

INPFC DOCUMENT
Ser. No. <u>2221</u>
Rev. No. _____

GENETIC VARIANTS OF PROTEINS IN CHUM AND CHINOOK SALMON FROM
THE BERING SEA: II ANALYSES OF 1978 COLLECTIONS AND ADDITIONAL
DATA FROM ASIAN POPULATIONS

by

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Submitted to the
INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION
by the U. S. NATIONAL SECTION

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October 1979

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INTRODUCTION

This report supplements an earlier report (Utter, 1978) based on the genetic analysis of protein variants of collections of chum and chinook salmon taken from the Bering Sea and the Yukon and Kuskokwim Rivers during 1976. The present report provides additional data from sources including (1) collections of these species from the Bering Sea during the summer of 1978, (2) juvenile chum salmon from Sakhalin Island, and (3) recent reports of Japanese studies of Asian chum salmon populations. These new data are examined relative to the earlier observations. The current picture of the genetic complexities of these species in the Bering Sea that emerges from these combined data is stated and recommendations are made for future studies directed towards the capability of identification of populations units of these species on the basis of genetic characters of such high seas collections.

SOURCES OF DATA

The sources of data of this report (plotted in Figure 1) have diverse origins. Much of the new data originated from samples of chum and chinook salmon collected during the 1978 cruise of the Japanese research vessel Riasu Maru on the Bering Sea; selected data from the 1976 cruise and from the Yukon and Kuskokwim Rivers (Utter, 1978) are also included for comparative purposes. Data were also obtained from 100 juvenile chum salmon shipped to the United States as eyed eggs from a hatchery on the Kalininka River in southwestern Sakhalin Island, USSR; these samples were provided by Oregon Aqua-Foods, Inc., Springfield, Oregon, who also supported the analysis of the data. This report also uses data from populations of Hokkaido and the Okhotsk Sea reported in Okazaki (in press).

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Chum salmon data

Data of seven polymorphic protein loci in chum salmon were presented in the first report (Utter, 1978). Considerable heterogeneity was observed in the distribution of genetic variants among samples collected within both of the Alaskan rivers for most of these loci, which generally ruled out the identification of river-specific characteristics. However, the frequency of many of the variants in some Bering Sea collections exceeded the ranges observed in Alaskan samples suggesting a substantial contribution of unsampled (and very likely Asian populations). Data from Asian populations are needed to estimate the proportions of Asian and American fish in Bering Sea collections, but those from the Asian populations most likely to be represented in these collections (i.e., from rivers near or entering the Bering Sea) were unavailable. Therefore, estimates of proportions of Asian populations had to be made from the limited data that had been collected by Soviet and Japanese workers from populations that were most likely unrepresented in the Bering Sea. These limited data suggested that variants of the MDH-3 locus existed at a pooled allelic frequency of approximately 5% in Asian populations, whereas these variants were not observed in the Yukon and Kuskokwim samples. Estimates of the relative proportion of Asian and American stocks in these Bering Sea collections, based on the assumption that the MDH-3 variation occurred at a frequency of 5% in Asian populations and was absent in Alaskan populations, suggested that Asian fish occurred at varying proportions in the earlier, more southerly collections, and were absent or infrequent in later collections.

The assumption that a 5% frequency of MDH-3 allelic variation is generally typical of Asian chum salmon populations needs re-examination. Okazaki (in press) has recently observed an average allelic frequency of only 3% for MDH-3 variants in a sampling of 900 fish from 9 areas of Hokkaido (Table 1) and has further noted that these variants occur at a frequency of less than 1% in collections representative of Amur River and Okhotsk Sea populations. Conversely, the data of the present report (Table 1) indicate a frequency of variant MDH-3 alleles of 16% in a population from Western Sakhalin Island. This broad frequency range coupled with the absence of samples from Asian populations known to contribute to the Bering Sea fishery makes the estimate of 5% presently unreliable.

A similar restraint is required in the interpretation of other recently obtained Asian data. For instance, it is initially tempting to speculate that the higher frequencies of the common alleles of LDH-1 and 6PGD observed in the Sakhalin samples than were seen in most of the Bering Sea collections and in any of the chum salmon populations from Alaskan rivers, are a reflection of a high incidence of Alaskan fish in the Bering Sea samples. However, such speculation would have to extend to the IDH and MDH-3 loci as well, where similar differences are observed among the Sakhalin, Bering Sea, and Alaskan samples. The same restrictions that affect the MDH-3 locus also apply to the IDH locus on the basis of the Hokkaido and Okhotsk Sea data (Table 1). It is therefore reasonable to assume that similar heterogeneity exists among Asian populations for most polymorphic loci, and that reliable estimates of the continental origins of Bering Sea chum salmon must await representative sampling of Asian populations that contribute to the Bering Sea fishery.

The present inability to proportionately allocate the continental origin of Bering Sea samples does not rule out considering the significance of the heterogeneity observed within and between the two sets of data from the Bering Sea in 1976 and 1978. It is pertinent first to briefly summarize the results of similar collections taken by Japanese investigators off the southern Kuril Islands. Analyses of these collections (Okazaki, in press) involved fewer biochemical genetic systems but included known allelic frequencies of major contributing populations and were supported further by data from tag returns, maturity states, migration routes and timing of runs. The combined data indicated that the maturing fish taken near the southern Kuril Islands were destined for rivers of Hokkaido while the immature fish probably originated from the Amur River. Substantial daily fluctuations of allelic frequencies of maturing fish coupled with the knowledge that these fish travel in excess of 60 miles per day further indicated a dynamic flux of maturing populations at this time. Daily fluctuations of allelic frequencies in the Bering Sea in both 1976 (e.g., IDH-100 and 75 alleles, Sta 40 vs. Sta 41) and 1978 (e.g., 6PGD, Set 11 vs. Set 12) suggests that a similar dynamic flux of populations also occurs here at least at some times and locations.

The collections of 1976 represent a much broader geographic range (Figure 1) and different timing than those made in 1978. It is not surprising for these reasons alone that a comparison of the 1976 and the 1978 data yields both similarities and differences in the distribution of allelic frequencies. Most of the loci (e.g., IDH, LDH-1, 6PGC, AGP-3, MDH-3) have similar ranges of allelic frequencies. The much higher incidence of invariant MDH-3 frequencies in 1976 (9/17 vs. 3/18) is readily explained by the absence of more northerly collections in 1978 where 6 of the 9 invariant collections occurred in 1976. It is more difficult to reconcile the very low frequency of PMI variation observed in 1978

with the relatively higher frequencies of the 1976 collections. It is interesting, however, that the only 1976 collection where PMI data were available which geographically coincided with the 1978 collections, was also the only collection of 1976 that lacked PMI variation. It is, therefore, possible that PMI may become a highly sensitive marker for differentiating Bering Sea populations of chum salmon, and it is pertinent to recall that PMI was the only genetic system that consistently differentiated between Kuskokwim and Yukon populations (Utter, 1978). Although the above factors very likely influenced the differences observed between the 1976 and 1978 collections, it is also probable that these differences reflect other variables such as different year-class strengths and migration routes.

Chinook Salmon Data

The interpretation of both the 1976 and the 1978 data of genetic variation of Bering Sea collections of chinook salmon relative to the continental origins of these fish is severely restricted by the absence of genetic data from Asian populations, and by the relatively limited set of data available on populations from the Yukon and Kuskokwim Rivers. Nevertheless, as with the chum salmon data, it is interesting to compare the heterogeneity within and between the 1976 and the 1978 data (Table 2). It is not surprising that some differences occur between the two sets of Bering Sea data given the temporal differences and the greater geographic range of the 1976 collections. Particularly noteworthy are the higher incidences of TO-1 and IDH variants, and the lower incidence of TO-2 variants in 1978. It is of further interest that three of the five Alaskan collections have a frequency of the common allele of PMI that exceeds .950, while this frequency is reached only by one of the 1976 and by none of the 1978 collections from the Bering Sea. These data cumulatively indicate that

the chinook salmon of the Bering Sea are a genetically heterogeneous group that contain varying proportions of fish originating outside of the Yukon and Kuskokwim drainages. However, realistic estimates of these proportions must await obtaining estimates of allelic frequencies from major Asian populations that migrate into the Bering Sea.

CONCLUSIONS

The present data in combination with the 1976 Bering Sea data, and baseline data from the Yukon and Kuskokwim rivers, represent an additional step towards the ultimate goal of using biochemical genetic data in the estimation of origins of chum and chinook salmon captured in Bering Sea fisheries, although this goal is presently unattainable because of the absence of appropriate Asian data of both species. The genetic heterogeneity of the Bering Sea data, plus differences observed between Bering Sea collections and Alaskan populations, both indicate that this approach will ultimately be useful if a commitment to continue this line of investigation is made. Once appropriate baseline data are available, the existing Bering Sea data can be analyzed more realistically.

We envision a multifaceted approach as the ultimate means of obtaining the most reliable answers concerning the geographic origins of the Bering Sea salmon. The genetic complexities of a particular region may initially preclude the use of genetic data alone as a reliable means of estimating origins; however, the data may become uniquely valuable when used in conjunction with other criteria. The report of Okazaki (in press) concerning the origins of chum salmon captured off the southern Kuril Islands is a useful model of this kind of combined investigation.

The recommendations of the first report (Utter, 1978) remain appropriate as a means of achieving the goal of using biochemical data to reliably estimate geographic origins of Bering Sea chum and chinook salmon; i.e.:

1. obtain collections of Asian salmon from at least three major Asian areas producing salmon which are known to contribute to the Bering Sea fishery, repeat for two or more years; and,

2. sample major contributing AYK drainages for at least two consecutive years in adequate detail to permit approximate definition of geographical and temporal population units.

LITERATURE CITED

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Estimation of geographic origins of mature and immature chum salmon (Oncorhynchus keta) captured in the autumn off the southern Kuril Islands. Bulletin, Far Seas Fisheries Research Laboratory, Shimizu, Japan. In Press.

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Table 1.--Allelic frequencies at nine polymorphic loci of chum salmon collected from the Bering Sea in 1978 plus selected data from other Bering Sea, Asian and American collections. Only the frequency of the most common allele is given except for multiple allelic systems.

Area	N	AAT ³ ^{4/}				IDH				LOCI				MEI				PGR
		100	75	95	50	LDH	PHI	6PGD	AGP	EMH3	100	75	126	85				
Bering Sea																		
1978																		
Set 1	20	5/	-	-	-	.900	1	.975	-	.975	.025	0	0	-	1			
2	55	.491	.368	.104	.028	.873	1	.918	.909	.950	.050	0	0	.782	1			
3	37	.486	.472	.028	.014	.892	.986	.916	.714	.982	.018	0	0	-	1			
4	50	.531	.398	.051	.020	.850	1	.950	.981	.930	.020	0	.050	.680	1			
5	60	.456	.378	.122	.044	.867	1	.983	.913	.983	.017	0	0	-	1			
6	54	.578	.355	.067	0	.879	1	.990	-	.944	.028	0	.028	.380	1			
7	55	.510	.375	.115	0	.882	.991	.973	.873	.918	.018	0	.064	.527	1			
8	55	.528	.377	.038	.047	.863	1	.955	.981	.927	.055	0	.018	.827	1			
9	55	.472	.453	.047	.028	.872	.991	.991	.867	1	0	0	0	-	1			
10	56	.530	.388	.082	0	.839	.991	.964	-	1	0	0	0	-	.991			
11	43	.423	.487	.090	0	.814	1	.919	.888	.919	.023	.035	.023	.937	1			
12	55	.536	.417	.047	0	.900	1	1	.902	.918	.018	.018	.016	.913	1			
13	55	.482	.427	.082	.009	-	1	.964	-	.964	.036	0	0	-	1			
14	55	.596	.394	0	.010	-	1	.936	-	.964	.018	0	.018	-	1			
15	55	.537	.278	.065	.120	.863	.991	.973	.864	.964	.018	0	.018	-	1			
16	55	.650	.300	.050	0	-	1	.982	-	.982	.018	0	0	.982	1			
17	55	.663	.245	.092	0	-	1	.955	-	1	0	0	0	.536	1			
18	55	-	-	-	-	.882	1	.955	.883	.982	0	0	.018	.882	1			
Bering Sea ^{1/}																		
1976																		
Station 24	37	.676	.576	.216	.108	0	1	.919	.946	.932	.973	.027	0	0	-	1		
25	40	.649	.705	.244	.051	0	.859	.936	.974	.961	.987	.013	0	0	-	1		
27	40	.559	.513	.372	.103	.012	.872	1	.937	.905	.987	.013	0	0	-	1		
28	27	.625	.463	.463	.074	0	.871	-	.942	.965	1	0	0	0	-	1		
29	28	.625	.577	.346	.077	0	.857	-	.944	.946	.982	0	0	.018	-	1		
30	40	.677	.438	.438	.040	0	.912	-	.950	.875	1	0	0	0	-	1		
31	22	.690	.500	.425	.025	.050	.886	-	.932	-	1	0	0	0	-	1		
33	40	.650	-	-	-	-	.925	.913	.988	.963	.950	.038	0	.012	-	1		
34	40	-	.463	.413	.100	.024	.850	.925	.988	.975	.988	.012	0	0	-	1		
36	21	.633	.429	.452	.048	.071	.904	-	.976	-	.976	.024	0	0	-	1		
37	19	.656	.368	.526	.106	0	.947	.868	.973	.973	1	0	0	0	-	1		
39	30	.672	.466	.466	.068	0	.900	.900	.967	.967	1	0	0	0	-	1		
40	34	.683	.603	.324	.059	.014	.897	.941	.956	.941	1	0	0	0	-	1		
41	25	.652	.405	.547	.048	0	.958	.958	1	.980	1	0	0	0	-	1		
42	38	.710	.389	.556	.042	.013	.868	.972	.931	.921	1	0	0	0	-	1		
Yukon-Kusk.																		
Low	2/	.378	.351	.323	0	0	.650	.826	.870	.886	1	0	0	0	-	-		
High	2/	.625	.675	.531	.086	.027	.835	.966	.977	.980	1	0	0	0	-	-		
Hokkaido ^{2/}																		
Mt. Av.	899	-	.503	.392	.024	.072	-	-	-	-	.973	.024	0	.003	-	-		
W. Okhotsk ^{3/}																		
	51	-	.480	.333	.118	.069	-	-	-	-	.990	0	0	.010	-	-		
N. Okhotsk ^{3/}																		
	78	-	.404	.481	.083	.032	-	-	-	-	.997	.003	0	0	-	-		
Sakhalin																		
	100	.636	.700	.267	0	.033	.984	1	.990	.860	.836	0	0	.164	1	1		

1/ From (Utter, 1978); two collections of 12 individuals have been omitted.

2/ Data are ranges of frequencies for each allele over both drainages, from (Utter, 1978).

3/ From Okazaki (in press); a fifth, infrequent, IDH allele is omitted.

4/ Abbreviations of enzyme systems include aspartate aminotransferase (AAT), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), phosphomannose isomerase (PHI), 6-phosphogluconate dehydrogenase (6-PGD), alpha glycerophosphate dehydrogenase (AGP), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM).

5/ Indicates no data.

Table 2.--Allelic frequencies at seven polymorphic loci of chinook salmon collected from the Bering Sea in 1978 plus selected data from Bering Sea and Alaskan collections of 1976.

Area	N	PMI	TO-1	^{3/} MDHB	IDH	GL-1	LGG	TO-2
Bering Sea								
1978								
Set 6,7	32	.859	.969	1	.984	.969	.953	-
8,9	41	.902	.988	1	1	.964	1	.964
15,16	26	.904	.962	1	1	1	.962	.944
17	85	.918	.971	1	.995	1	1	1
18	105	.881	.948	1	.995	1	1	1
19	22	.909	1	.954	-	1	1	-
20	54	.880	.963	1	.990	1	1	1
21	25	.860	1	1	.990	1	1	1
22	28	.911	.946	.982	.982	1	1	1
23-26	21	.857	1	1	1	1	1	1
1976								
Station 24 ^{1/}	29	.983	1	1	1	-	-	.966
25	20	.825	1	1	1	-	-	.950
27-29	21	.881	.952	1	1	-	-	.929
30	38	.882	-	1	1	-	-	.921
31-33	31	.839	1	1	.984	1	-	.886
34,37-42	25	.920	1	.960	1	1	-	.900
Yukon-Kuskokwim ^{1/}								
Low	<u>2/</u>	.909	.965	.942	.939	.989	-	.932
High		1	1	1	.974	.989	-	(single data point)

1/ Data from (Utter, 1978).

2/ See footnote 2/, Table 1.

3/ Abbreviations of enzyme systems not included in Table 1 are tetrazolium oxidase (TO), peptidase-glycyl leucine substrate (GL), peptidase-leucylglycylglycine substrate (LGG).

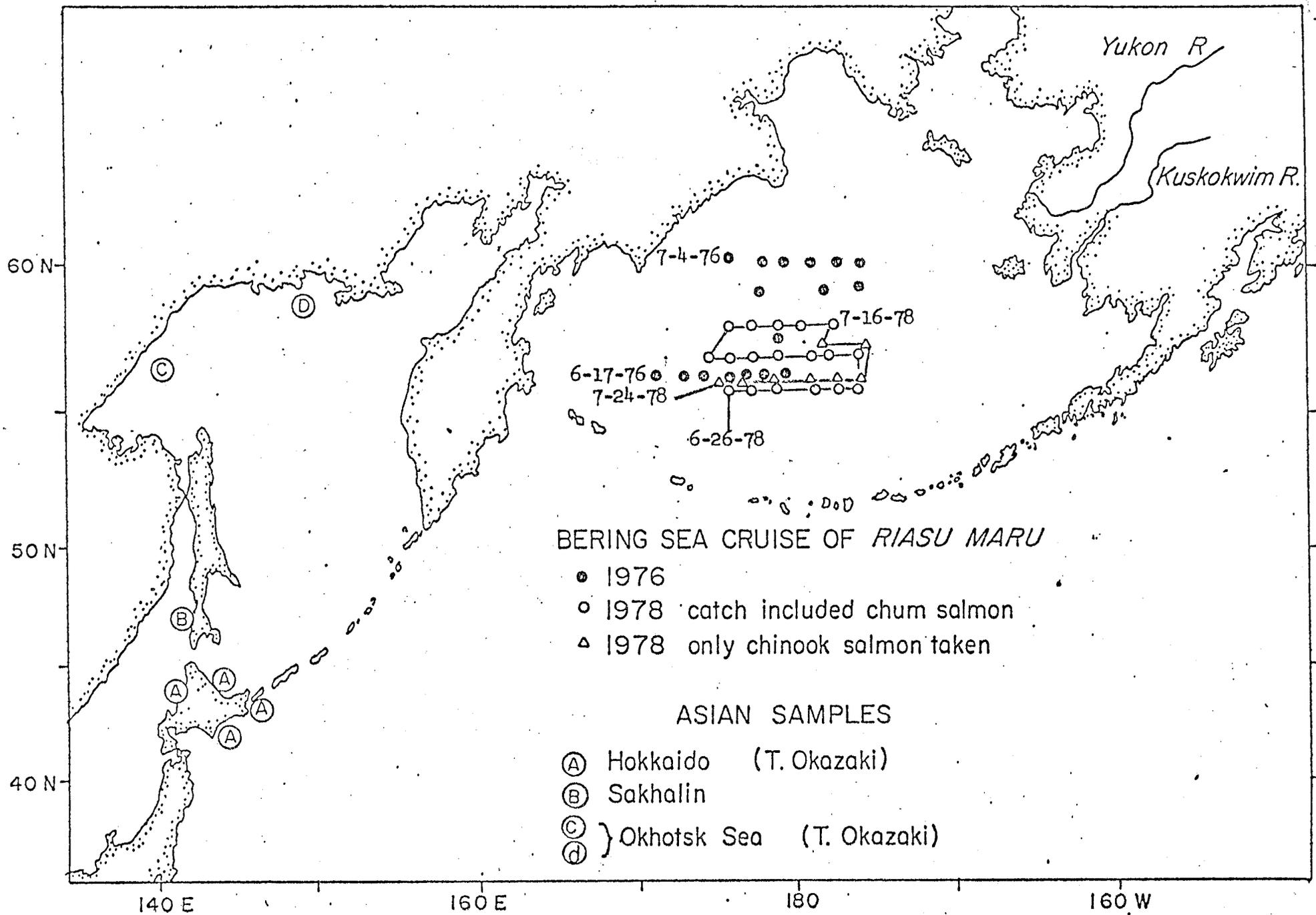


Figure 1.--Location of collections of chum and chinook salmon in the Bering Sea, and of chum salmon in Alaskan and Asian waters. Bering Sea collections of 1976 began at the extreme southwest and ended at the extreme north-west. Sequence of 1978 collections can be followed by line connecting starting and terminal sets.