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**Age-specific effects of sockeye abundance on adult body size of selected British
Columbia sockeye stocks**

by

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Abstract

Most of the growth of anadromous sockeye salmon (*Oncorhynchus nerka* W.) occurs during the marine life history phase. There are significant correlations of mean annual hypural lengths among neighbouring and widely separated sockeye stocks in northern and central British Columbia. The correlations are greatest between sexes within rivers, followed by age-classes among rivers. A common factor or factors affecting sockeye size in the North Pacific Ocean is suggested. Between 1912 and the 1960's, the mean size of sockeye salmon caught annually in the fisheries of central and northern British Columbia (Nass River, Skeena River and Rivers Inlet) was negatively correlated with the magnitude of western Alaska (Bristol Bay) sockeye catches. This effect applied only to sockeye returning after 3 years in the ocean. Those sockeye returning after 2 years did not show any significant reduction in size in years when Bristol Bay sockeye abundance was high. Age 1.3 sockeye were significantly further offshore (away from their natal streams) than age 1.2 sockeye during the spring of maturation, and therefore were closer to the main distribution of Bristol Bay sockeye in the Gulf of Alaska. The pattern of annual marine growth measured from Skeena River sockeye scales collected during the 1960's provides additional evidence that the adult size of age 1.3 sockeye was a function of Bristol Bay sockeye abundance in the year of maturation. No such correlation was evident in scales collected from age 1.2 sockeye. These results suggest that aggregations of sockeye in the North Pacific may be more structured than previously reported.

Introduction

The size at age of sockeye salmon (*Oncorhynchus nerka* W.) in the North Pacific Ocean is and has been an area of active research (Godfrey 1958, Rogers 1980, Ricker 1981, Peterman 1984b, Ishida et al. 1993). Issues concerning salmon production in the North Pacific Ocean continue to stimulate interest. Studies, currently being developed under the auspices of the North Pacific Marine Science Organization (PICES), are hoping to determine the limits to production of salmon and other nekton in the subarctic North Pacific (Anonymous 1994). In particular, joint PICES/GLOBEC science plans are under development to examine, among other things, the relationship between large-scale climatic change and the ability of the North Pacific to produce salmon.

Maturing sockeye are known to return at smaller mean size when the abundance of sockeye in the Gulf of Alaska is high (Peterman 1984a) or when abundances within stocks are high (Krogius 1962, Rogers 1980, Peterman 1984a), or in Russia when pink salmon abundances are high (Krogius 1962, 1964). Previous studies have suggested that the observed reduction in mean body size of sockeye populations occurs either in the final year at sea (Rogers 1980) or earlier in marine life (Peterman 1984b).

After analyzing interannual variation in mean size of Bristol Bay sockeye, Rogers (1986) reported that the magnitude of the western Alaska sockeye run and the mean April-May sea surface temperature at Women's Bay on Kodiak Island accounted for 31% of interannual variation in mean length of age 1.2 and 53% of age 1.3 sockeye returning to Bristol Bay from 1959 to 1983. He noted that the mean annual length of age 1.2 sockeye was more affected by temperature than by abundance and that the reverse was true for age 1.3

sockeye. That Rogers (1984) found strong density-dependent growth until 1978 and thereafter found increases in average size (relative to abundance) is significant in light of current and planned studies on decadal scale productivity shifts in the North Pacific.

This paper explores density-dependent effects on marine growth of adult sockeye salmon by age-class from 1912 to the late 1960's in three of the largest sockeye producing river systems in British Columbia: the Nass River, the Skeena River, and Rivers Inlet. Although it would be desirable to include them, the time series used in this study are not yet available for more recent decades. Nonetheless, this study may serve as a basis for comparison with more recent periods as the data become available. In this paper, I am attempting to show that (1) the density-dependent reductions in growth of adult sockeye in these stocks were age-specific, (2) that age-specific differences in ocean migration patterns provide a plausible mechanism, and (3) that the density-dependent reductions in length of specific age-classes resulted from reduced growth in the final year at sea, previously reported by Rogers (1980) for Bristol Bay sockeye, and may also have resulted from reduction in the second ocean growth season.

Data

The most comprehensive data on the size at age of B.C. sockeye was summarized in Bilton et al. (1967). They standardized and reported the mean hypural lengths by age-class and sex for sockeye salmon caught in coastal fisheries of British Columbia from 1912 to 1963. I selected data for the Nass River, the Skeena River, and Rivers Inlet because of the completeness of the time series over the period. Measures of annual sockeye density in the

North Pacific Ocean were taken from two sources. Sockeye catches (numbers) for Bristol Bay, Western Alaska, Central Alaska, Southeast Alaska, and B.C. were taken from INPFC (1979). Reconstructed minimum ocean abundances of sockeye were estimated from figures presented in Peterman (1984a:Figs.15 & 16).

Ocean distributions of known aged sockeye from the Nass and Skeena Rivers and from Rivers Inlet were determined from tagging data. The scientific programs of the former International North Pacific Fisheries Commission (INPFC) reported salmon tagging information for the period 1956 to 1991. Records of tagged sockeye recovered in INPFC General Area 71 (Nass River - D.F.O. Statistical 3), General Area 72, (Skeena River - D.F.O. Statistical Area 4) and General Area 74, (Rivers-Smith Inlets - Statistical Areas 9/10) were extracted for all years. Only sockeye tagged in the North Pacific and recovered in coastal fisheries during the same year were used. The recoveries of tagged Nass River sockeye were not so numerous (n=69), so the analysis of marine distributions focused on Skeena River (n=303) and Rivers Inlet (n=240) sockeye.

To examine when the reduction in mean length of sockeye salmon might have occurred during their life history, I used biological data collected by the former Fisheries Research Board of Canada (FRB). Biological samples of salmon caught in the commercial and test fisheries in British Columbia were collected by staff of the FRB for the period 1957 to 1972. Between 1960 and 1969, subsamples were selected and various attributes of salmon scale growth were measured, including the number of circuli and the width of each annulus. Mean annual width of each annulus, mean total scale widths (focus to edge), and mean hypural lengths were computed by age-class for samples of age 1.2 and 1.3 sockeye taken in

the Skeena River gillnet fishery. Data from the Tyee test fishery on the Skeena River were used in 1964 as no samples of the commercial fishery were found in the database.

Methods

Historical trends in annual mean length by age-class and sex in the Skeena and Nass Rivers, and Rivers Inlet sockeye fisheries were examined using a LOWESS smoothed curve (tension= 0.2) as implemented in Wilkinson (1990a). The correlation matrix of annual mean lengths stratified by river, sex, and age-class (12 strata) was computed using pairwise deletion to account for rare years of missing data in some series. To determine which correlations were significant, Bonferroni-adjusted probabilities were computed to adjust for the large number of correlations being computed. Multiple dimensional scaling of this correlation matrix was used to examine the historical pattern of covariation in the strata. Lagged cross-correlations of mean annual lengths between strata were computed to determine whether lags other than zero years produced significant correlations. Partial autocorrelations within strata were used to check for cyclic interannual patterns in length at catch and correlations in size between years within strata.

The density-dependent component of interannual variation in mean annual length at catch was estimated by examining the relationship between the \log_e of the annual catch of Bristol Bay sockeye, in numbers (INPFC 1979), versus the annual mean hypural length of sockeye by sex and age-class caught in Nass, Skeena, and Rivers Inlet fisheries. Linear trends in mean length versus abundance were tested using analysis of covariance in the MGLH

(multivariate general linear hypothesis) module in the SYSTAT 5.03 statistical package (Wilkinson, 1990b).

Recoveries of age 1.2 and 1.3 sockeye, pooled across years, were stratified by month of tagging. Notched box and whisker plots were used to determine if age 1.2 and 1.3 sockeye were tagged at similar distances from the coast. There were insufficient tag recoveries of age 2.2 and 2.3 sockeye (and of all ages from the Nass River) to thoroughly examine marine tagging distributions in any of these stocks. For each tagged sockeye, the shortest (great circle) path (Robinson et al. 1978) between the tag release and recovery locations (Skeena River (54°30'N, 131°W) or Rivers Inlet (51°30', 127°30')) was calculated along with the elapsed time. Kernel smoothing, as implemented in Wilkinson (1991b), was used to examine the temporal and spatial concentration of tags by age-class. Only tags from the terminal fishing areas within each INPFC General Area were used. Subarea 1, defined as inside the net boundary of Area 4 up to the Mowitch Pt.-Veitch Pt line, was used in the Skeena River. Subareas 1 and 2, defined as inside the net boundary of Area 9 and inside Rivers Inlet, were used in Rivers Inlet. This avoided the complications of including recoveries from tributaries that would bias the ocean migration timing estimates.

Results

Interannual variation in mean length of sockeye

Between 1912 and 1963, the annual mean lengths of sockeye caught in Nass and Skeena River and Rivers Inlet fisheries were variable (Fig. 1). The mean lengths of Nass

River sockeye were larger at age than Skeena River sockeye which, in turn, were larger than Rivers Inlet sockeye. Male sockeye were larger than female sockeye in these rivers except for age 1.2 sockeye in the Skeena River where the mean length of age 1.2 males was 0.2 cm smaller than females. The standard deviations of annual length at age were larger for male sockeye than female sockeye, except age 1.3 male sockeye from the Skeena River. Standard deviations tended to be greater for age $x.3$ sockeye than age $x.2$ when compared within freshwater age-classes. Differences in mean length among stocks and age-classes were greater than differences between sexes. Sockeye caught after 3 years at sea were larger than those caught after only two years at sea except for a period in the early history of the Nass River fishery when the mean length of age 2.2 sockeye was larger than that of age 1.3 sockeye. Sex-specific differences had little effect in determining the pattern of interannual variation in mean length.

LOWESS smoothing of annual mean lengths produces trend lines that increase and decrease with considerable synchrony between sexes and among age-classes and stocks. Nass and Skeena River sockeye size trends are more easily compared as data from four age-classes are available for both stocks. The Nass River history differs from the Skeena River in a number of ways. The most notable difference is that freshwater age, or something related to freshwater age, seems more important in determining the adult size of Nass River sockeye than Skeena River sockeye. In the Skeena River, there is much less difference between the mean lengths of age 1.2 or age 2.2 sockeye, or age 1.3 and age 2.3 than in the Nass River where the magnitude of the differences in length among age-classes are greater. The mean length of age 2.2 Nass River sockeye decreased about 4 cm from the mid-1930's to 1963. By

the early 1960's, there was less difference in mean length between ages 2.2 and 1.2 and more similar to the situation in the Skeena River.

The range between the annual mean lengths of age 1.2 and age 1.3 sockeye from Rivers Inlet is greater than that in the Nass and Skeena Rivers. Age 1.2 sockeye from Rivers Inlet decreased in length from 1912 to the late 1940's then increased during the 1950's. Mean lengths at age of 2.x sockeye were not reported in Rivers Inlet catches until 1957, presumably because of their infrequency. So few age 2.x individuals were sampled between 1957 and 1963 that the reliability of these mean lengths is low.

Correlations between annual mean lengths at catch for all strata were highest between the sexes within age-class and river (Table 2). All male/female pairs, stratified by age-class and river, ordinated as tightly coupled pairs (Fig. 2). Age-classes ordinated on dimension 2 and rivers on dimension 1. The pattern of covariation in mean lengths showed that the history of variation of an age-class in one river was often more similar to the same age-class in another river than to another age-class within the same river. For example, the pattern of interannual variation in length for age 1.3 sockeye in the Skeena River was almost identical to age 1.3 sockeye from the Nass River and more similar to age 1.3 sockeye from Rivers Inlet than to age 1.2 sockeye in the Skeena River.

Lagged cross-correlations of annual mean lengths of sockeye among rivers, stratified by age-class and sex reveal complex temporal and spatial relationships. When the Nass and Skeena Rivers are compared, age 2.x strata were not significantly correlated at any lags including zero, however, when age 1.x strata were compared, these series were significantly correlated at zero lags. Only annual mean lengths of age 1.3 sockeye (both sexes) were

significantly correlated between rivers at non-zero lags (Table 3). Cross-correlations involving Rivers Inlet sockeye and either the Skeena or the Nass River had frequent correlations in mean length at lags other than zero. Partial autocorrelations within series were significant at a 1 year lag for all Nass River series, for all age x.3 series in the Skeena River, and 2 of 4 series in Rivers Inlet (Table 4). The autocorrelations were highest in the Nass River, lowest in Rivers Inlet, and intermediate in the Skeena River.

Density-dependent marine growth of sockeye salmon

The mean annual hypural lengths of age 1.3 sockeye salmon from the Nass River, the Skeena River, and Rivers Inlet were reduced ($P < 0.10$) reduced in those years (between 1912 and 1963) when Western Alaska (Bristol Bay) sockeye catches were high (Table 5). This effect was not evident in sockeye from these rivers that had spent only 2 years in the ocean. All age 1.3 sex/age-classes from the 3 rivers showed this density-dependent effect. Of the 2.3 age sockeye in the Skeena and Nass Rivers, only Skeena males showed a significant effect ($P = 0.07$). The decrease in length of age 1.3 sockeye was greater in the Skeena River and Rivers Inlet than in the Nass River. The slopes of the regressions of mean annual hypural lengths (cm) of age 1.3 sockeye on the \log_e of Bristol Bay sockeye catches (numbers) were: in the Skeena River (σ^2 : -0.901, φ : -0.830), in the Nass River (σ^2 : -0.561, φ : -0.464), and in Rivers Inlet (σ^2 : -0.809, φ : 0.892).

Spatial distribution in the North Pacific Ocean

Age 1.2 sockeye from the Skeena River and Rivers Inlet were closer to the B.C. coast

than age 1.3 fish when tagged on the high seas in the spring of maturation. Kernel smoothing of time at sea versus distance from the Skeena River revealed two modes (concentrations) of tag release locations for both age 1.2 and 1.3 fish (Fig. 3). One mode appears common to both age-classes at about 250 km and 10 days from the Skeena River. The second mode is closer to the Skeena River in time and space for age 1.2 (675 km, 55 days) sockeye than age 1.3 (850 km, 75 days). The concentration of tagging locations in the mode closer to shore includes a higher proportion of the tags than the concentration in the more distant mode for age 1.2 fish. The concentrations of tagging locations for age 1.3 fish are more equitably shared between the two modes.

Kernel smoothing of time at sea versus distance from Rivers Inlet for tag recoveries in Subareas 1 and 2 revealed that the main concentration of age 1.2 fish was centred near 800 km, 30 days offshore (Fig. 3). Lesser concentrations were found further away. The centre of tagging concentration for most age 1.3 fish was approximately 1250 km, 63 days away at tagging. Both age-classes showed evidence of concentrations closer to the fishery at about 15 days and 200 km. The median distances from the recovery locations were significantly different between age 1.2 and age 1.3 fish during May and June for both Skeena River and Rivers Inlet sockeye (Fig. 4). For tagging during April, the differences between age-classes were consistent in trend but not significant.

Timing of the density effect on sockeye length

Sockeye salmon scales collected from the Skeena River commercial salmon fishery from 1960 through 1969 were used to examine interannual variations in growth of individual

sockeye as well as summary statistics of growth for the Skeena River stock. Summary statistics of scale morphometric characters and mean hypural lengths of returning age 1.3 and age 1.2 sockeye are reported in Tables 6 and 7. From 1960 to 1969, the mean length of age 1.3 sockeye, along with two measures of mean annual growth in the final year at sea (scale width in Zone 5 and the proportion of total scale width in Zone 5), and two measures of sockeye abundance (catches in Western Alaska, and minimum abundance of age 2+3 sockeye in the Gulf of Alaska during second ocean year) loaded highest on the dominant factor from principal component analysis (Table 8). The signs and the strengths of the loadings were consistent with what might be expected for density-dependent reductions in growth in the final spring. The magnitude of the Skeena River sockeye run (approximated as D.F.O. Statistical Area 4 catch + escapement at the Babine River fence) did not load on the dominant principal component.

The factors responsible for determining the annual mean length of age 1.2 sockeye appear different from those affecting age 1.3 fish. For age 1.2 sockeye, annual mean length, annual mean scale growth in the final year at sea (both absolute and proportional), and Western Alaska sockeye catches loaded on independent components (Table 9). The highest positive correlation between annual scale growth and mean length of age 1.2 sockeye was $r=0.53$ in Zone 3 (Table 2). The dominant principal component for age 1.2 sockeye resulted from a strong negative correlation between scale growth in the year prior to maturity and scale growth 2 years prior to maturity. A similar component was also evident in age 1.3 sockeye.

Discussion

Density-dependent reductions in the mean length of sockeye salmon caught in the major sockeye fisheries in central and northern British Columbia, associated with high abundances of western Alaska sockeye, were age-specific. Sockeye salmon that spent three years at sea were susceptible to density-dependent reductions in growth whereas sockeye returning after only two years did not. The causal mechanism appears to be related to temporal and spatial disaggregation of these age-classes in the North Pacific. The geographic distribution of age 1.3 sockeye from the Skeena River and Rivers Inlet was centred further west in the Gulf of Alaska than age 1.2 sockeye in the spring of maturation, and nearer to the main distribution of western Alaska sockeye. Western Alaska sockeye averaged 51% of total North American abundance (range 13-79%) from 1950 to 1977 and 65% (range 45-82%) from 1978 to 1984 (Rogers 1986).

Those sockeye that remain at sea for more than two years continue to feed and grow. In those years when western Alaska sockeye abundances were high, the normal growth resulting from an additional year at sea was less than in those years when western Alaska sockeye were less abundant. The factors affecting the mean length of older maturing sockeye do not appear to affect younger maturing sockeye from these rivers, or at least not in the same manner. Did these differences arise from a lifetime of exposure to different factors, or was some period during the life history more critical?

When lagged cross-correlations were computed for the mean length data, there were no significant correlations between age-classes within rivers. So, the mean size at maturity of different life history types from the same brood year are not correlated. Consider two extreme

life history options to explain this result. One possibility is that age 1.2 and age 1.3 individuals from a brood share common environmental influences from the time of entry into the ocean as smolts until the onset of maturation of the age 1.2 component. Thereafter, maturing sockeye are known to grow more than immature sockeye of the same age-class (Lander et al. 1966). Following the onset of maturation of the age 1.2 component, independent rather than common influences would presumably dominate to establish a final size at maturity. The correlation structure that would arise from this option would produce positive correlations between age-classes until the onset of maturity of the age 1.2 component. The period of common environmental influence while both components were immature and the growth achieved by both age-classes during that period shared in common would not be sufficient to establish a correlation in mean size between these age-classes at maturity. Considering the other extreme life history option, the mean sizes at maturity may have resulted from factors acting independently from the initial period of ocean entry such that very little of the life histories of age 1.2 and age 1.3 sockeye from the same river were shared in common.

Correlation analysis of the sockeye scale growth data collected from 1960 to 1969 from the Skeena River supports the first option. The mean scale annulus widths of ages 1.2 and 1.3 sockeye were significantly correlated at a lag of 1 year during their first and second ocean years (zone 2: $r=0.82$, zone 3: $r=0.80$) but not in the third year of marine growth. In other words, the scales collected in year x from age 1.2 sockeye reflected the same growth conditions for the first and second years of ocean life as scales collected from their siblings returning in year $x+1$. Thus the cross-correlation signal in mean size that was missing at the

adult stage was present during the first two years of marine life for Skeena River sockeye. The factors affecting growth of maturing age 1.2 sockeye appear to be independent of those affecting the growth of age 1.2 sockeye that do not mature. The data support a model where both age 1.2 and age 1.3 sockeye are subject to a common environment up to the end of the second marine growth season. The significance of the partial autocorrelations in mean length time series suggests that the environmental conditions that affected growth at some point in the life of maturing fish were also experienced by sockeye that remained immature for at least one additional year.

In contrast, Peterman (1984b) reported that density-dependent effects were acting on early ocean life history stages. From the mid-1950's to the mid-1970's the mean size at return of age 1.3 sockeye in the Skeena River was negatively correlated with the total abundance of age 2+3 sockeye in the Gulf of Alaska two years prior to maturation. There was some evidence of this in my analysis of Skeena River catch data from 1960 to 1969. The 3 years of highest Gulf of Alaska sockeye abundance (1958, 1959 and 1963) were also the years of lowest mean size of age 1.3 sockeye two years later (1960, 1961, and 1965). There was no evidence of a relationship between Peterman's total Gulf of Alaska abundance and the mean length of age 1.2 sockeye in the Skeena River at any lags. This suggests that a density-dependent effect on growth was operating at some early ocean life history stage, however, none of the scale growth data or the correlation analyses reported here suggest that early ocean life was the most critical period for determining mean length at return. Although the first 15 months of ocean life is the time of greatest increase in sockeye length (and scale width), and could therefore have a strong influence on the mean length attained by a given

cohort, scale growth data indicated that the coefficients of variation were greatest for annulus widths formed in the year of maturation for both age 1.2 and 1.3 sockeye stock mixtures caught in the spring and early summer in the mid-1960s in the Gulf of Alaska (unpublished data). A satisfactory explanation for the apparent density-dependent effects on growth during early ocean life has so far eluded me. None of the other data sets provide support for this effect.

Size-dependent survival and age at maturity might also potentially affect the mean size of sockeye salmon. Peterman (1982) reported that most of the mortality from smolt to adult in Skeena River sockeye must occur during the 15 month between late May (approximately) in the year of ocean entry and August of the following year when the returning jacks appear. Abundances of different ocean age sockeye were significantly correlated thereafter. I found no indication that the proportion of a brood year maturing at age 1.2 had any effect on the mean size of that age-class or sibling age 1.3 sockeye. That is, if a high proportion of a brood matured at age 1.2, there was not significant relationship between that event and the mean size of that age-class or the mean size of age 1.3 fish that returned the following year.

What model for the migration and growth of sockeye salmon from central and northern British Columbia stocks is most appropriate? The 'traditional' model of sockeye migration in the North Pacific by (French et al. 1976, Forrester (1987), Burgner (1991)) suggests that sockeye from 3 broad geographical regions (Asian, Western Alaska, and northeastern Pacific) have different general migration patterns determined by ocean age and maturity. Stock-specific variations in migration patterns within these regions are not considered. Despite this, Burgner (1991) considered evidence for density-dependent

interactions among stocks in the North Pacific (eg. Peterman 1984a,b) to be speculative because different general migration paths for Bristol Bay and northeastern Pacific sockeye would reduce the possibility of interaction between populations of sockeye.

The traditional model of sockeye migration appears unable to produce the observed patterns of interannual variation in sockeye size reported here. The observed annual variations in size at maturity appear to require a model of greater complexity which maintains the observed hierarchy of size correlations between strata. Sexes within age-classes and rivers are the most highly correlated, followed by age-classes among rivers, followed by correlations between adjacent rivers. The simplest model for maintaining the observed correlation structure between annual mean lengths of sockeye would be for those groups with the highest correlations to remain closer together over the marine life history. The same model would support the high correlation between age-classes from different rivers. Age 1.3 sockeye from different rivers presumably covary more than age 1.2 sockeye from the same river because age 1.3 sockeye have more in common (an additional year of common environmental effects while immature) with their brood year than other age-classes in the same population.

Unlike sockeye from central and northern B.C., Peterman (1984a) reported density-dependent growth of age 1.2 sockeye in two Fraser River sockeye stocks (Chilko and Stellako). Why should age 1.2 Fraser River sockeye experience density-dependent growth in the presence of large numbers of western Alaska sockeye when other more northerly populations do not? In part, the answer may be suggested by data in the INPFC tagging database. Age 1.2 Fraser River sockeye were not homogeneously distributed throughout the Gulf of Alaska. They were found in the northwestern Gulf of Alaska, overlapped in time and

space with western Alaska sockeye to a greater extent than age 1.2 sockeye from northern and central British Columbia (Fig. 5). Density-dependent growth was age-specific in sockeye salmon but evidence from tagging data also suggests that the effects at age might also be stock-specific as well.

Western Alaska sockeye form the most abundant sockeye populations in the North Pacific. In cycle years when they are very abundant, several major populations of sockeye in the Gulf of Alaska return at smaller size. The degree to which the reduction affects various sockeye populations appears to depend on the extent of the spatial and temporal overlap with western Alaska sockeye. That a reduction in size occurs implies that resources were limiting in the region of overlap. The recent high productivity of the North Pacific Ocean (Brodeur and Ware 1993) appears to have contributed to the logarithmic scale increase in western Alaska sockeye abundances. Plans for continued rebuilding of Fraser River stocks to historically high levels will further increase sockeye population densities. A sudden shift to lower productivity in the Gulf of Alaska, in combination with large abundances of sockeye, could bring about interesting changes in sockeye productivity. The PICES-GLOBEC plan to study carrying capacity of the North Pacific seems timely.

Evidence already exists that populations of salmon may be contagiously distributed in time and space in the Gulf of Alaska. Sockeye smolts leaving lakes do not do so randomly as there is normally a structured run (Wood et al. 1993). In early marine life, Jaenicke and Celewycz (1994) found contagious distributions of juvenile salmon in southeastern Alaska. Percy (1984) reported that 19 juvenile coho salmon (*O. kisutch*) from the Columbia River, Oregon, were caught in a single purse seine haul 140km and 31 days after their release from a

hatchery. Steelhead trout (*O. mykiss*) released together as juveniles from the same hatchery at the same time have been recovered together during the same gillnet fishing operation up to 2 years after release (McKinnell, in prep.). Peterman (1987) argued that Fraser River pink salmon (*O. gorbuscha*) must be a relatively cohesive group. Finally, during their homeward spawning migration, sockeye appear in coastal waters in aggregates. It seems possible to suggest that marine distributions of salmon may be more highly aggregated than previously thought. The methods for examining finer scale distributions of sockeye stocks in the ocean currently exist to test this, however, real improvements in our knowledge of sockeye distribution, abundance, and more importantly survival during the marine phase will not be made without the use of technologies yet to be developed.

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Table 1. Mean and standard deviation of the mean annual hypural lengths (cm) of sockeye caught in the Nass and Skeena Rivers and Rivers Inlet from 1912-1963.

Age-class	1.2		1.3		2.2		2.3	
	♂	♀	♂	♀	♂	♀	♂	♀
Nass R.	49.2	47.8	53.2	51.3	51.9	50.4	55.5	53.3
	0.92	0.83	1.30	1.01	1.35	1.37	1.78	1.51
Skeena R.	47.7	46.9	52.4	50.7	48.8	47.5	52.5	50.6
	0.92	0.64	1.01	0.87	0.79	0.88	1.19	1.16
Rivers Inlet	44.8	45.0	51.4	50.1	46.0	45.7	51.5	49.5
	1.11	0.90	1.40	1.13	-	-	-	-

Table 2. Pearson correlation coefficients between annual mean hypural lengths at catch where sizes have been stratified by sex, age-class and river for the Nass, Skeena, and Rivers Inlet fisheries. Correlations with significant Bonferroni-adjusted probabilities are written in bold type face.

	♂1.2SKN	♀1.2SKN	♂1.3SKN	♀1.3SKN	♂2.2SKN	♀2.2SKN	♂2.3SKN	♀2.3SKN	♂1.2NAS
♂1.2SKN	1.000								
♀1.2SKN	0.756	1.000							
♂1.3SKN	0.217	0.436	1.000						
♀1.3SKN	0.276	0.481	0.945	1.000					
♂2.2SKN	0.343	0.436	0.393	0.389	1.000				
♀2.2SKN	0.411	0.527	0.498	0.470	0.830	1.000			
♂2.3SKN	0.017	0.149	0.777	0.716	0.329	0.413	1.000		
♀2.3SKN	-0.014	0.131	0.656	0.592	0.268	0.378	0.827	1.000	
♂1.2NAS	0.395	0.402	0.232	0.236	0.299	0.156	0.098	0.084	1.000
♀1.2NAS	0.331	0.356	0.152	0.188	0.188	0.090	-0.005	0.068	0.783
♂1.3NAS	0.061	0.102	0.583	0.518	0.175	0.126	0.641	0.446	0.429
♀1.3NAS	0.077	0.182	0.529	0.495	0.177	0.116	0.583	0.423	0.468
♂2.2NAS	0.439	0.292	-0.093	-0.059	0.222	-0.013	-0.161	-0.164	0.712
♀2.2NAS	0.493	0.370	-0.146	-0.115	0.253	0.035	-0.184	-0.149	0.649
♂2.3NAS	0.104	0.022	0.186	0.149	0.150	-0.009	0.246	0.147	0.529
♀2.3NAS	-0.002	-0.074	0.135	0.114	0.140	-0.024	0.346	0.246	0.526
♂1.2RIV	0.420	0.288	-0.105	-0.083	0.025	0.038	-0.219	-0.278	0.135
♂1.3RIV	0.186	0.209	0.496	0.459	0.035	0.161	0.452	0.276	0.065
♀1.2RIV	0.304	0.277	-0.077	-0.039	-0.084	-0.083	-0.194	-0.171	0.094
♀1.3RIV	0.049	0.137	0.456	0.429	-0.075	0.033	0.398	0.249	-0.003

Table 2. Continued

	♀1.2NAS	♂1.3NAS	♀1.3NAS	♂2.2NAS	♀2.2NAS	♂2.3NAS	♀2.3NAS	♂1.2RIV	♂1.3RIV
♀1.2NAS	1.000								
♂1.3NAS	0.252	1.000							
♀1.3NAS	0.358	0.812	1.000						
♂2.2NAS	0.514	0.223	0.254	1.000					
♀2.2NAS	0.509	0.093	0.189	0.931	1.000				
♂2.3NAS	0.359	0.660	0.611	0.525	0.422	1.000			
♀2.3NAS	0.438	0.682	0.703	0.454	0.395	0.763	1.000		
♂1.2RIV	0.004	-0.126	-0.136	0.297	0.362	-0.037	-0.031	1.000	
♂1.3RIV	-0.029	0.484	0.467	-0.038	-0.062	0.140	0.165	0.389	1.000
♀1.2RIV	0.005	-0.124	-0.090	0.148	0.256	-0.065	-0.054	0.791	0.373
♀1.3RIV	-0.017	0.376	0.457	-0.114	-0.134	0.090	0.116	0.358	0.911
	♀1.2RIV	♀1.3RIV							
♀1.2RIV	1.000								
♀1.3RIV	0.420	1.000							

Table 3. Correlation coefficients between lagged series of mean annual hypural lengths at catch (1912-1963) where significant correlations occurred at annual lags other than zero for age 1.2 and 1.3 sockeye. Significant correlations at zero lag are also reported.

Strata		Lag	r
Skeena / Nass	♂ 1.3	-1	.455
		0	.583
Skeena / Nass	♀ 1.3	-1	.425
		0	.495
Skeena / Rivers	♂ 1.2	-2	.568
		-1	.346
		0	.425
	♂ 1.3	-2	.354
		-1	.419
		0	.496
Skeena / Rivers	♀ 1.2	-2	.361
		-1	.341
	♀ 1.3	0	.429
		1	.348
Nass / Rivers	♂ 1.2	-2	.329
		-1	.404
		0	.484
	♀ 1.3	-1	.362
		0	.457

Table 4. Significant partial autocorrelations in mean annual hypural lengths from 1912 to 1963 stratified by age-class, sex, and river.

<u>River</u>	<u>Sex</u>	<u>Age</u>		<u>Class</u>	
		<u>1.2</u>	<u>1.3</u>	<u>2.2</u>	<u>2.3</u>
Nass	♂	0.323	0.549	0.628	0.423
	♀	0.336	0.377	0.558	0.573
Skeena	♂	0.430		0.423	
	♀	0.367		0.322	
Rivers	♂	0.326		n/a	n/a
	♀	0.348	n/a	n/a	

Table 5. Analyses of variance from regressions of mean annual hypural lengths of B.C. sockeye salmon by age and sex on \log_e of the numbers of Western Alaska sockeye caught annually from 1912 to 1963.

River		Males				Females			
		1.2	1.3	2.2	2.3	1.2	1.3	2.2	2.3
Skeena	Slope	0.149	-0.901	0.113	-0.538	-0.198	-0.830	-0.023	-0.374
	Std. Error	0.174	0.197	0.198	0.293	0.129	0.176	0.222	0.287
	n	51	51	44	43	51	51	44	44
	P (2 tail)	0.395	0.000	0.570	0.073	0.131	0.000	0.918	0.200
Nass	Slope	-0.077	-0.561	0.270	0.199	0.006	-0.464	0.504	0.273
	Std. Error	0.220	0.305	0.333	0.433	0.195	0.243	0.326	0.358
	n	44	44	44	44	44	44	44	44
	P (2 tail)	0.730	0.073	0.422	0.648	0.975	0.063	0.129	0.451
Rivers	Slope	0.168	-0.862			-0.046	-0.809		
	Std. Error	0.253	0.328			0.212	0.261		
	n	43	44			43	44		
	P (2 tail)	0.510	0.012			0.829	0.004		

Table 6. Mean zonal widths of scales, mean hypural lengths, and sample sizes of age 1.2 sockeye salmon taken from the Area 4 (Skeena River) commercial fishery samples¹ of catch from 1960 to 1969.

<u>Year</u>		<u>Zone 1</u>	<u>Zone 2</u>	<u>Zone 3</u>	<u>Zone 4</u>	<u>Hypural Length (mm)</u>
1960	Sample size	66	66	66	66	66
	Mean	41.1	114.5	88.0	43.1	462.4
1961	Sample size	132	132	132	132	132
	Mean	37.9	99.5	100.9	47.1	474.5
1962	Sample size	443	443	443	443	479
	Mean	38.6	106.2	90.6	42.6	465.4
1963	Sample size	484	484	484	484	694
	Mean	40.0	107.1	86.8	47.8	454.1
1964	Sample size	379	379	379	379	812
	Mean	39.8	105.9	81.4	43.1	443.5
1965	Sample size	428	428	428	381	863
	Mean	37.4	107.4	90.7	42.7	479.6
1966	Sample size	741	741	741	741	1013
	Mean	37.9	111.5	82.4	44.9	469.3
1967	Sample size	512	512	512	512	623
	Mean	39.9	119.3	93.2	41.0	465.1
1968	Sample size	50	50	50	50	98
	Mean	38.8	119.9	84.4	48.6	476.9

Table 6. Continued

<u>Year</u>	<u>Zone 1</u>	<u>Zone 2</u>	<u>Zone 3</u>	<u>Zone 4</u>	<u>Hypural Length (mm)</u>
1969 Sample size	388	388	388	388	426
Mean	39.3	111.9	98.0	48.0	477.8

¹ No commercial fishery samples were found in the historical data so samples from the Tyee test fishery were used.

Table 7. Mean zonal widths of scales, mean hypural lengths, and sample sizes of age 1.3 sockeye salmon taken from the Area 4 (Skeena River) commercial fishery samples¹ of catch from 1960 to 1969.

<u>Year</u>		<u>Zone 1</u>	<u>Zone 2</u>	<u>Zone 3</u>	<u>Zone 4</u>	<u>Zone 5</u>	<u>Hypural Length (mm)</u>
1960	Sample size	37	37	37	37	37	37
	Mean	38.8	112.5	91.2	58.1	24.5	511.8
1961	Sample size	45	45	45	45	45	45
	Mean	36.3	108.4	79.0	64.1	27.1	505.9
1962	Sample size	831	831	831	831	831	831
	Mean	35.9	97.6	95.6	64.9	25.4	523.6
1963	Sample size	168	168	168	168	168	168
	Mean	38.2	111.8	86.4	60.6	28.3	532.1
1964	Sample size	851	851	851	851	851	1733
	Mean	39.0	108.2	80.5	59.9	30.6	529.1
1965	Sample size	271	271	271	271	271	606
	Mean	37.4	103.1	74.9	65.4	24.4	509.1
1966	Sample size	1159	1159	1159	1159	1158	1357
	Mean	35.8	104.1	86.2	60.0	29.8	527.2
1967	Sample size	575	575	575	575	575	730
	Mean	37.4	115.8	79.2	70.6	29.0	528.2
1968	Sample size	47	47	47	47	47	524
	Mean	39.8	115.3	86.3	65.3	31.7	530.0

Table 7. continued

<u>Year</u>	<u>Zone 1</u>	<u>Zone 2</u>	<u>Zone 3</u>	<u>Zone 4</u>	<u>Zone 5</u>	<u>Hypural Length (mm)</u>
1969 Sample size	338	338	338	338	338	386
Mean	38.0	118.3	80.1	69.0	31.1	529.7

1. No commercial fishery samples were found in the historical data so samples from the Tyee test fishery were used.

Table 8. Rotated loadings from a principal components analysis of scale growth and sockeye abundance variables for age 1.3 Skeena River sockeye caught in the Area 4 commercial fishery between 1960 and 1969.

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
GOA 2 years prior	-0.947	0.127	0.186	0.068	0.052
Mean hypural length	<u>0.931</u>	-0.066	0.130	-0.110	0.060
W. Alaska catch	<u>-0.909</u>	-0.025	0.051	0.054	0.334
Zone 5 width	<u>0.849</u>	0.201	0.284	0.276	0.210
Prop. (Zone 5)	0.749	0.130	0.210	0.306	0.427
Zone 4 width	0.111	0.924	0.026	-0.105	-0.003
Prop. (Zone 4)	-0.266	0.848	-0.130	-0.172	0.258
Skeena catch	-0.050	0.743	0.147	0.036	0.203
B.C. catch	0.392	0.712	-0.003	0.260	0.051
Prop. (Zone 3)	-0.000	-0.650	-0.649	-0.230	-0.241
Zone 3 width	0.271	-0.555	-0.514	-0.199	-0.433
GOA 3 years prior	-0.020	-0.090	-0.887	0.096	0.115
Zone 1 width	0.227	-0.232	0.838	0.094	-0.090
Prop. (Zone 2)	-0.038	0.276	0.786	0.327	-0.210
Zone 2 width	0.347	0.318	0.679	0.262	-0.392
Prop. (Zone 1)	-0.422	-0.471	0.616	0.016	0.362
Prop. (BY-age 1.3)	0.083	0.129	0.185	0.931	0.172
GOA previous year	0.141	-0.341	0.413	0.706	-0.100
GOA current year	0.495	-0.068	0.459	-0.671	-0.095
S.E. Alaska catch	0.009	0.313	-0.082	0.074	0.875
C. Alaska catch	0.076	0.139	-0.243	0.047	0.787
Variance explained	22.918	19.788	20.623	11.470	11.831

Table 8. continued,

Legend:

Zones	Mean annual widths of scale annuli (freshwater growth in Zone 1)
Prop. (Zone x)	Mean annual proportion of the total scale width by zone.
GOAxxxx	Estimated total Gulf of Alaska sockeye abundance of age 2+3 sockeye (Peterman 1984a).
Catch	Annual commercial sockeye catch in numbers.
Skeena run size	Babine fence count + Area 4 sockeye catch.
Prop. (BY-age 1.2)	Proportion of brood year that returned at age 1.2.

Table 9. Rotated loadings from a principal components analysis of scale growth and sockeye abundance variables for age 1.2 Skeena River sockeye caught in the Area 4 commercial fishery between 1960 and 1969.

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
Prop. (Zone 1)	-0.876	-0.393	0.163	0.003	0.110
Skeena run size	0.792	0.165	-0.134	-0.251	0.024
Mean hypural length	<u>0.750</u>	0.436	-0.106	0.047	-0.334
Zone 3 width	0.741	-0.233	0.096	-0.534	-0.217
B.C. catch	0.694	0.128	0.262	0.343	0.466
C. Alaska catch	0.181	0.868	0.016	0.288	-0.033
Zone 1 width	-0.299	-0.854	0.132	0.289	0.206
S.E. Alaska catch	0.068	0.717	0.325	0.258	-0.067
GOA 3 years prior	-0.109	0.635	0.033	-0.473	0.203
Prop. (Zone 4)	-0.106	0.158	<u>-0.913</u>	-0.215	0.119
Zone 4 width	0.286	-0.027	-0.893	-0.068	0.149
GOA current year	0.051	-0.186	-0.778	0.468	0.150
Prop. (Zone 2)	-0.216	0.127	0.253	0.897	0.227
Zone 2 width	0.235	-0.090	0.172	0.885	0.232
Prop. (BY-age 1.2)	0.260	0.028	0.408	-0.775	0.299
Prop. (Zone 3)	0.498	-0.092	0.146	-0.770	-0.307
W. Alaska catch	-0.001	0.270	0.229	-0.108	<u>-0.918</u>
GOA 2 years prior	0.223	-0.002	0.176	-0.173	-0.903
GOA previous year	-0.274	-0.433	0.170	0.048	0.119
Variance explained	19.814	16.831	15.201	21.157	13.143

Table 9. Continued.

Legend:

Zones	Mean annual widths of scale annuli (freshwater growth in Zone 1)
Prop. (Zone x)	Mean annual proportion of the total scale width by zone.
GOAxxxx	Estimated total Gulf of Alaska sockeye abundance of age 2+3 sockeye (Peterman 1984a).
Catch	annual commercial sockeye catch in numbers.
Skeena run size	Babine fence count + Area 4 sockeye catch.
Prop. (BY-age 1.2)	Proportion of brood year that returned at age 1.2.

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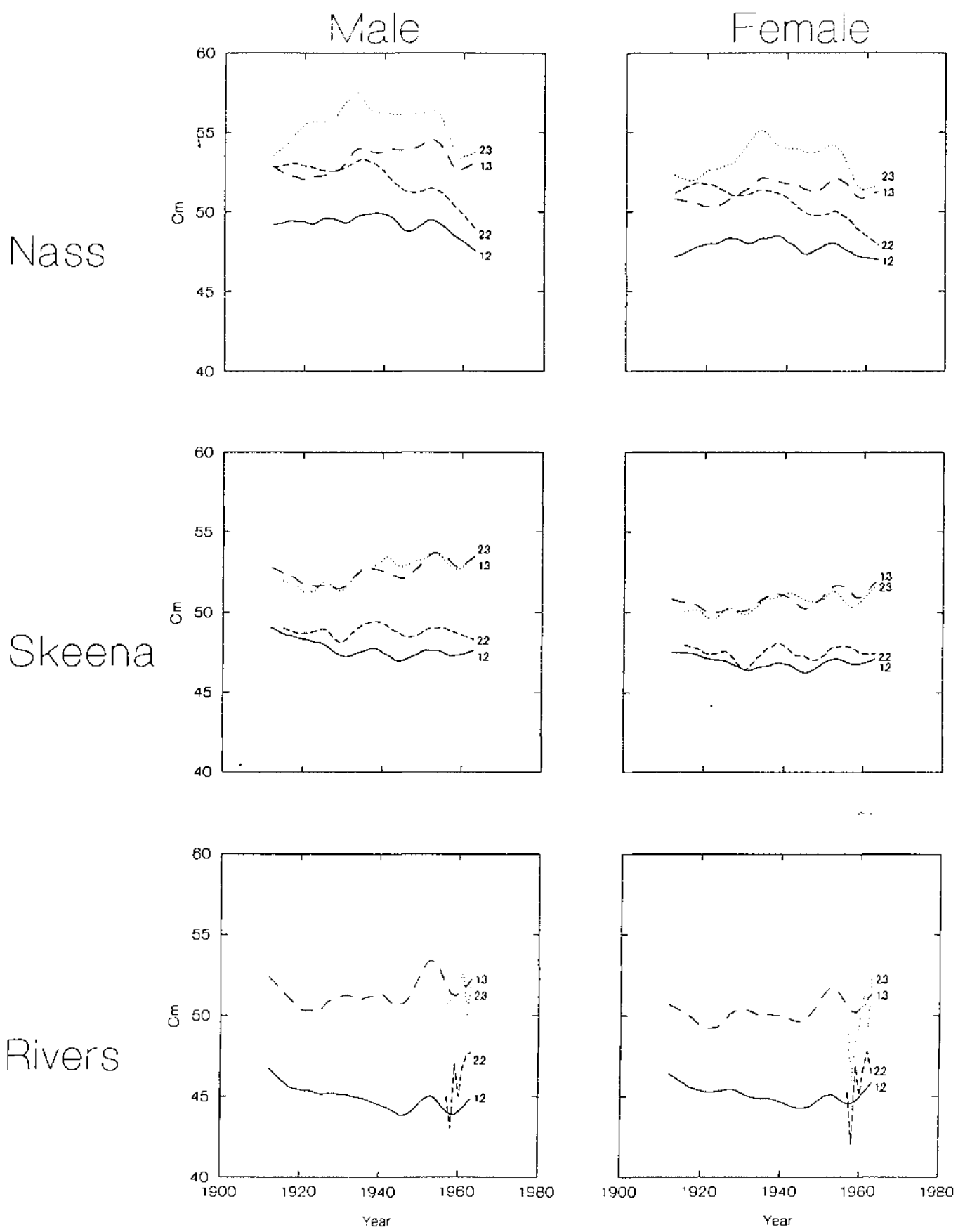
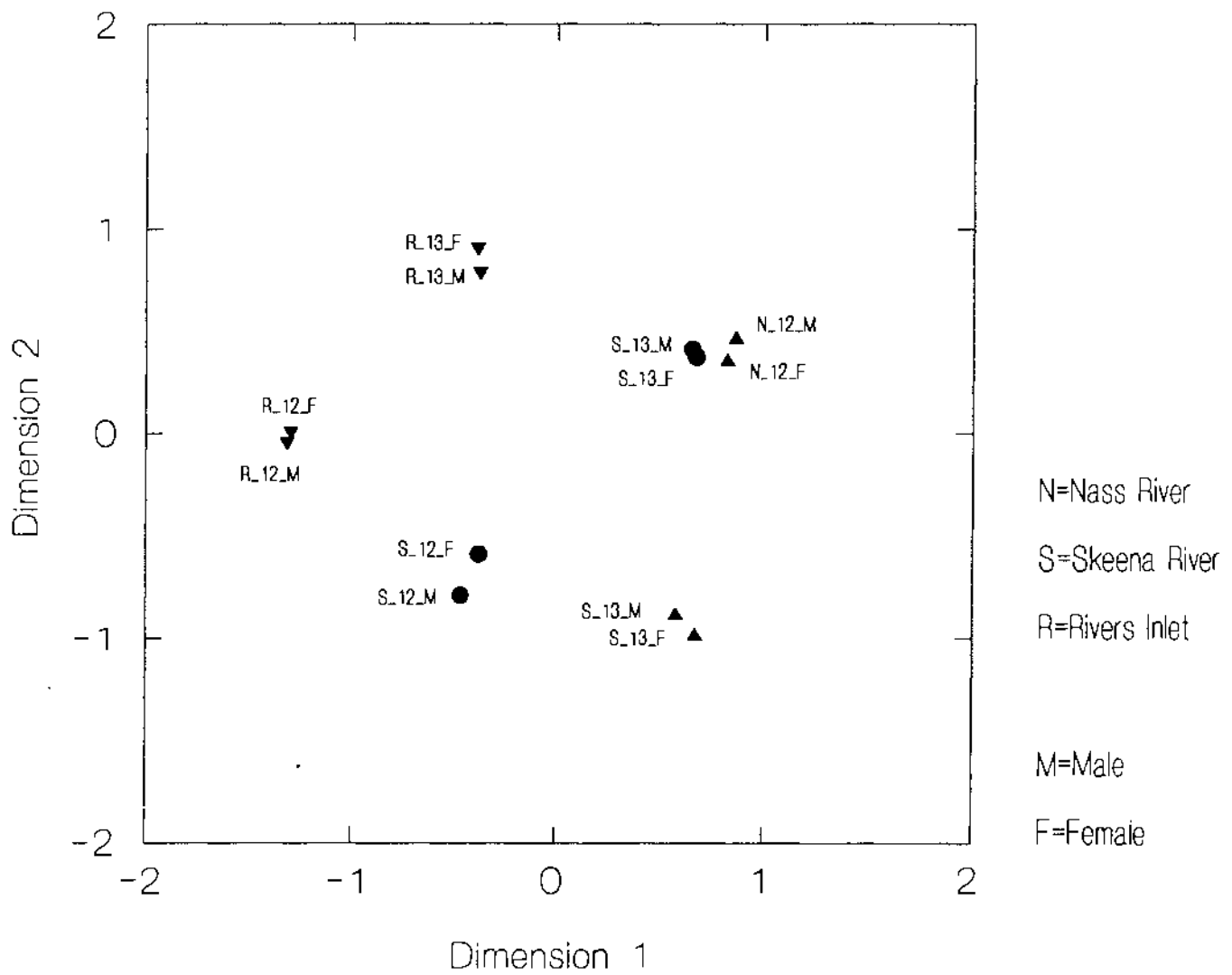
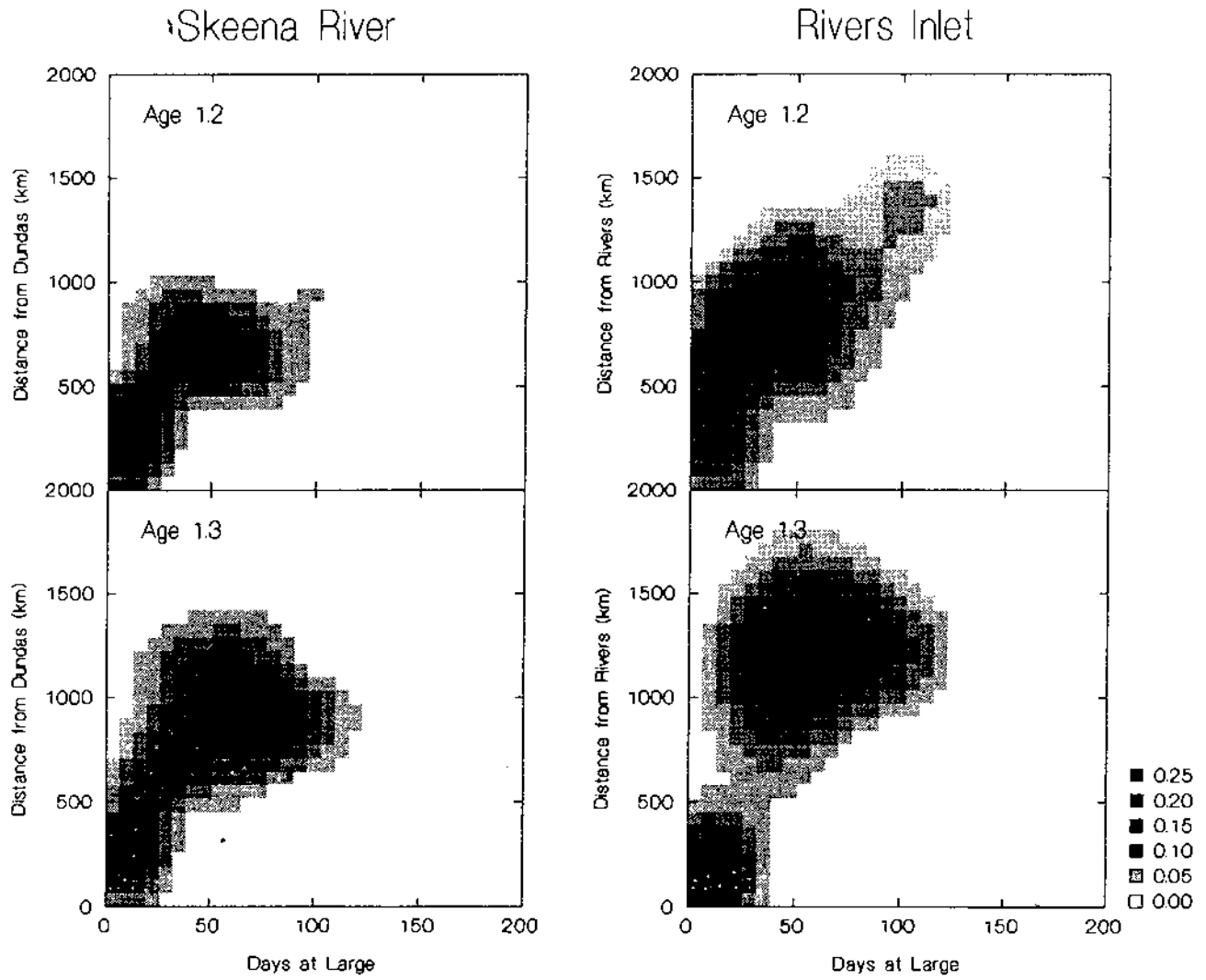
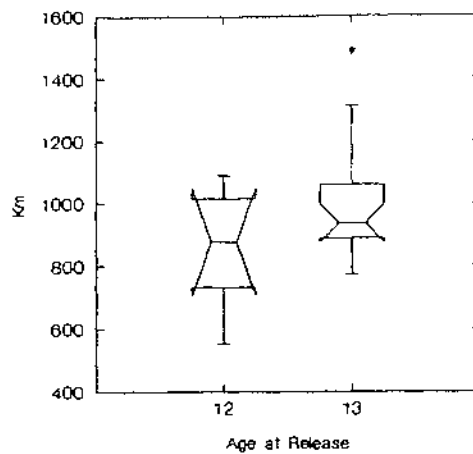
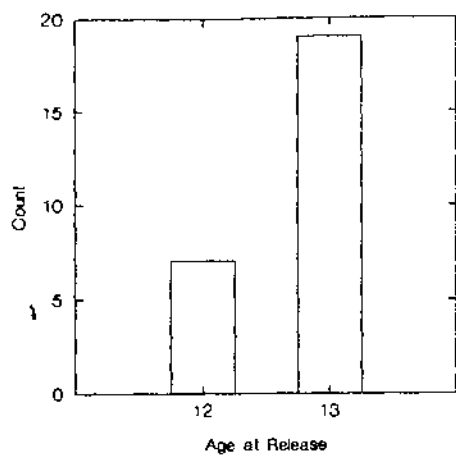


Figure 2

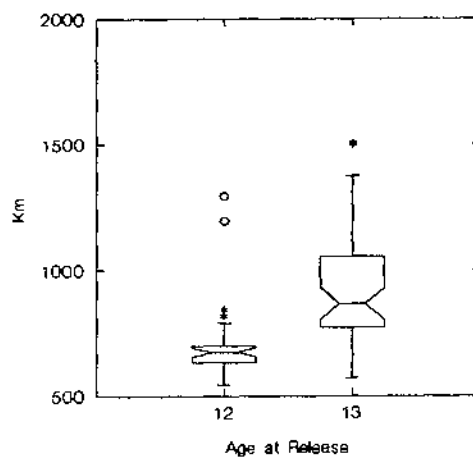
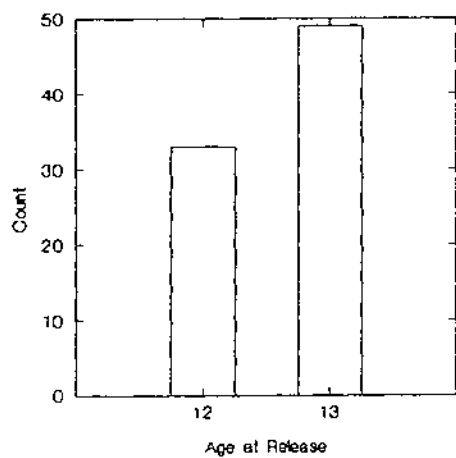




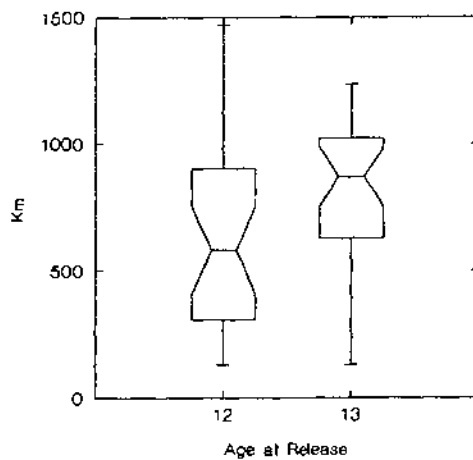
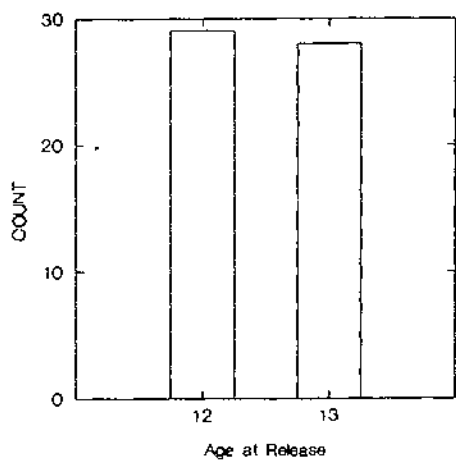
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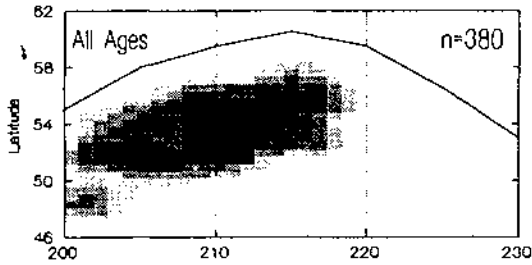
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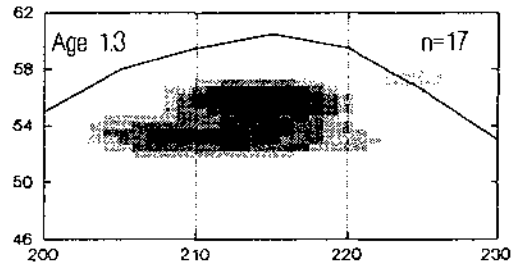
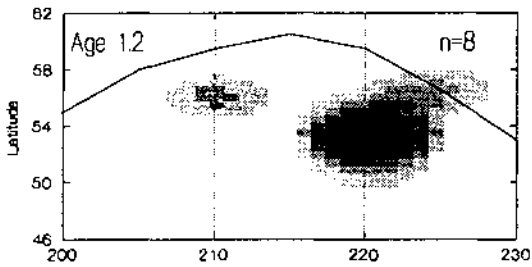
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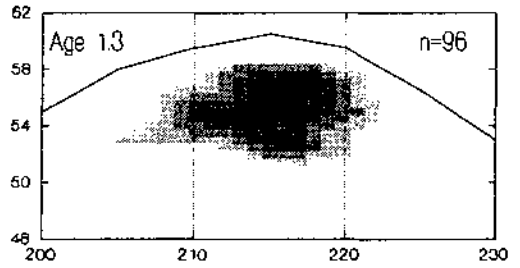
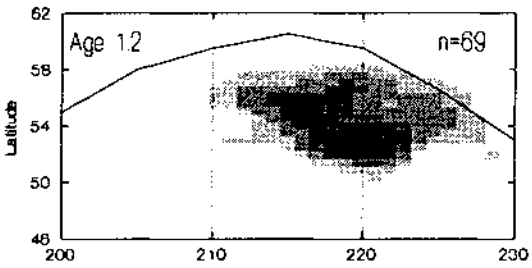
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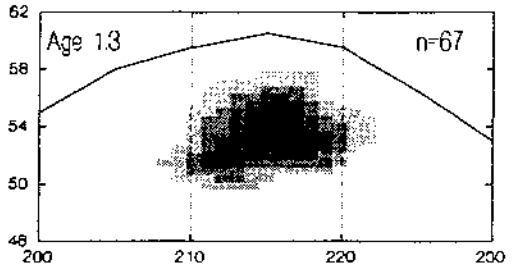
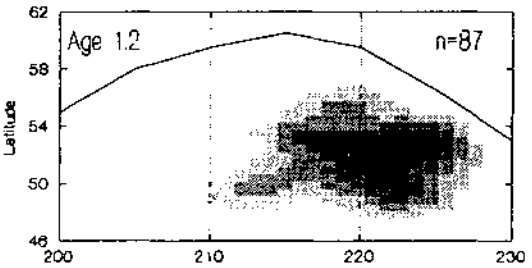
Nass River



Skeena River



Rivers Inlet



Fraser River

