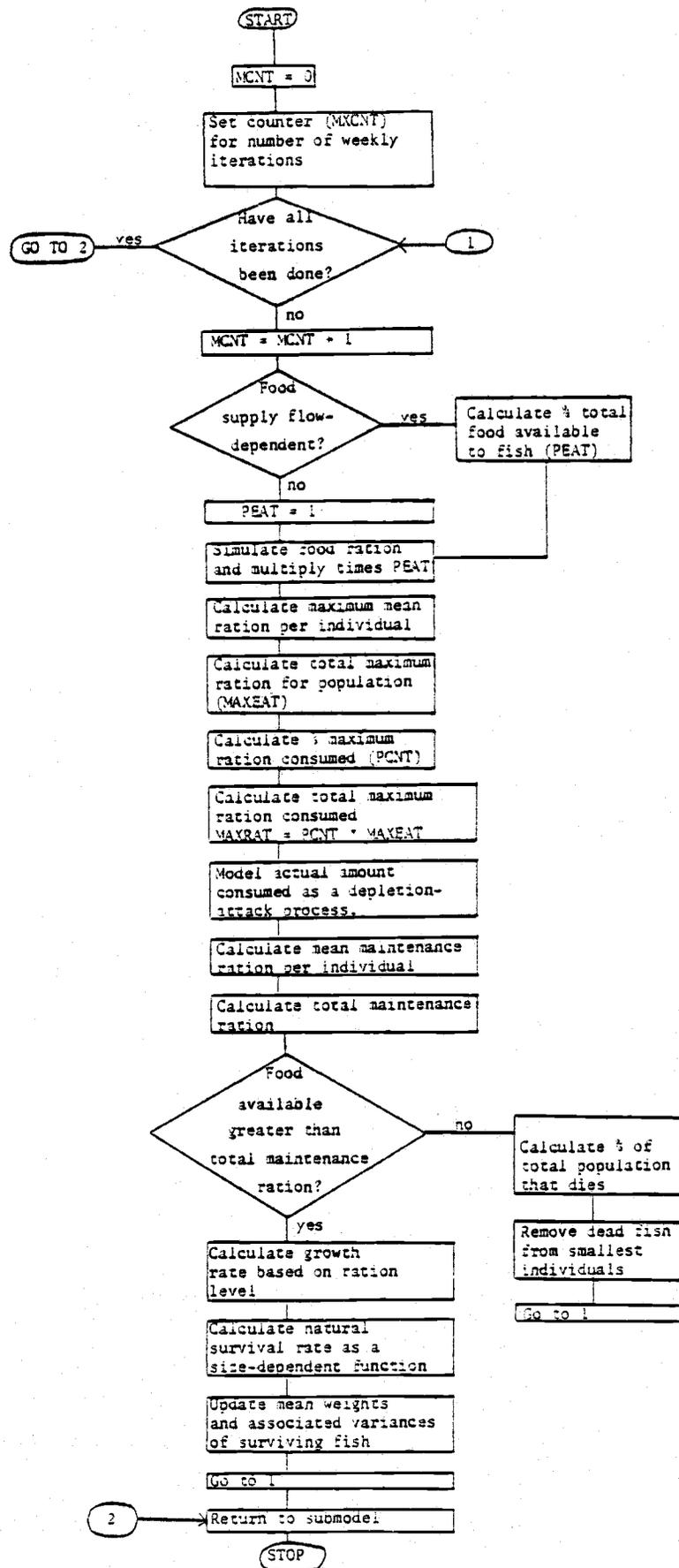


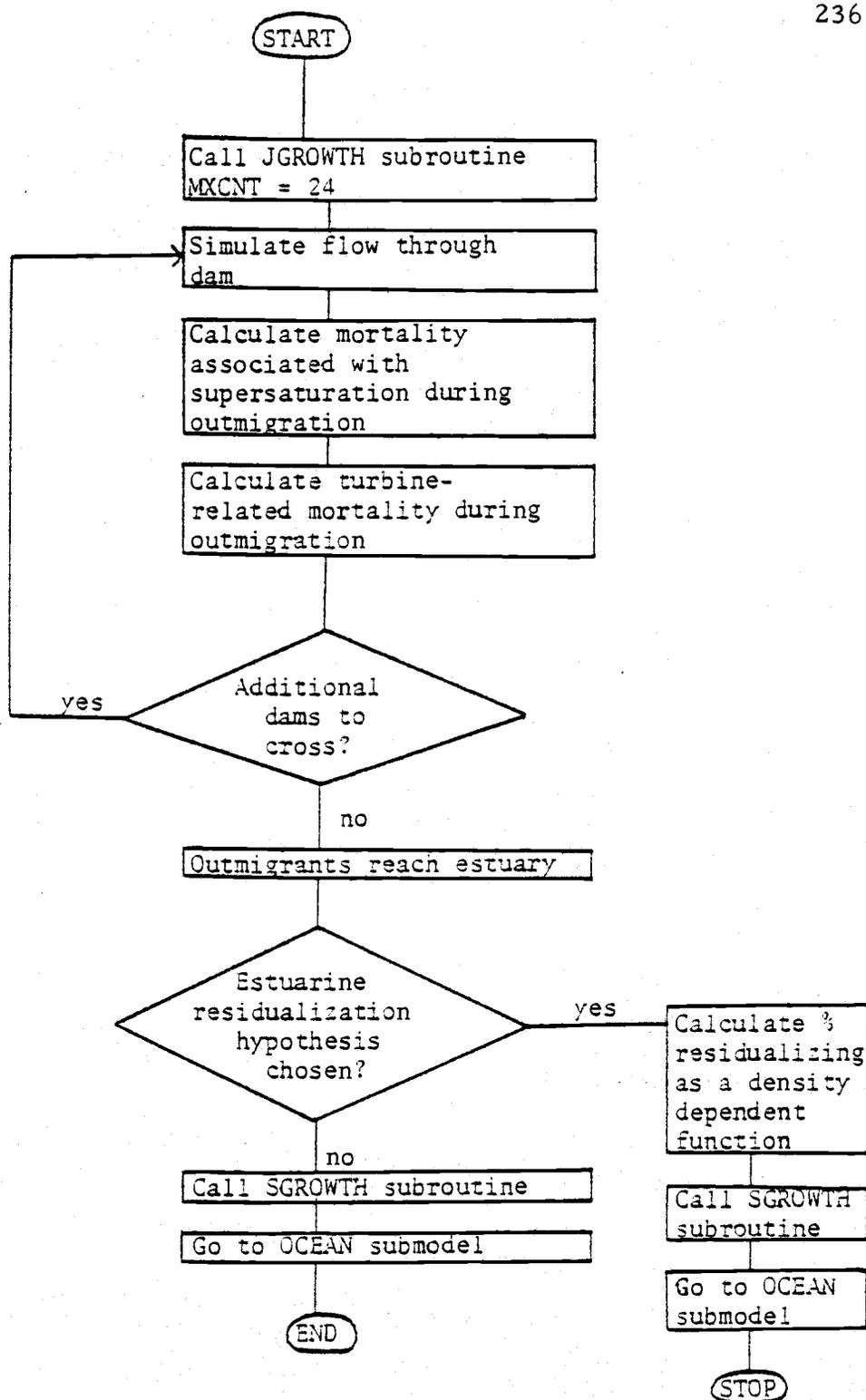
Appendix III-1. A flow diagram illustrating the flow of events internal to the SPAWN subroutine.



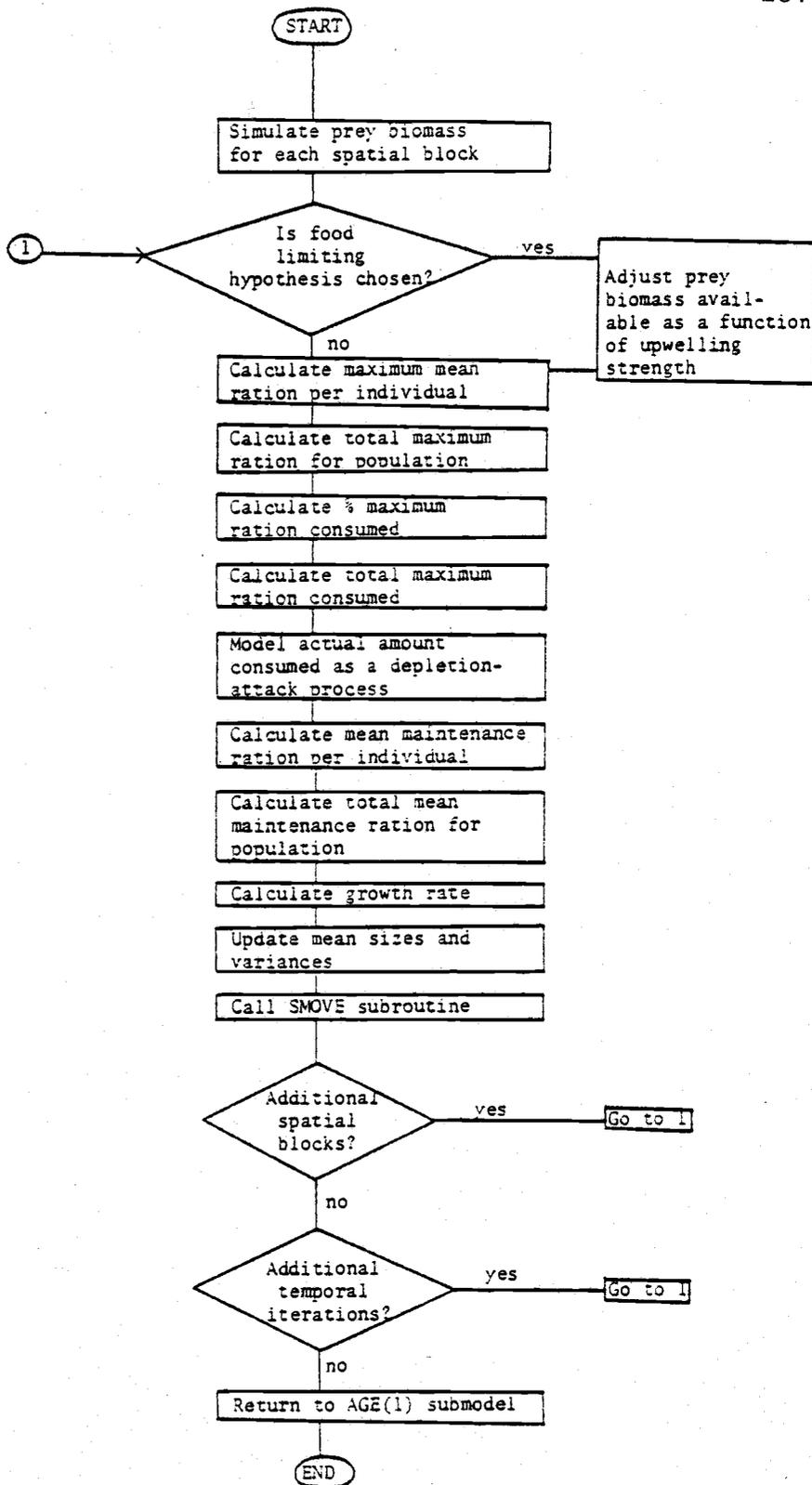
Appendix III-2. A flow diagram illustrating the flow of events internal to the UPDATE subroutine.

Appendix III-3. A flow diagram illustrating the flow of events internal to the JGROWTH subroutine.

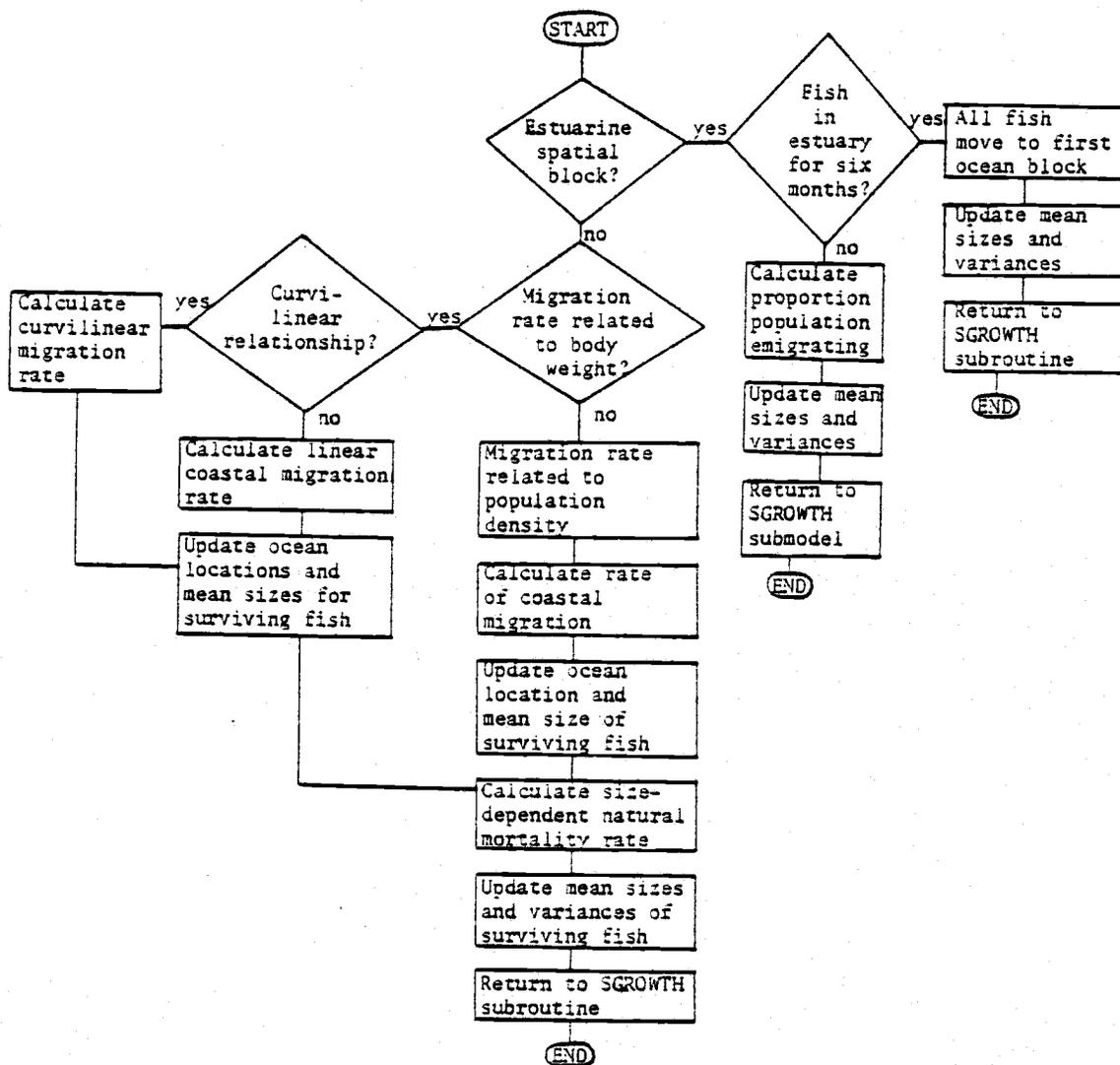




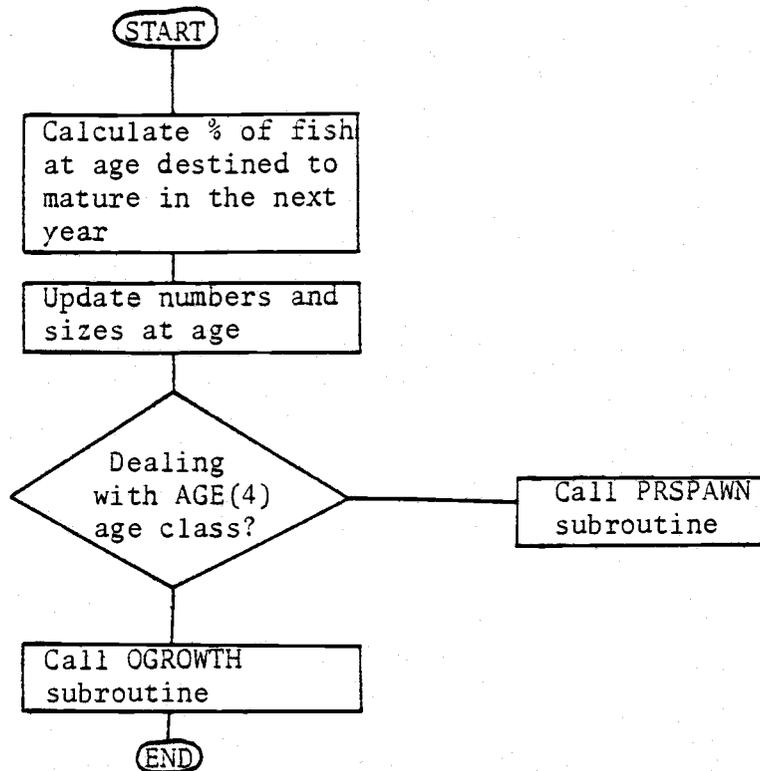
Appendix III-4. A flow diagram illustrating the flow of events internal to the AGE(1) submodel.



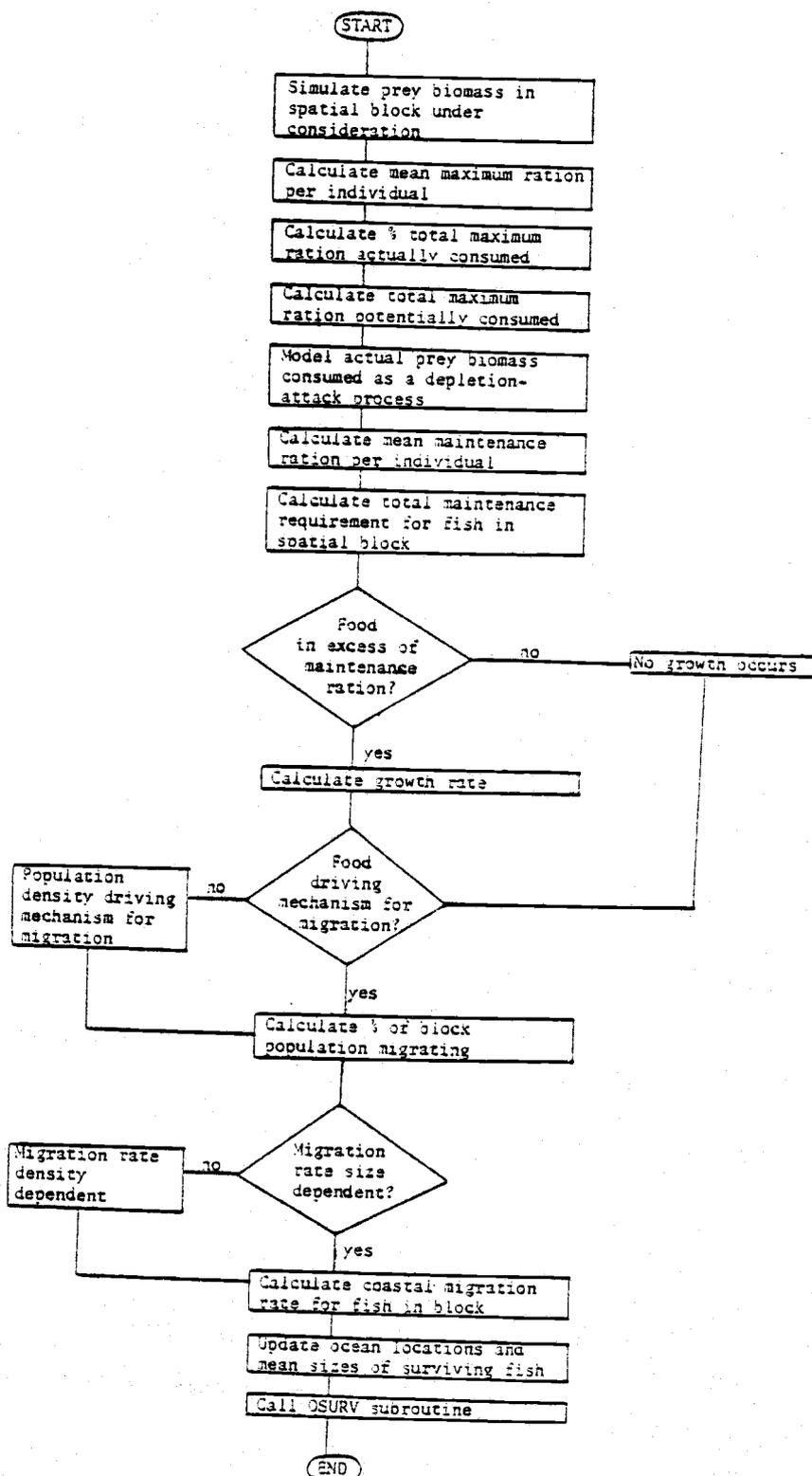
Appendix III-5. A flow diagram illustrating the flow of events in the ocean smolt growth (SGROWTH) subroutine.



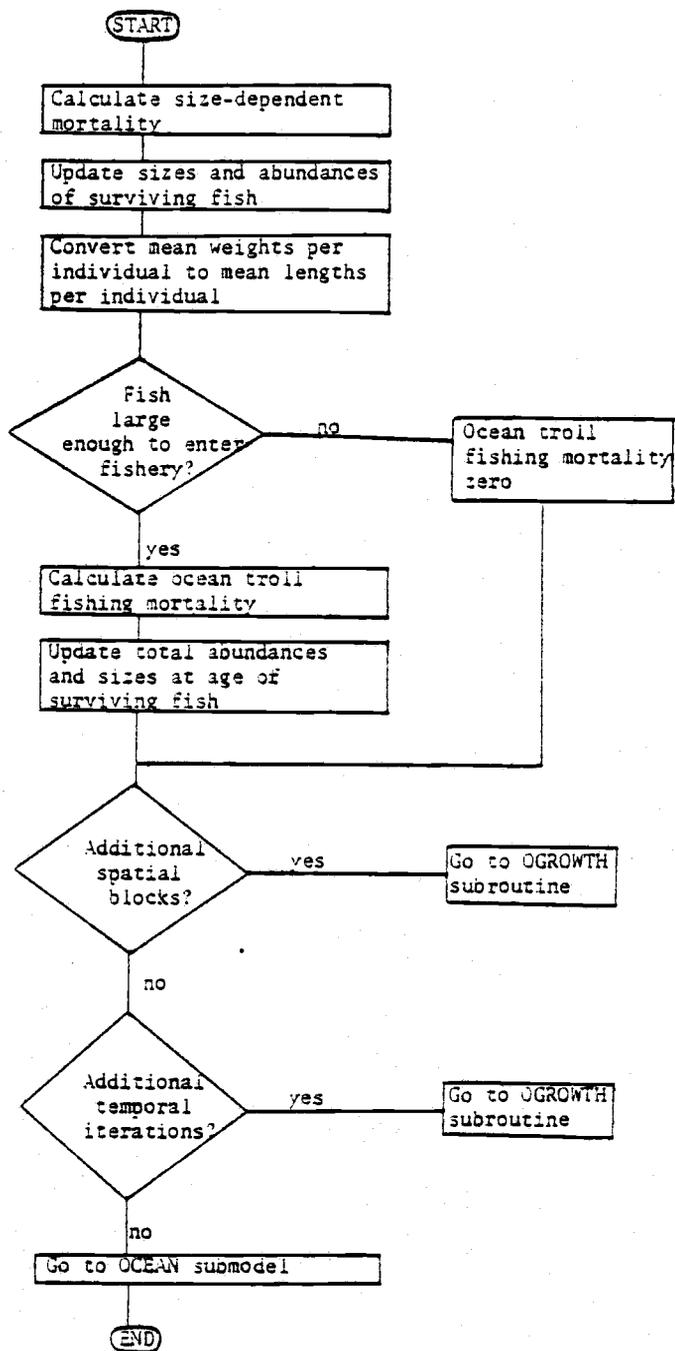
Appendix III-6. A flow diagram illustrating the flow of events in the SMOVE subroutine.



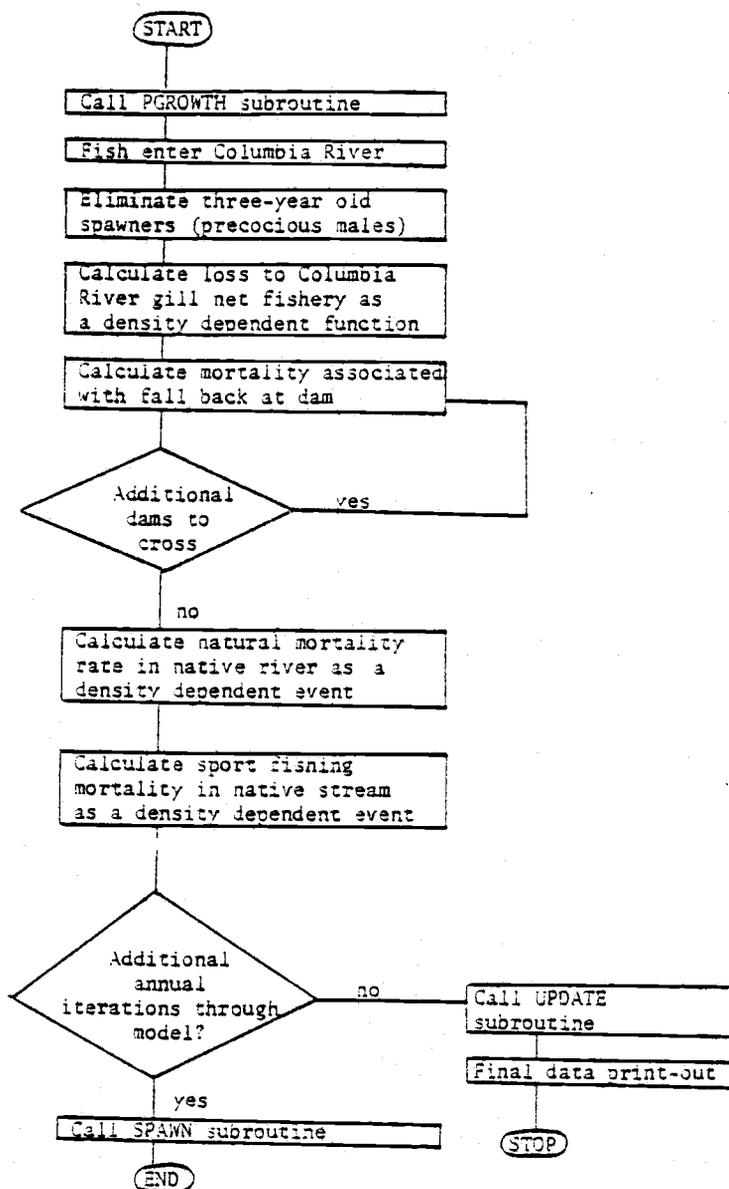
Appendix III-7. A flow diagram depicting the flow of events in the OCEAN submodel.



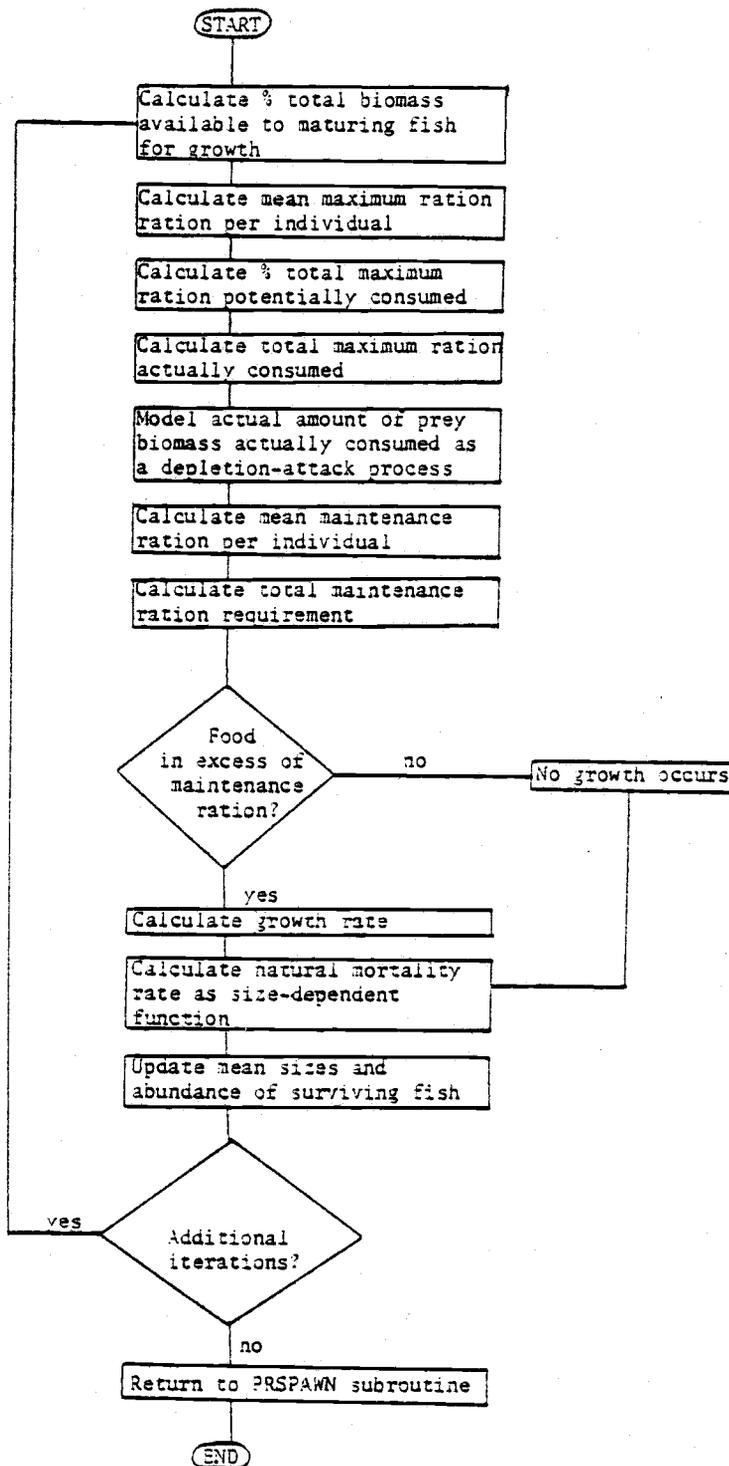
Appendix III-3. A flow diagram illustrating the flow of events in the OGROWTH subroutine.



Appendix III-9. A flow diagram illustrating the flow of events in the OSURV subroutine.



Appendix III-10. A flow diagram illustrating the flow of events in the PRSPAWN submodel.



Appendix III-11. A flow diagram illustrating the flow of events in the PGROWTH subroutine.