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INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION

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BULLETIN NUMBER 51

DISTRIBUTION AND ORIGINS OF STEELHEAD TROUT (*Oncorhynchus mykiss*) IN OFFSHORE WATERS OF THE NORTH PACIFIC OCEAN

by

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IN OFFSHORE WATERS OF THE NORTH PACIFIC OCEAN

BY R.L. BURGNER, J.T. LIGHT, L. MARGOLIS, T. OKAZAKI, A. TAUTZ AND S. ITO

Corrections to Text

P. 45, Section 7. (Rates of Travel at Sea), paragraph 1:
- line 14, change 13 to 12
- line 16, change 50 to 33
- line 18, change 1,438 to 1,059
- line 19, change 85 to 62
- line 20, change 762 to 435 and change 15.2 to 8.7

P. 64, paragraph 4, line 1:
- change 13 to 12

paragraph 4, line 6:
- change 50 to 33
- change 85 to 62

Corrections of Appendix Table 2 (page 91 & 92) attached.

Appendix Table 2. Release and recovery information for steelhead tagged on the high seas during Japanese, U.S., U.S.S.R., and Canadian research vessel cruises, 1956-1989 (n=78).

	RELEASE			RECOVERY				
Tag Number	Date MDY	N. Latitude	Longitude	Date MDY	N. Latitude	Longitude	Elapsed Time (Days)	Distance to Recovery Pt (km)
M23341	071962	55°13´	134°35´W	073162	51°19´	127°48´W	12	625
27882	071461	56°56´	136°03´W	072761	54°06´	130°29´W	13	471
M17101	062362	52°05´	135°20´W	071062	46°16´	123°45´W	17	1,059
M49086	070667	55°30´	135°30´W	072967	54°38´	130°52´W	23	310
M19338	070962	51°58´	135°30´W	080562	52°15´	128°20´W	27	490
70149	070965	49°45´	132°05´W	080665	45°38´	121°31´W	28	912
M20382	071162	53°00´	136°10´W	081362	46°17´	123°39´W	33	1,167
MW3649	072361	54°21´	150°32´W	082961	54°05´	130°08´W	37	1,321
C21632	070688	44°59´	146°58´W	081288	49°10´	123°20´W	37	1,840
M31826	053163	51°00´	140°35´W	071063	46°15´	123°40´W	40	1,346
74310	051066	52°00´	137°00´W	062166	50°40'	126° --´W	42	777
M49068	070567	55°33´	134°40´W	082467	55°05´	127°50´W	50	435
81593	070566	58°00´	142°30´W	091666	55°15´	129°05´W	73	874
M39786	042863	45°56´	137°52´W	071063	41°50´	124°25´W	73	1,168
43774	061762	57°33´	141°40´W	090162	55°06´	127°47´W	76	896
M45387	060165	53°01´	137°20´W	082065	56°45´	131°45´W	80	547
M47766	052765	49°00´	132°30´W	081665	46°12´	123°25´W	81	749
M50148	050565	52°00´	139°00´W	072765	55°02´	130°00´W	83	683
M44836	051865	50°57´	137°33´W	081265	52°45´	128°40´W	86	641
M27057	041063	44°55´	136°08´W	071163	46°15´	123°35´W	92	986
S00667	060988	45°54´	156°18´W	090988	48°40´	125°53´W	92	2,298
M47350	050165	47°00´	150°00´W	081165	45°57´	124°00´W	102	1,984
M14811	050262	49°35´	151°00´W	081462	54°34´	130°28´W	104	1,501
74539	052466°	50°58´	137°28´W	092466	54°25´	126°48´W	123	813
M09667	041862	47°00´	141°05´W	082062	48°40´	125°40´W	124	1,163
M37740	041165	49°00´	152°30´W	082065	46°10´	123°50´W	131	2,159
M09599	041262	44°55´	130°40´W	090662	42°51´	124°34´W	147	540
L08995	090670	51°00´	177°17´E	030571	46°57´	123°50´W	180	4,203
81885	070866	56°30´	145°00´W	011067	42°03´	124°16´W	186	2,183
Y8353	071985	46°28´	169°30´E	012286	47°20´	124°19´W	187	4,869
M11975	062162	49°42´	156°50´W	010163	47°20´	123°15´W	194	2,465
33516	052664	49°10´	147°00´W	121064	46° --´	124° --´W	198	1,752
T2732	070784	45°30´	178°26´W	013185	46°04´	123°44´W	208	4,154
N4285	062579	45°31´	179°28´E	011980	45°34´	122°22´W	208	4,424
M28926	052263	47°00´	159°00´W	122963	46°55´	122°35´W	221	2,737
M28318	051663	49°00´	135°30´W	122763	43°20´	123°30´W	225	1,116
MW1625	062562	48°25´	154°00´W	020663	47°13´	122°20´W	226	2,350
MW6205	060162	48°00´	141°50´W	011663	46°11´	122°54´W	229	1,443
M29261	052663	49°00´	141°04´W	011064	40°55´	124°06´W	229	1,603
M45455	060265	52°08´	137°33´W	012266	54°10´	127°25´W	234	711
A00183	080858	56°17´	150°08´W	033059	48°32´	122°25´W	234	2,049
1777	071957	50°17´	174°45´W	031358	47°00´	126°00´W	237	3,534
M39723	042763	48°06´	136°00´W	122563	39°29´	123°46´W	242	1,368
S1315	050682	43°31´	176°22´W	010783	47°21´	124°18´W	246	4,007

.../continued

Appendix Table 2, continued.

	RELEASE			RECOVERY				
Tag Number	Date MDY	N. Latitude	Longitude	Date MDY	N. Latitude	Longitude	Elapsed Time (Days)	Distance to Recovery Pt (km)
33502	052564	47°05′	145°45′W	012765	36°30′	123°00′W	247	2,209
M29747	011364	51°00′	135°00′W	092264	55°26′	126°41′W	253	740
M28240	051563	50°00′	139°00′W	012564	55°26′	126°41′W	255	1,023
BB0107	061788	42°30'	176°30'W	031289	47°55'	124°32'W	268	4,035
M28686	052063	47°00′	153°08′W	021364	46°05′	123°43′W	269	2,238
M28689	052063	47°00′	153°08′W	022564	47°20′	124°18′W	281	2,166
M36003	040465	51°35′	132°30′W	011566	46°10′	122°55′W	286	922
M28190	051563	50°00′	139°00′W	022964	40°37′	124°15′W	290	1,549
S1210	070482	46°30′	169°31′E	042683	47°20′	124°20′W	296	4,865
AA3928	061987	45°19′	176°36′W	041688	47°00′	122°38′W	302	4,075
M20706	072062	53°01′	142°52′W	052663	47°33′	124°20′W	310	1,444
M27132	041263	46°08′	140°00′W	022364	43°05′	123°15′W	317	1,365
50117	071564	55°00′	147°25′W	071365	50°55′	127°50′W	363	1,382
M67485	070767	54°27′	134°18′W	071768	54°59′	130°02′W	376	280
M29766	011464	47°13′	133°50′W	020665	43°40′	123°40′W	389	885
51898	051565	46°00′	142°25′W	061366	42°29′	124°21′W	394	1,487
N0992	061079	43°32′	177°33′E	100580	45°35′	120°55′W	483	4,756
46288	090558	55°42′	151°49′W	020560	44°26′	124°05′W	518	2,317
P3930	053180	44°36′	177°29′W	111781	45°40′	121°30′W	535	4,299
MW1567	062262	47°15′	156°57′W	122663	39°05′	123°12′W	552	2,856
M20720	072062	53°01′	142°52′W	012564	39°00′	123°41′W	554	2,136
M50363	052965	47°00′	142°30′W	123166	45°27′	122°18′W	581	1,558
38927	071464	55°00′	150°05′W	021666	43°20′	123°15′W	582	2,319
M45422	060265	52°08′	137°33′W	010767	42°08′	124°11′W	584	1,497
M47671	052465	47°00′	137°30′W	011367	40°06′	123°48′W	599	1,341
T0624	062883	43°31′	179°29′W	022485	46°12′	123°45′W	607	4,309
51914	051765	46°02′	137°30′W	011567	46°01′	122°53′W	608	1,126
58048	050765	48°06′	143°05′W	010867	45°44′	122°24′W	611	1,587
M11950	062162	49°42′	156°50′W	022264	40°30′	124°00′W	611	2,744
S17312	062862	56°10′	148°00′W	071364	54°09′	130°05′W	746	1,156
M12021	041062	48°53′	133°15′W	03–63	54°25′	126°45′W	—	760
M27978	051163	47°39'	129°35'W	63	44°25'	124°00'W	—	561
33596	052664	49°10′	147°00′W	01–65	44°22′	124°00′W	—	1,822
C21638	070688	44°59′	146°58′W	10–88	45°38′	121°56'W	—	1,950

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PREFACE

This bulletin is the culmination of studies intensified after 1982 when the Commission endorsed a recommendation to initiate preparation of a joint comprehensive report on distribution and origins of steelhead trout in offshore waters of the North Pacific Ocean. With the recent assignment of this species to the genus *Oncorhynchus*, this report becomes the eighth in a series of new comprehensive reports published by the Commission on this genus in the high seas of the North Pacific Ocean and on closely related oceanographic conditions. The first seven in this series concerned coho salmon (Bulletin 31), oceanography (Bulletin 33), sockeye salmon (Bulletin 34), chum salmon (Bulletin 35), chinook salmon (Bulletin 38), pink salmon (Bulletin 40), and masu salmon (Bulletin 43).

Research reports submitted to the Commission for publication in the Bulletin must first receive approval by three scientific referees. Referees for this Bulletin were: Dr. R.J. Beamish, Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, B.C.; Dr. Jun Ito, National Research Institute of Far Seas Fisheries, Fisheries Agency of Japan, Shimizu, Japan; and Dr. Loh-Lee Low, Alaska Fisheries Science Centre, National Marine Fisheries Service, Seattle, Washington. Following approval for publication by the scientific referees, reports must receive approval by the Commission. Approval for publication by the Commission does not necessarily constitute endorsement of the views of the authors.

Bulletins of the Commission are published separately in English and Japanese and accuracy of translation is the responsibility of the Secretariat. The original language of this Bulletin was English.

INPFC Secretariat
March 1992

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DISTRIBUTION AND ORIGINS OF STEELHEAD TROUT (*Oncorhynchus mykiss*) IN OFFSHORE WATERS OF THE NORTH PACIFIC OCEAN

I. INTRODUCTION

In 1978 a revision of the Protocol of the International Convention for the High-Seas Fisheries of the North Pacific Ocean broadened the scope of investigations under the auspices of the International North Pacific Fisheries Commission (INPFC) to allow consideration of the high-seas distribution and origin of salmonid species in addition to the seven species of Pacific salmon. As a result of the amended Protocol, attention was directed to the high-seas distribution and origins of steelhead trout (*Oncorhynchus mykiss*). Research vessel catch data and tagging results soon provided increasing evidence of the widespread distribution of this species in the offshore waters of the North Pacific Ocean. Beginning in 1981, the Fisheries Agency of Japan provided statistics of the annual catch of this species by the Japanese landbased drift-net salmon fishery. This information, together with data from the Japanese mothership salmon fishery and from research investigations, allows a more complete description of steelhead ocean life history.

Since 1975 the Commission has published comprehensive reports that contain broad syntheses of information on the distribution and origins of species of Pacific salmon encountered offshore in the North Pacific Ocean. Because of the rapidly growing information base on steelhead and the need for a unified synthesis of this information, the INPFC in 1982 approved the recommendation of its Sub-Committee on Salmon, Committee on Biology and Research, to initiate the preparation of a joint comprehensive report on the distribution and origins of steelhead trout similar to those prepared for the Pacific salmon species.

As with the series of INPFC Bulletins on Pacific salmons, an introductory section summarizing life history information is included. Considerably less is known of the relatively less abundant Asian steelhead than of North American steelhead. In discussions and statistics regarding high-seas areas where the two forms may have been present together but not distinguished, they will be referred to collectively as "steelhead trout" for convenience. Much effort since initiation of this study has been directed to methods of determining the overlap in high-seas distribution and the relative abundance of the two forms, and in determining distributions of individual North American steelhead stocks, races, and regional groups.

II. LIFE HISTORY BACKGROUND

1. Distribution and Taxonomic Relationships

Steelhead trout, the anadromous form of rainbow trout, originate in Pacific coast streams of North America and Asia (Carl *et al.* 1959; Needham and Gard 1959; Scott and Crossman; 1973 Okazaki 1983). The native range of steelhead is more restricted than that of resident rainbow trout (Fig. 1). In North America, rainbow trout are distributed from the Kuskokwim River, Alaska, to the Rio del Presidio at 24° N, Mexico (Needham and Gard; 1959 MacCrimmon 1971). The historical distribution of spawning stocks of North American steelhead has been reported to have extended from the Bristol Bay area, Alaska, to the California-Mexico border (Carl *et al.* 1959), but according to Sheppard (1972), Sutherland (1973), and Behnke (1984), the northwestern limit of their spawning range did not extend north of the Alaska Peninsula. However, recent information reveals that steelhead spawn on the south side of the Alaska Peninsula as far west as Russell and Trout creeks, Cold Bay (Van Hulle 1985), and on the north side of the Alaska Peninsula northeast as far as Bear and Sandy rivers (Van Hulle 1985), and on the north side of Unimak Island west to Urilia Bay streams (personal communication, Arnie Shaul, Alaska Department of Fish and Game, Cold Bay, Alaska). They have not been reported in Bristol Bay lake drainages (Van Hulle 1985). The reported northern limit of spawning is in a tributary of the Gulkana River in the Copper River system, Prince William Sound, Alaska, at about 63° N (Burger *et al.* 1983; Van Hulle 1985). The present southern limit of spawning is in Malibu Creek, Santa Monica Bay, California, at 34° N (Franklin and Dobush 1989). The center of abundance of North American steelhead is the Columbia River basin and adjacent rivers to the north and south (Light 1987a).

Asian populations of rainbow trout, known locally as Kamchatkan trout or mikizha, are unevenly distributed in northeastern Asia, and occur in greatest abundance on the Kamchatka Peninsula (Fig. 1). A few scattered populations are found in streams on the mainland coast of the Sea of Okhotsk and also in streams on Greater Shantar Island and on the Commander Islands (Berg 1948; Savvaitova *et al.* 1973; Alekseev and Sviridenko 1985).

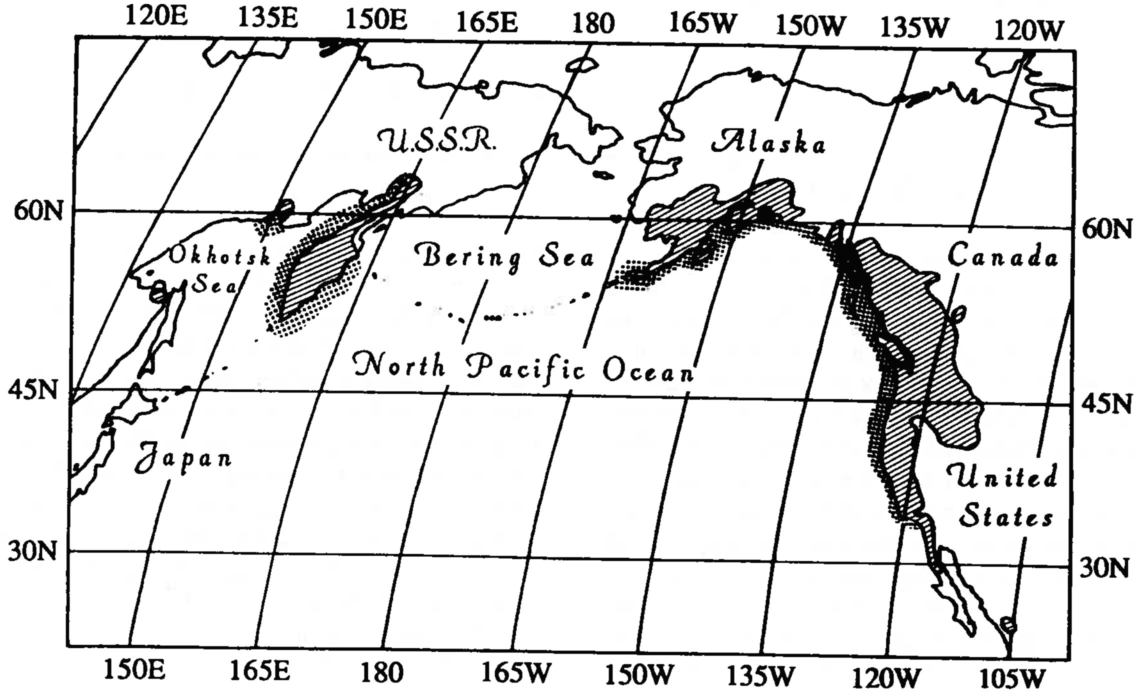


Figure 1. Endemic range of rainbow trout, *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) (shaded). Stippled areas indicate coastal areas where watersheds containing anadromous forms empty into the sea (modified from Okazaki 1983).

Anadromous populations are most abundant in streams of western Kamchatka between the Penzhina and Bol'shaya rivers (Savvaitova *et al.* 1973). They also occur in lower abundance in rivers of the east coast of Kamchatka south of the Ozernaya River (Berg 1948) and in scattered areas along the northern Okhotsk Sea coast westward to the Lonkovaya River near the Ola River (Savvaitova *et al.* 1973). Possibly, steelhead are found in the Commander Islands (Suvorov 1912).

The taxonomic relationship between the Asian and North American forms of steelhead has been the subject of considerable review and discussion (Behnke 1966; Savvaitova *et al.* 1973; Savvaitova 1975; Okazaki 1986). Formerly, the two forms were considered as different species. After a review of the evidence supporting the separation of the two forms, the Names of Fishes Committee of the American Fisheries Society resolved to recognize the two forms as a single species (Smith and Stearley 1989). On the basis of nomenclatural priority, *mykiss* was chosen as the proper scientific name for this species. Further, after concluding that there was "no biological basis" for distinguishing rainbow trout from Pacific salmon (*Oncorhynchus* spp.) at the generic level, the committee also resolved that all trout and salmon of Pacific lineages were to be considered to belong to a single genus, namely *Oncorhynchus*. In response to these changes, and for the practical reason that Asian and North American steelhead are externally indistinguishable (Okazaki 1983), they will be treated collectively in this report as *Oncorhynchus mykiss*.

Resident rainbow trout, that is, fish that do not migrate to the sea during their life span, co-occur with anadromous steelhead throughout the range of steelhead trout. Current genetic, morphological, and morphometric evidence suggests that resident trout and anadromous steelhead are simply different life history forms within the same species (Rybock *et al.* 1975; Parkinson *et al.* 1984; Reisenbichler and Phelps 1985; Currnes *et al.* 1988). If the two forms occur together in streams where they are not separated by physical barriers, it is possible that offspring of resident fish may migrate to the sea, and offspring of steelhead may remain in streams as resident fish. At the northern edge of rainbow trout distribution in Bristol Bay streams, wild populations inhabit systems with other anadromous salmonid species, yet the trout remain in fresh water throughout their lives and often grow to large size (Gwartney 1983; Van Hulle 1985).

2. Major Life History Subgroups

Within the general range of steelhead there exist distinctive ecological subgroups that are distinguished by life history or genetic differences. A general description of these subgroups is provided below as background for later discussions. These subgroups include seasonal races, regional groups, and populations with restricted ocean migration patterns.

(1) Seasonal Races

Seasonal races of steelhead occur within the range of this species (Neave 1944; Shapovalov and Taft 1954; Bali 1959; Withler 1966; Smith 1968; Sheppard 1972; Savvaitova *et al.* 1973; Chilcote *et al.* 1980; Van Hulle 1985). The races (usually two) are principally defined by the timing of adult returns to spawning streams and by the state of sexual maturity of these fish upon entry into fresh water. Fish that return to fresh water between May and October are termed "summer" steelhead and those that return between November and April are referred to as "winter" steelhead (Withler 1966; Smith 1968). This terminology is somewhat arbitrary, because steelhead populations are sometimes referred to as "spring-run" or "fall-run" according to season of entry (Shapovalov and Taft 1954; Savvaitova *et al.* 1973; Van Hulle 1985). Regardless of terminology, the fundamental differences between seasonal races are the sexual maturity of the fish upon freshwater entry and the time between entry and spawning. The gonads of summer steelhead (including fall-run fish) are only slightly developed when they enter fresh water, and there is usually a delay of several months between the time when most fish enter the river and the time spawning begins (Shapovalov and Taft 1954; Withler 1966). Summer steelhead also appear to have a higher percentage of body fat than winter steelhead at time of river entry (Smith 1968). Winter steelhead (including spring run fish) have well developed gonads when they enter fresh water, and there is much less time between freshwater entry and spawning. All seasonal races spawn at approximately the same time (principally January to May).

Although both races are widespread, summer and winter steelhead distributions do not completely coincide (Fig. 2). In some streams the native populations are exclusively winter steelhead, whereas in others only summer steelhead are found. However, many streams support both forms (Withler 1966; Everest 1973; Leider *et al.* 1984; Van Hulle 1985). Historically, summer steelhead were more prevalent in larger drainages such as the Sacramento, San Joaquin, and Klamath systems in California (Murphy and Shapovalov 1950; Kesner and Barnhart 1972), the Rogue and Umpqua rivers in Oregon (Bali 1959; Everest 1973), the Columbia River and its tributaries in Oregon, Idaho, and Washington (Bryant and Parkhurst 1950; Crawford 1979; Howell *et al.* 1985), the upper Fraser and Skeena systems in British Columbia (Withler 1966; Parkinson 1984), and a few of the larger rivers in southeastern Alaska south of Yakutat (Van Hulle 1985). A few scattered summer populations inhabit shorter coastal streams from northern California to southeastern Alaska (Pautzke and Meigs 1940; Shapovalov and Taft 1954; Bali 1959; Withler 1966; Crawford 1979; Van Hulle 1985). Steelhead north of Yakutat, Alaska, and westward to the Alaska Peninsula and into Asia are virtually all summer-run fish that return to spawning streams in the fall (primarily September-October) before the streams have frozen over, and then overwinter in these streams before spawning the following spring (Savvaitova *et al.* 1973; Burger *et al.* 1983; Van Hulle 1985).

Winter steelhead typically inhabit the abundant small streams that drain the Pacific coast of North America between Yakutat, Alaska, and central California (Murphy and Shapovalov 1950; Bali 1959; Carl *et al.* 1959; Withler 1966; Crawford 1979; Van Hulle 1985). Some winter-run fish are present in Asian streams along the west coast of the Kamchatka Peninsula (Maksimov 1976) and in some Alaska streams north of Yakutat (Van Hulle 1985), but these runs are relatively minor.

(2) Inland and Coastal Groups

Extensive genetic studies of North American steelhead have revealed the existence of two major genetic groups that are distinguished geographically by a line approximately coinciding with the crest of the Cascade Mountains (Fig. 2). These two groups are referred to as inland and coastal, and have been defined on the basis of the frequencies of LDH-4 and SOD alleles (Allendorf 1975; Parkinson 1984; Okazaki 1984b). Inland populations are exclusively summer-run and are found only in the Fraser and Columbia River drainages.

(3) Subgroups With Restricted Ocean Migration Patterns

Two notable life history subgroups of steelhead,

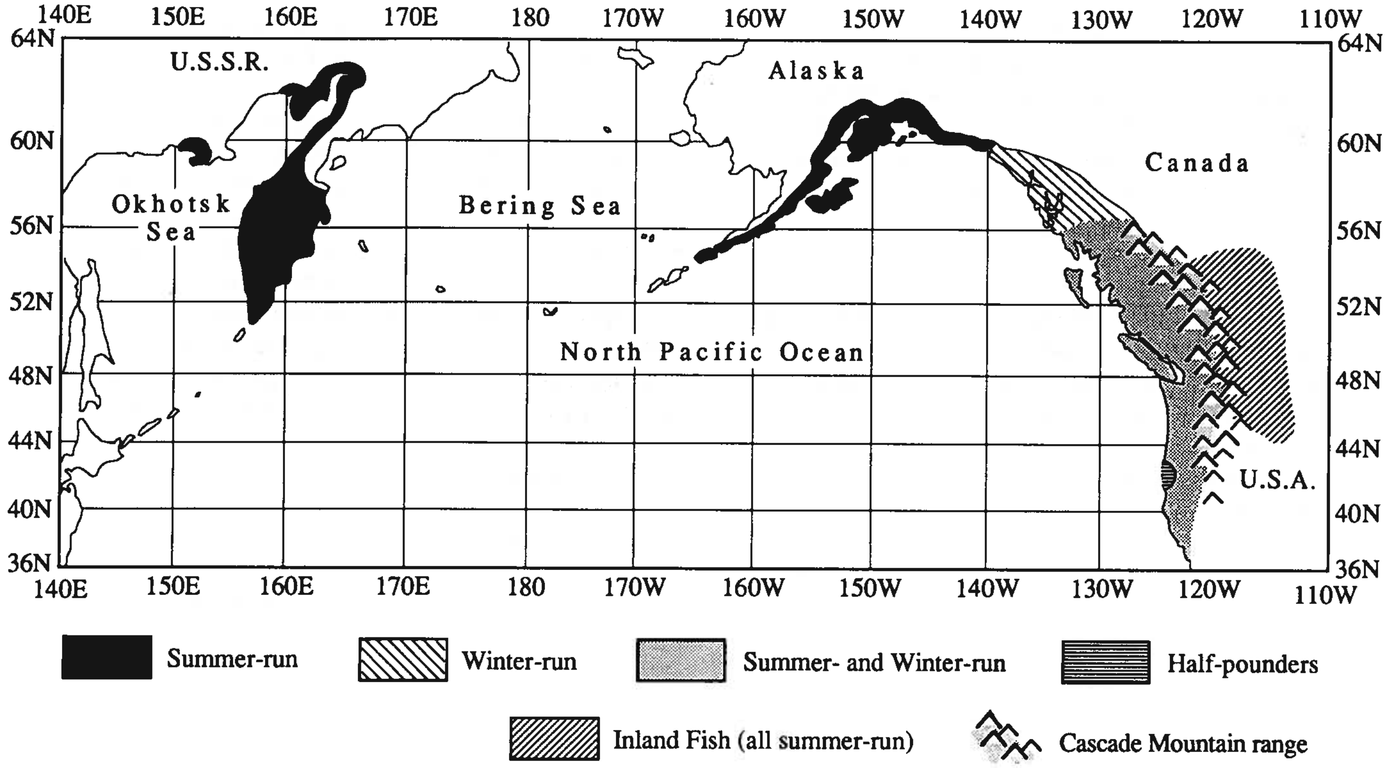


Figure 2. Geographic distribution of major steelhead life history subgroups (see text for subgroup definitions and characteristics).

namely the "half-pounder" populations of North America and coastal populations in Asia, are distinguished by unique behaviors that involve an anomalous aspect of the marine migration phase of their life histories.

(a) Half-Pounders

Steelhead in certain river systems in southern Oregon and northern California are peculiar in that a large fraction of the population (nearly 100% in some cases) returns to fresh water only a few months after entry into the ocean as smolts (Kesner and Barnhart 1972; Everest 1973). During their brief ocean residence, these fish grow to an average weight of approximately one-half pound (.23 kg), hence the common name "half-pounders." They are usually sexually immature and do not spawn on their initial return migration, but instead return to the sea the following spring. Some precocious males have been observed spawning with adult females (Everest 1973). Half-pounders later return to fresh water after their second summer at sea as maturing adults on their first spawning migration. Scale patterns of these fish are distinctive due to resorption of the edge of the scale while the fish are in fresh water. This resorption causes a check resembling a spawning check to form on the scale cutting into the periphery of the first year's ocean growth region. Once half-pounders have returned to sea after their first upstream migration their whereabouts are unknown, but they may migrate offshore before returning as mature adults.

(b) Asian Coastal Populations

This life history subgroup is composed of anadromous steelhead in Asian populations that do not migrate as extensively as do the majority of Asian steelhead (Savvaitova *et al.* 1973). These fish, identified on the basis of scale features, appear to undertake brief, localized marine migrations similar to the migration patterns of anadromous cutthroat trout (*Oncorhynchus clarki*) in North American coastal streams (Johnston 1982). Much less is known about Asian coastal steelhead than is known of the half-pounders in North America. As with half-pounder steelhead, the ecological reasons for this peculiar life history pattern are unknown.

3. Spawning and Freshwater Life History

Steelhead possess an array of life history features that reflect extreme adaptability to a wide variety of environmental conditions. These features combine to make steelhead life history the most complex and diverse of all the species of *Oncorhynchus*. In this section, freshwater life history is summarized to provide necessary background for an understanding of ocean life history. Much of the information presented here has been summarized elsewhere (Sutherland 1973; Behnke 1984; Okazaki 1986), but new information from recent studies and a re-examination and synthesis of earlier information is included where appropriate. Emphasis is placed on naturally-produced "wild" steelhead, although some examples from hatchery fish are used.

(1) Adult Return to Fresh Water

After maturing for one to several years in the ocean, steelhead depart their distant feeding areas and return to their natal streams to spawn. The timing of their return to the coast and the degree of sexual maturity at return are largely governed by the seasonal race to which the fish belong. Although there are probably steelhead returning to some Pacific Rim streams throughout the year (Withler 1966; Savvaitova *et al.* 1973), the timing of returns of populations to individual streams is more compressed and reflects the presence of seasonal races within each population. The period of freshwater entry for most steelhead populations encompasses several months and is composed of many minor peaks in numbers of immigrants rather than one major peak. Available evidence suggests that steelhead do not tend to linger in their home estuary prior to stream entry if stream flow is favorable (Shapovalov and Taft 1954; Everest 1973; Gatto *et al.* 1976; Oguss and Evans 1978). However, their entry timing can be influenced by tides and stream discharge (Shapovalov and Taft 1954; Withler 1966; Everest 1973).

Steelhead typically remain at sea for two to four summer growing seasons (one to three winters) before returning to fresh water to spawn. The duration of ocean residence is apparently independent of time spent in fresh water (Sutherland 1973; Okazaki 1984a).

Prior to their first spawning migration, immature steelhead of all age groups and both sexes are referred to as "maiden" fish. If maiden steelhead survive their first spawning and successfully return to the sea, they are called "kelts". Kelts may return to spawn in the season immediately following their previous spawning (consecutive spawners), or they may remain at sea for an additional year before a subsequent spawning migration (alternate spawners). Scales from the former group have consecutive spawning checks separated by a single summer growth zone, whereas those from the latter group have an ocean annulus (and two summers of ocean growth) between spawning checks. Kelts are predominantly female (Withler 1966; Jones 1972-1976; Hooton *et al.* 1987; Didier 1990); females outnumbered males by over four to one among repeat spawners in wild fish samples from 14 Vancouver Island streams (Hooton *et al.* 1987), and in Alaskan streams typically comprised 65 to 80 percent of repeat spawning fish (Didier 1990).

The frequency of repeat spawning varies greatly among populations. So few summer-run fish in the Columbia Basin survive spawning that these populations are effectively semelparous (Long and Griffin 1937), whereas repeat spawners comprised well over 30% of returning winter-run steelhead to Petersburg Creek and summer run steelhead to Karluk River in Alaska (Jones 1972-1976; Van Hulle 1985).

The average size (fork length) of adult steelhead returning to fresh water is usually between 625 and 750 mm. Summer-run fish from the Clearwater River in Idaho and the Kispiox and Thompson rivers in British Columbia achieve a particularly large size. (Average length: Clearwater River wild fish, 831 mm, Ball and Pettit 1974; Thompson River males, 912 mm, McGregor 1986; Kispiox River combined sexes, 850 mm, Whately 1977). Some steelhead returning to the Clearwater and Kispiox rivers exceed a meter in length (Ball and Pettit 1974; Whately 1977). In general, fish size correlates with the number of years spent in the ocean. In Idaho, two groups of summer run steelhead are recognized, group A, returning past Bonneville Dam primarily between July 1 and August 25 after only one winter in the ocean, and group B, much larger fish returning primarily after August 25 and after two winters in the ocean (Idaho Fish and Game 1992).

(2) Homing and Upstream Migration

Homing behavior is characteristic of salmonids and is linked with the suite of population-specific traits that they display. The most thorough study of homing to the natal site in wild steelhead was conducted by Shapovalov and Taft (1954) on Waddell and Scott creeks, two small coastal California creeks with winter steelhead runs. During this twelve year study (1931-1942), 476 (98.1%) steelhead marked at Waddell Creek returned there and 9 (1.9%) strayed to Scott Creek. Of the Scott Creek steelhead, 932 (97.1%) returned there and 28 (2.9%) strayed to Waddell Creek. In contrast, coho salmon (*Oncorhynchus kisutch*) from these two creeks strayed much more than did the steelhead (85.1 and 73.2% homing to Waddell and Scott creeks, respectively). Repeat-spawning steelhead also exhibit the ability to home accurately to their natal stream or stream of previous spawning (Everest 1973). Although homing generally prevails, circumstantial evidence indicates that the degradation of water quality and spawning habitat following the eruption of Mt. St. Helens, Washington State, led to increased straying of steelhead from the affected area (Leider 1989). In the Rogue River, Oregon, half-pounder steelhead appear to have less fidelity to their river of origin than maturing fish (Satterthwaite 1988).

Many studies have shown that a large proportion of hatchery steelhead incubated, reared, and released in a river will return there as adults (e.g., Leider *et al.* 1985; Lirette and Hooton 1988; see reviews by Lister *et al.* 1981 and Slatick *et al.* 1988). Fish captured during downstream migration and trucked to release sites below dams on the Columbia River tend to return to their hatchery of origin (Ebel *et al.* 1973; Slatick *et al.* 1975). Fish reared at one site but released as smolts after an additional rearing period at another site tend to return to the release site (Wagner 1969; Cramer 1981). However, in Oregon there is reported to be a significant problem of hatchery fish straying into streams where no hatchery smolt releases have occurred (Chilcote 1992).

Although most evidence indicates that steelhead and other salmon imprint as smolts, there are indications that the homing behavior of transplanted or "artificially imprinted" fish reflects a tendency to return to both the release site and the natal site. Fish released away from the natal site stray more than do those reared and released at the same site, and those that stray often go back to their rearing site. In general, the closer the rearing and release sites are to each other, the greater the tendency to stray from the release site and return to the rearing site (Lister *et al.* 1981).

After a period of upriver migration, steelhead appear to "hold" in specific sections of rivers during the winter. This seems to be the case for both summer runs (Spence 1981; Burger *et al.* 1983; Lough 1983; Wallis and Balland 1984) and winter runs (Hooton and Lirette 1986). Spence (1981) reported that individual summer-run fish were stationary for up to six months in the Chilcotin River system, B.C. Fish did not all hold in the same place but rather were spread out over 60 km of river in the Chilcotin and lower Chilko rivers. The holding areas chosen by steelhead on their upriver migrations often contain deep pools with an abundance of cover (large boulders, ledges, overhanging vegetation, etc.) (Savvaitova *et al.* 1973; Dunn 1981; Freese 1982; Burger *et al.* 1983). In the spring, steelhead typically move from holding areas to spawning areas. These movements are usually upstream, but complex riverine movements have been noted by several authors (Burger *et al.* 1983; Lough 1983; Wallis and Balland 1984).

(3) Spawning

Steelhead spawn primarily in late winter and spring, with some regional (latitudinal, altitudinal) variation produced by stream temperature or flow regimes. For example, for summer steelhead populations in southern Oregon and California, spawning begins as early as December and is finished by April-May, whereas in the cooler climates of Alaska and Asia, spawning of summer steelhead begins in late April or May after the ice melts and continues into June. Racial differences are also apparent. Summer steelhead in the Kalama River, Washington, and the Rogue River, Oregon, spawn substantially earlier than winter populations in the same streams (Everest 1973; Leider *et al.* 1984, 1986).

Steelhead typically spawn in moderate to high gradient sections of streams at the heads of riffles or the tails of pools where hydraulic conditions are conducive to intragravel flows adequate to maintain an oxygenated environment during egg incubation (Greeley 1932; Orcutt *et al.* 1968). Within these general areas, steelhead redd sites occur within a range of habitat characteristics that include water velocity and depth, cover, and substrate size.

Other factors that appear to influence redd site selection include presence of escape cover (See 1987), size of fish (Orcutt *et al.* 1968), water temperature (Dodge and MacCrimmon 1971; Reiser and Bjornn 1979; Cederholm 1984), and number of fish in the spawning population (Orcutt *et al.* 1968). Water temperatures during spawning normally range between 3.9° and 9.4°C (Bell 1973), although successful spawning has been known to occur at temperatures as low as 0.3°C (Dodge and MacCrimmon 1971) and as high as 20°C (Cederholm 1984).

Female steelhead generally construct a single redd in which they dig several nests. Occasionally, a female will not deposit all of her eggs in a single redd, and will construct a second redd to finish spawning (Reingold 1964). The female chooses the redd site and performs all digging (Shapovalov and Taft 1954). The dominant male attends the female during nest digging and egg deposition/fertilization, while satellite males, if present, arrange themselves downstream. Precocious steelhead and resident trout males (and occasionally, in populations where they occur, half-pounder males) often participate in fertilization and are sometimes a large fraction of the satellite male population (Everest 1973). Steelhead do not guard the nests after spawning. Individual males may remain on the spawning ground for some time to mate with several females. Females typically leave the spawning area immediately and move passively downstream (Shapovalov and Taft 1954; Everest 1973; Hooton and Lirette 1986).

(4) Embryonic Development and Emergence

Steelhead egg development generally occurs on an increasing stream temperature schedule. Temperature requirements for development from time of egg deposition to alevin emergence range from about 583 to 661 temperature units (cumulative degree-days above 0° C) depending on mean incubation temperature (data from computer program, Jensen 1988). Brannon (1987) noted that, unlike Pacific salmon embryos, steelhead trout embryos incubated at constant temperatures required fewer temperature units to yolk absorption at higher incubation temperatures (e.g., 650 units at 5°C, 608 units at 10.4°C). The numbers of degree days required for embryonic development of steelhead to the emergence stage are considerably fewer than for the Pacific salmons (see Brannon, 1987, Fig. 2). At emergence the alevins have grown to approximately 23-26 mm in length (Shapovalov and Taft 1954), and are generally smaller than alevins of the Pacific salmons at the same stage.

The timing of emergence of juvenile steelhead from redds is dependent on spawning season and on incubation temperatures. Peak emergence occurs in April and May in two Rogue River, Oregon, tributaries (Everest 1973), whereas in some Puget Sound streams of Washington, emergence from wild stock spawning is heavier in June and July (R. L. Burgner, unpublished data). Alevins with absorbed yolk sacs were found in the Utkholok River, west Kamchatka, by mid-June (Savvaitova *et al.* 1973). In the Anchor River, Cook Inlet, Alaska, emergence was estimated to peak in July (Wallis and Balland 1984). In the Salmon River, Idaho, steelhead emerge from the gravel from July to September (Howell *et al.* 1985).

(5) Stream Residence and Emigration of Smolts

The stream residence of juvenile steelhead lasts from one to five or more years, with the majority of fish spending two to three years in fresh water before departing to the sea (Sutherland 1973; Savvaitova *et al.* 1973). Freshwater age generally increases along the coast from south to north. In most naturally-produced populations, few fish leave the stream after only one year of freshwater growth, but in wild populations of the Rogue River and many California streams, there occurs a sizeable number of one-year smolts (9-29%) (Shapovalov and Taft 1954; Hallock *et al.* 1961; Kesner and Barnhart 1972; Everest 1973). In colder or less productive streams such as those occurring in northern British Columbia and Alaska, a noticeable percentage of fish remain in streams for four and, less frequently, five years (Whately 1977; Van Hulle 1985).

In their first year in the stream, steelhead typically grow to about 100 mm. Fry that emerge late in the year, such as those in the headwaters of some Columbia River tributaries, do not grow appreciably before winter and are only about 50 mm in length the following spring. Fish raised in hatcheries usually exceed 150 mm by the completion of their first year of growth, and are released in the spring following hatching (Wahle and Smith 1979). By the end of their second winter in the stream, most naturally-produced steelhead are larger than 150 mm, and at this size many will become smolts and leave the system (Wagner 1968; Chrisp and Bjornn 1978).

Size, far more than age, is the critical determinant in the initiation of smolt outmigration. A coastwide survey of smolt size at outmigration reveals that despite the great variation in steelhead age at emigration, the size (fork length) of most wild smolts is consistently near 160 mm (Wagner 1968; Everest 1973; Chrisp and Bjornn 1978; Seelbach 1987; Ward and Slaney 1988; Peven and Hays 1989), ranging from 125 to 225 mm (Peterson and Lyons 1968; Narver 1969; Maksimov 1976). Studies of hatchery fish indicate that survival is highest for fish larger than 150 mm at time of release (Wagner 1968; Seelbach 1987). Size at emigration also appears to affect the number of years spent at sea, and consequently the size at return; larger smolts produce adults that return sooner than adults of smaller smolts (Shapovalov and Taft 1954; Chapman 1958; Bali 1959; Ward and Slaney 1988).

Once steelhead reach the proper size and begin the physiological transformation that enables them to live in sea water, they begin their movement downstream to the sea. The migration occurs for the most part in the spring, from mid-March to mid-July, but the peak of the migration usually occurs between mid-April and mid-May, coincident with spring runoff. In populations from southeastern Alaska to Asia, and in headwaters of interior streams in the Columbia and Fraser River basins, smolts migrate in June, somewhat later than populations elsewhere along the coast (Maksimov 1972; Jones 1973; Savvaitova *et al.* 1973; Fish Passage Center 1986). In some streams, larger smolts appear to leave earlier than smaller ones (Jones 1973; Howell *et al.* 1985). Coincident with smoltification, young steelhead attain a silvery coloration that is retained until they develop nuptial coloration upon their return to fresh water to spawn.

III. METHODS AND INFORMATION SOURCES

1. Age Designation Terminology

A large part of what is known of steelhead life history has come from the study of scales. The age and spawning history of a fish are recorded in scale features, and many terminologies have been developed to describe the diversity of life history characteristics peculiar to fish of a given stock. In this report, the age designation format developed by Koo (1962) for Pacific salmon will be used. By this method, the number of years spent in fresh water, identified by winter annuli (annuli are typically formed in March, Maher and Larkin 1955), is denoted by a numeral followed by a dot (period). To the right of the period another numeral denotes the number of winters spent at sea. For example, the age class of a fish that had spent 2 years (i.e., winters) in fresh water before entering the sea as a smolt, followed by three full winters (which implies 3 summers of ocean growth) in the ocean before being caught at sea in its 4th summer of ocean growth is denoted as 2.3.

2. Information from High-Seas Research

Information on ocean distribution and abundance of steelhead largely derives from catch, effort, and biological data collected since 1955. Oceanographic and tag-recovery information is also used to help interpret the observed distribution patterns and to gain insight into movements of specific stocks, groups, or races. Most of the ocean catch, effort, and biological data were obtained from published or unpublished records of fishing operations of salmon research vessels of the three member nations of the INPFC: the United States, Canada, and Japan. Other information was obtained from records of non-INPFC sponsored research both in offshore (U.S.-U.S.S.R. cooperative research in 1983-1990) and in nearshore waters (Fisher *et al.* 1983, 1984; Miller *et al.* 1983; Fisher and Pearcy 1985a, b; Margolis *et al.* 1989). Gillnets, longlines, and purse seines were used during fishing operations. Longlines and purse seines were principally used to capture fish alive for tagging whereas gillnets were used to obtain relative abundance data and biological information. Effort data used in this report include the number of sets of each particular gear type and the total amount of gear deployed. For purse seines, a single set was used as the unit of effort. For gillnets, the unit of effort was a 50-m tan (U.S. and Canadian 50-fm gillnet "shackles" were converted accordingly). A 49-hook hachi (called a "skate" in the U.S. and Canada) was the unit of effort for longlines.

A brief description of the three gears, fishing methods, and limitations in use of steelhead catch data for abundance comparisons is given in Sutherland (1973). Additional discussions of differences in the respective gears used and effect on salmon catch-per-unit-of-effort (CPUE) are given by Godfrey *et al.* (1975); French *et al.* (1976); and Takagi *et al.* (1981).

High-seas research conducted by INPFC member nations initially focussed on the Pacific salmons, and steelhead trout received little attention until the Protocol revision of 1978, which addressed all salmonids in Convention waters. Consequently, only portions of the total high-seas salmonid data set are relevant to steelhead. Much of the catch, effort, and biological data for steelhead prior to 1981 were taken from annual reports and shipboard sampling sheets. When biological data are used, the data will include U.S. and Canadian data for the years 1955-1990, but Japanese data will generally be restricted to the period 1981-1989 because earlier data are incomplete. However, in some areas, particularly those along the coast of the Soviet Union and in the Sea of Okhotsk, early Japanese catch data are crucial to an understanding of the total distribution of steelhead (Okazaki 1983). Where appropriate, these early data are included but identified as incomplete.

Basic biological information (scale samples, length measurements) was collected from all steelhead caught. More detailed biological information, such as body and gonad weight and sex, was taken from dead fish, i.e., all fish caught with gillnets or those fish caught with purse seines or longlines that perished during tagging operations. In some years or on some vessels, fish were sampled in greater detail to obtain stomach contents, tissue samples and kidneys for genetic or parasitological studies, and otoliths or other non-routine information. Routine biological sampling procedures aboard Japanese research vessels are described by Light and LeBrasseur (1986).

Three separate analyses of the seasonal distribution of steelhead were performed. The first analysis, based on available catch and effort data for the years 1955-1990 (Canada and U.S.A.), 1981-1989 (Japan), and 1983-1990 (U.S.S.R.), included fish from all ocean age groups and spawning histories. In the second and third analyses, ocean age and spawning history information obtained from scales collected in 1955-1985 (Canada and U.S.A.) and 1981-1985 (Japan) was used to group fish prior to CPUE calculations. In the ocean age analysis, fish were grouped into three ocean age categories based on the number of annuli present in the ocean growth portion of their scales: age .0 (first year at sea), age .1 (second year at sea), and age .2 or older (three or more years at sea). Steelhead were presumed to form an annulus on their scales in February or March, thereby becoming members of the next older age group by the time they were sampled in spring. Insufficient numbers of ocean ages .3, .4, and .5 fish were present in the samples to warrant separate groupings, and the seasonal distribution pattern for these older fish was much the same as for age .2 fish. In the spawning history analysis, all ocean age groups were pooled, and immature fish that had not yet spawned (maidens) were separated from those fish with spawning checks on their scales (kelts) to compare the distributions of pre- and post-spawning fish.

Sampled steelhead with useable scales constituted the foundation of the age and spawning history distributional analysis, and were the "catch" in these CPUE calculations. These fish were often a subset of the total catch because some fish (ca. 8 %) had damaged scales or unreadable ocean ages. We assumed that the proportion of fish with damaged or unreadable scales did not differ enough in occurrence across all ocean ages and spawning history groups to affect the inferences drawn on seasonal distribution and abundance.

Age and spawning information for scales used in the analyses of distribution by ocean age or spawning history were determined by biologists from the Fisheries Research Institute (FRI), University of Washington. This included U.S. and Canadian samples from 1955-1985 and Japanese samples from 1981-1985 (Davis and Light 1985).

(1) Calculation of CPUE Indices

The lack of uniformity in fishing times and locations for each gear type over the more than 30 years of sampling necessitated pooling of both catch and effort data over all years. In all three analyses (all fish, ocean age, and spawning history), catch and effort data were stratified by INPFC 2°-latitude by 5°-longitude (2°X5°) statistical areas and by season. Seasons were chosen as the best means of showing broad shifts in abundance throughout the year. The months used to define each season (spring = March-May, summer = June-August, autumn = September-November, winter = December-February) correspond to meaningful periods of steelhead life history.

To account for differences in the efficiency and selectivity of each of the three gear types (Sutherland 1973), CPUE values were not expressed as numbers per set (operation). Instead, dimensionless CPUE rankings were calculated for each gear type and then averaged for all gear types fished in each season-area combination to produce a single weighted average CPUE value for each time-area combination. To do this, after appropriate stratification according to the aim of each analysis, the total catch of steelhead by each gear type was divided by the total effort of that gear type in each time-area combination. The resultant CPUE values for each gear type for all areas and time periods were then ranked, and non-zero values were divided into quartiles. CPUEs in the first quartile (lowest CPUE values) were given an index of "1", CPUEs in the second quartile were given an index of "2", and so on up to the fourth quartile "4" (highest CPUE values).

This "within-gear type" ranking is not without its bias for research vessel gillnet data. Sampling by U.S. and Canadian vessels was conducted primarily in earlier years when multifilament nets were used. Multifilament nets were determined to be less efficient for salmon than the monofilament nets used by Japan in more recent years (see discussion in Takagi *et al.* 1981). Further, in order to provide more data on steelhead distribution, the steelhead catch data for Japanese research vessels used in this analysis include catches in "commercial" gear (111-121 mm mesh) in addition to the multi-mesh "non-selective" gear (Ishida *et al.* 1966). Since gear set nightly in a Japanese research vessel operation consisted primarily of "commercial " gear, commonly 102 of 132 tans, overall CPUE, size, and age composition of the steelhead catch was influenced by inclusion of total catch of both gear types. These biases must be kept in mind.

To calculate average CPUE values in time-area combinations where more than one gear caught steelhead, the CPUE indices for each gear type were averaged, weighting by the number of sets of each gear type. For example, if in INPFC area E7048 in spring, both gillnets and longlines caught ocean age .1 steelhead, and the relative CPUE indices in this time-area stratum were calculated to be "1" for gillnets and "3" for longlines, and if 25 gillnet sets and 5 longline sets had been made in that area in spring, then the average CPUE index for age .1 fish in this time-area combination would be "1", calculated as follows:

$$\frac{(\text{CPUE index for gear 1 X no. of sets, gear 1}) + (\text{CPUE index for gear 2 X no. of sets, gear 2})}{\text{no. of sets gear 1 + no. of sets gear 2}}$$

$$= \frac{1(25)\text{ gillnets} + 3(5)\text{ longlines}}{25 + 5}$$

$$= \frac{40}{30}$$

$$= 1.33 \text{ (rounded to 1)}$$

If any gear type was fished in a particular time-area combination but no steelhead were caught, then the number of sets of that gear type would be included in the above equation with a corresponding zero CPUE index. For each of the three analyses, the relative sizes of the final average CPUE quartiles provide a measure of the relative abundance of steelhead in each area across all seasons and sampling years. The literature was reviewed for further information on distribution and migration with respect to life history, area of origin, and temperature.

(2) Distribution of Sampling Effort

The distribution of fishing effort by purse seines, gillnets, and longlines over all years (United States and Canada 1955-1990, Japan 1981-1989, U.S.S.R. 1983-1990) is shown in Figs. 3-5. Distribution of effort (gillnets and longlines) for the analyses using age data, in which data are restricted to years prior to 1986, is shown in Appendix Figs. 1 and 2. From these summaries it is apparent that sampling was not uniform with regard to area or gear type. FAJ sampled mostly in the western and central North Pacific with gillnets and longlines, whereas Canadian and U.S. research vessels operated more frequently in the eastern North Pacific and Bering Sea (Bristol Bay area) using purse seines, longlines, and some gillnets. The U.S.S.R. purse seine sampling was conducted primarily in the Bering Sea and south of the Aleutians. The composite effort distribution for all gear types is presented by season in Appendix Figs. 3-6 and 7-9 for the overall analyses and the analyses using age data, respectively. Winter sampling effort shown in Appendix Fig. 6 was the same as in the analysis using age data. Summer sampling was heaviest (principally in June and July), with lesser effort in spring and autumn, and only scattered or infrequent sampling during winter months. No purse seines were fished during winter. The area south of 48°N between 160°W and 175°W was not well sampled during high-seas surveys, and because CPUE data for steelhead are generally very low and thus sensitive to differences in effort and abundance (Light 1989a), the CPUE index values for the 2°X5° areas in this region are probably less accurate than areas where more thorough sampling occurred. Ranges of actual CPUE values within each quartile for each gear type are given in Appendix Tables 1A-C for each of the three analyses: total catch, distribution by ocean age group, and distribution by maturity stage.

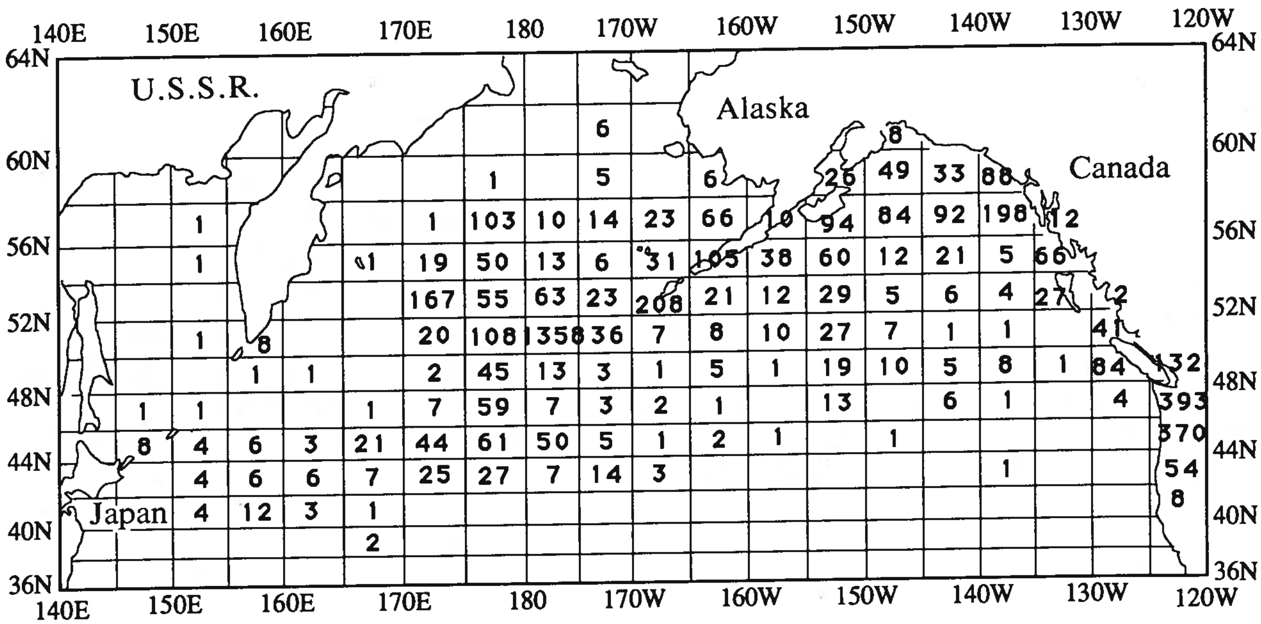


Figure 3. Distribution of purse seine effort (number of sets) by U.S. and Canadian (1955-1985), U.S.S.R. (1983-1990) and Japanese (1989) research vessels operating in the North Pacific Ocean and Bering Sea.

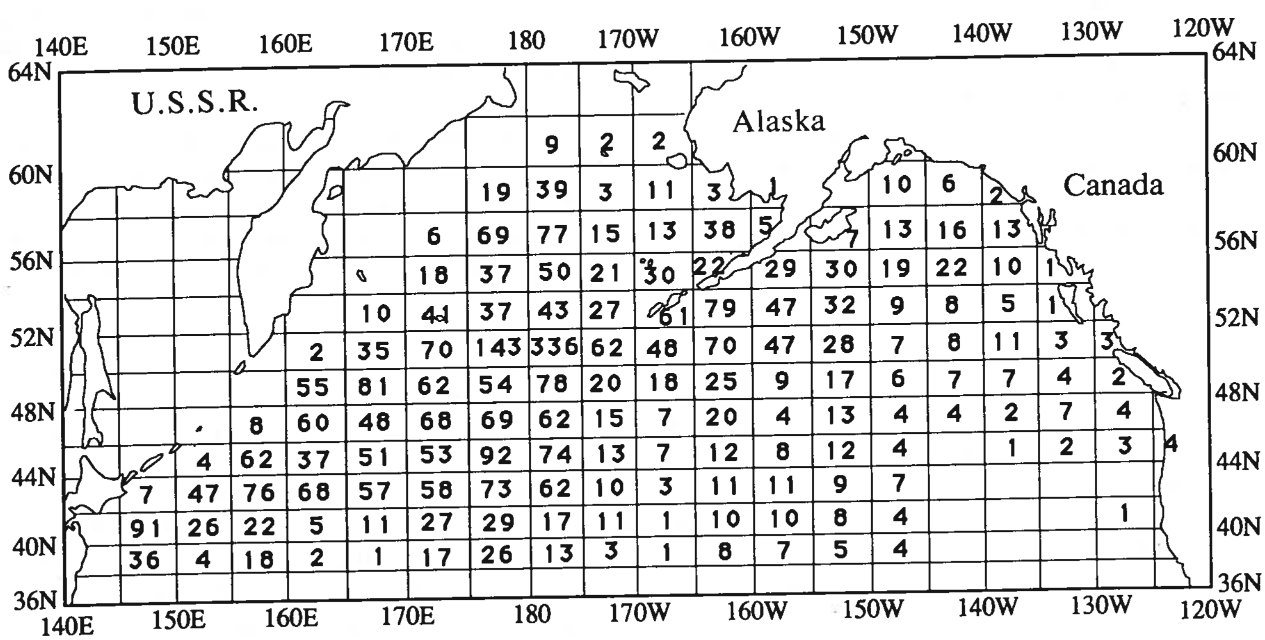


Figure 4. Distribution of gillnet effort (number of sets) by U.S. and Canadian (1955-1990) and Japanese (1981-1989) research vessels operating in the North Pacific Ocean and Bering Sea.

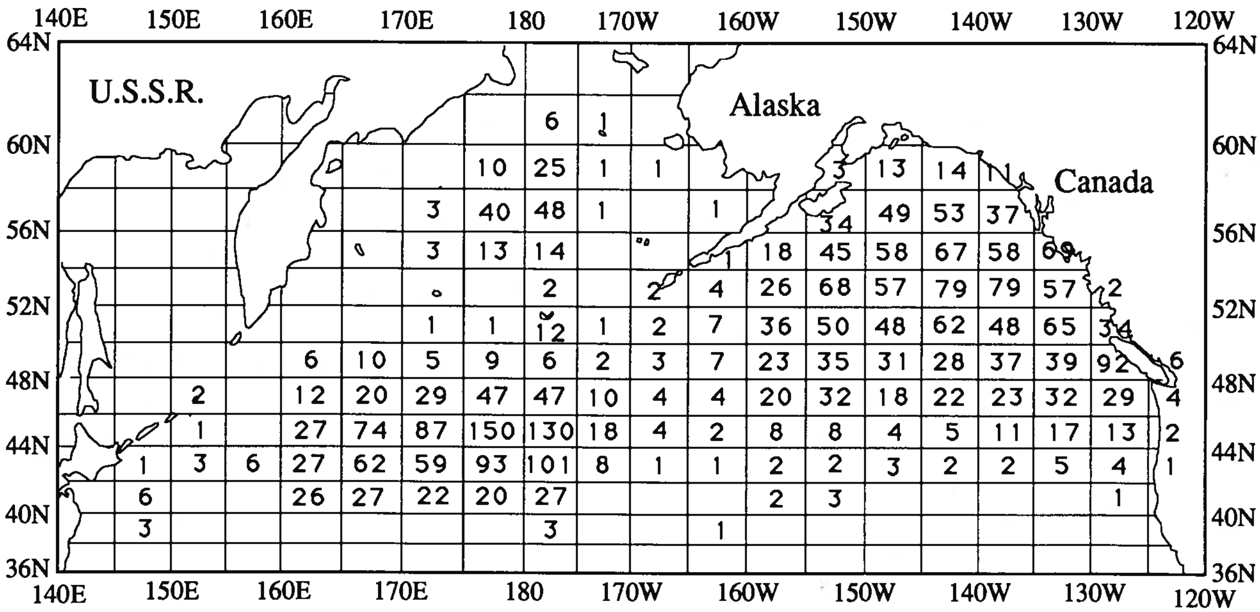


Figure 5. Distribution of longline effort (number of sets) by U.S. and Canadian (1955-1990) and Japanese (1981-1989) research vessels operating in the North Pacific Ocean and Bering Sea.

(3) Estimated and Reported Catch by Japanese High-Seas Salmon Fisheries

Steelhead catch data from Japan's salmon driftnet fisheries operating in the North Pacific and Bering Sea were used in this report. The mothership driftnet fishery, using fleets of catcher boats to deliver salmon catches to their respective assigned motherships, operated in June and July only in areas northwest of 46°N, 175°E in the North Pacific and Bering Sea except in the Bering Sea north of 56°N. The landbased driftnet fishery vessels operated in May, June, and July in areas southwest of 46°N, 175°E in the North Pacific Ocean. A detailed description of these fisheries was given by Harris (1989).

Research vessel catch and effort data were provided on computer tape by the FAJ. Mothership and landbased effort data were also provided on computer tape by FAJ. Catch data for the landbased fishery were obtained from FAJ publications (1982-1988a, 1989a, 1990). Mothership catch data for steelhead were obtained from unpublished reports by United States salmon fishery observers aboard motherships in 1984-1986.

Reported catches of steelhead by the landbased driftnet fishery were available for 1981 through 1989. Catches in 1981 were derived by expanding the reported catches of 139 of the 207 licensed vessels. Both weighted and unweighted average CPUE values were calculated from research vessel data for 1981-1985 (stratified by 2°-latitude X 5°-longitude areas, by month, and by 10-day period), and estimated catches were derived by multiplying these values by the reported commercial landbased effort in the same time-area strata. Prior to 1986, the length of a tan of gillnet was not uniform and varied between 30 and 45 m. Standardized (1 tan = 45 m) effort data for 1984 and 1985 were used in this analysis, but this was not possible for the 1981-1983 data.

For motherships, unweighted average CPUE values (i.e., an average of the mean CPUE values in each year) from research vessels operating in the mothership area over a 5-year period (1981-1985), stratified by 1 degree latitude X 5 degree longitude areas, by month (June, July), and by 10-day period (days 1-10, 11-20, and 21-31 of each month) were used. Catch estimates were then derived by combining these CPUE values with total commercial effort (stratified in the same way) for the three years (1984-1986) that steelhead were returned to the motherships for sampling. Direct estimates of catch by the mothership fishery in 1984 and 1986 were possible because research vessels operated in the same time-area strata in which landings by motherships were reported.

3. Description of Tagging Programs

The two groups of marked or tagged steelhead discussed in this report are differentiated on the basis of where they were marked or tagged, i.e., offshore or inshore.

(1) Offshore Tagging

(a) Release

In contrast to inshore marking and tagging programs, where a large number of juvenile fish are released from a broad area along the coast, offshore tagging experiments capture and release relatively few fish from a limited number of widely-scattered research vessels operating in a vast area. The effectiveness of these tagging experiments for determining continent of origin can be reduced if tagged fish are intercepted by a high-seas fishery before reaching their spawning streams, or if these fish return to remote spawning areas where recovery is unlikely (Davis *et al.* 1990). Despite these drawbacks, data collected from the inshore recoveries of steelhead tagged on the high seas has provided invaluable information on the offshore distribution of North American steelhead.

In offshore tagging experiments, fish are captured alive during research vessel operations with purse seines or surface longlines, tagged (primarily with Peterson disk tags), and released (Davis *et al.* 1990). United States research vessels from the University of Washington's Fisheries Research Institute (FRI) fished with purse seines between 1956 and 1982 (excluding 1979 and 1981, when no tagging experiments were conducted). Between 1983 and 1988, FRI scientists participated in cooperative U.S.-U.S.S.R. tagging studies sponsored by the Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO) (Walker *et al.* 1988). These cooperative studies were conducted on board Soviet research vessels using purse seines. The combined U.S. and U.S.-U.S.S.R. purse seine effort during tagging experiments between 1956 and 1988 totalled 4,225 sets.

Surface longlines were used by Canada (Department of Fisheries and Oceans [DFO], formerly Fisheries Research Board of Canada) in tagging experiments from 1961 until 1967 (Sutherland 1973), and again in 1987-1988 when their tagging program was resumed (LeBrasseur *et al.* 1987, 1988). Japan (FAJ) has used longlines exclusively to capture salmonids for tagging since 1962, but reliable records of the numbers of steelhead captured, tagged, and released are not available for years prior to 1976. FRI also made limited use of longlines from 1963 through 1970, and in 1980 and 1982 (INPFC 1970, 1971, 1972; Sutherland 1973; Harris *et al.* 1980; Harris 1982). In 1953, 1964, and 1965, NMFS fished with longlines but a small number of sets were made and only a few steelhead were caught (Sutherland 1973). For the years between 1961 and 1988, for which complete data on the number of steelhead tagged and released are available, the combined longline tagging effort of all three nations totalled 3,344 sets. (Japanese longline effort data for the years 1962-1975 were available but were not included because the numbers of steelhead caught during longline operations in these years were not consistently recorded.)

A thorough description of fishing gear and methods was given by Hartt (1962, 1963) and Kondo *et al.* (1965), and was summarized by Sutherland (1973). Tagging procedures were described by Davis *et al.* (1990). Most tagging experiments were conducted in spring and summer. Between 1956 and 1988, the combined purse seine and longline tagging efforts of all three nations resulted in a minimum of 1,722 steelhead being tagged and released at sea (Fig. 6).

(b) Recovery

Fish tagged offshore are recovered inshore by commercial and sport fisheries when the fish return to spawn. In North America, the inshore recovery program is coordinated by FRI in conjunction with federal, state, and provincial fisheries agencies. The steelhead recovery program relies heavily upon the cooperation of sport fishermen because, with the exception of a limited number of tribal or commercial fisheries, steelhead is not a commercial species. In Japan, the high-seas tag recovery program is administered by FAJ and in the U.S.S.R. by TINRO.

(2) Inshore Marking and Tagging

(a) Release

Steelhead smolts are marked or tagged inshore prior to their seaward migration. Most of these fish

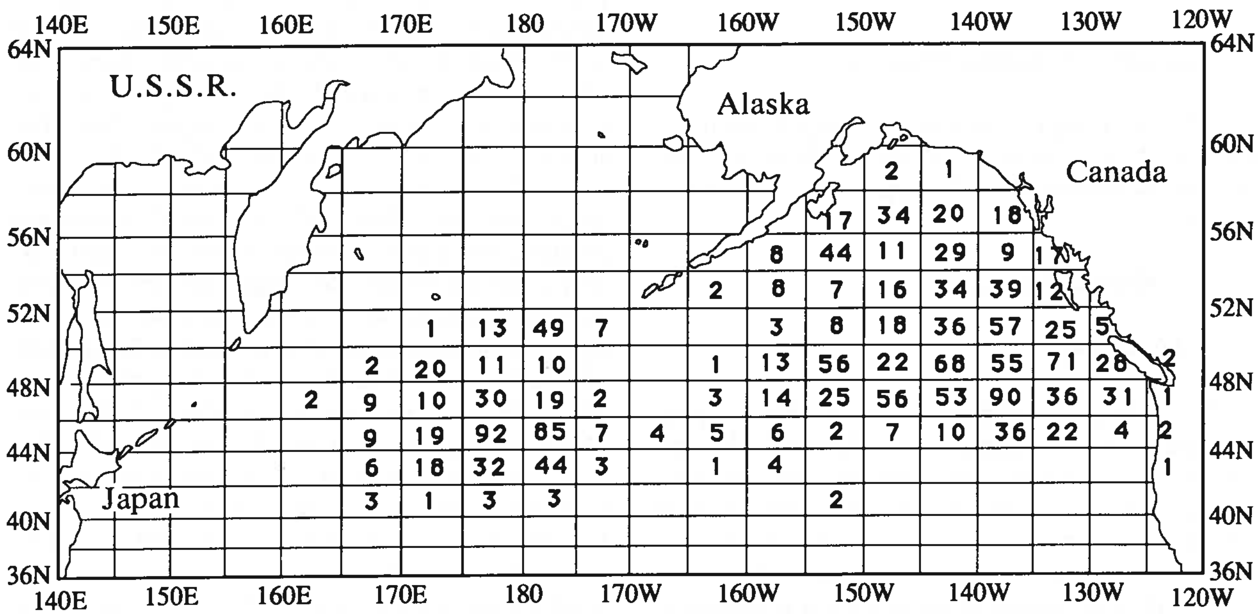


Figure 6. Number and distribution of steelhead tagged and released during INPFC high-seas tagging experiments, 1956-1988. N=1722. Japanese data for 1962-1975 were not included because steelhead catches in these years were not consistently recorded.

are reared in hatcheries, and so offshore recoveries primarily reflect the ocean distribution of hatchery fish, which may be somewhat different than that of naturally-produced (wild) fish. Fish are typically marked by removal of fins (singly or in combination) or maxillary bones (Johnson 1987). Occasionally, external dyes, freeze brands, or spaghetti tags are used for marking (Johnson and Longwill 1988), but no marks of this type have been reported for steelhead recovered offshore. Coded-wire tags (CWT), which are small metal wires inserted into the snouts of juvenile fish prior to their seaward migration, are the internal tags most frequently used by fisheries agencies (Johnson and Longwill 1988). These tags are typically used in combination with some form of external mark, usually a clipped adipose or left ventral fin, to identify the presence of the tag within the fish. Fin-clipped steelhead, especially those with adipose fin clips, carry a strong implication of North American origins because natural fin loss rates are suspected to be low (Foerster 1935; Ricker 1972) and there is no deliberate fin-clipping program in Asia.

Substantial numbers of marked or tagged steelhead from North American hatcheries have been released, in addition to much smaller numbers of wild steelhead, since inshore tagging programs began. The duration of ocean residence for most steelhead is 1 to 3 years (Sutherland 1973), and for this reason fish released by inshore tagging programs between 1978 and 1989 were the most likely to have been at sea since offshore recovery efforts began in 1981. In the 12-year period from 1978 through 1989, nearly 139 million marked or tagged steelhead smolts were released (Table 1; Johnson and Longwill 1988; Pacific States Marine Fisheries Commission [PSMFC] unpublished data). The majority of these fish (89.0%) were missing their adipose fin, and 22,285,000 (18.0%) carried CWTs. Although none of these inshore tagging experiments were designed to investigate the offshore distribution of steelhead, the recovery of fish from these studies has greatly supplemented the information obtained from high-seas tagging studies, especially the information obtained from steelhead carrying CWTs.

Table 1. Annual releases (x1,000) of marked or tagged steelhead smolts along the Pacific coast of North America, 1978-1989, and the proportions of these fish that had clipped fins[1] and that carried a coded-wire tag[2].

Year of Release	Total Number Marked or Tagged[3]	Number of Adipose-Clipped Smolts Released (% of marked fish)	No. of Adipose-Clipped Smolts with a Coded-Wire Tag (% of adipose-clipped fish)
1978	2,990	2,041 (68.3)	1,704 (83.5)
1979	4,619	2,783 (60.2)	1,866 (67.0)
1980	3,613	2,521 (69.8)	1,729 (68.6)
1981	3,834	2,303 (60.1)	1,647 (71.5)
1982	4,397	3,379 (76.9)	2,031 (60.1)
1983	5,616	4,345 (77.4)	1,937 (44.6)
1984	12,995	10,615 (81.7)	1,683 (15.9)
1985	18,738	17,501 (93.4)	2,161 (12.4)
1986	19,007	18,234 (95.9)	1,866 (10.2)
1987	19,295	18,126 (93.9)	2,044 (11.3)
1988	20,761	19,558 (94.2)	2,122 (10.9)
1989	23,088	22,210 (96.2)	1,494 (6.7)
Total	138,953	123,616 (89.0)	22,285 (18.0)

1 Some of the fin-clipped fish also had clipped maxillary bones.

2 All data on marked and tagged fish were provided by J. Kenneth Johnson, Pacific Marine Fisheries Commission, Portland, Oregon. Releases include marked or tagged wild fish which varied between 0.8 and 20.2% of total annual releases of CWT steelhead. Since 1983, CWT Columbia Basin steelhead must bear a left ventral fin clip but do not require a clipped adipose fin.

3 The actual number of fish marked and released in a given year may be somewhat less than shown because agencies conducting marking experiments often release fewer fish than projected and do not report final totals. This qualification does not apply to releases of coded-wire tagged fish.

(b) Recovery

Fish marked or tagged inshore by fin clipping and coded-wire tagging are recovered offshore during fishing operations of research and commercial vessels. Since 1981, scientists aboard salmon research vessels from the United States, Japan, and Canada, as well as U.S. observers aboard foreign fishing vessels, have routinely searched for adipose fin-clipped fish among salmonid catches as part of an intensive CWT recovery effort. The program is coordinated by the National Marine Fisheries Service (NMFS) in Auke Bay, Alaska, in conjunction with PSMFC, an agency that coordinates salmonid tagging and marking programs along the North American Pacific coast. Additionally, Margolis *et al.* (1989) reported recoveries of coded-wire tagged steelhead incidentally caught in an experimental squid driftnet fishery conducted in the vicinity of the outer limits of the Canadian and U.S.A. 200-mi. (320 km) zones off British Columbia, Washington, and Oregon. Recovery efforts have focused on adipose-clipped fish because in the past this particular fin clip was commonly used to identify steelhead carrying CWTs and because it is the most frequently used fin clip for identifying hatchery fish (Johnson and Longwill 1988).

When an adipose-clipped steelhead was found in the catch of a research or commercial vessel, basic biological data and the capture location were recorded, and the snout was removed and stored (salted or frozen or both) for later inspection to detect the presence of a CWT. The snouts of fish potentially carrying a CWT are usually sent to the NMFS laboratory in Auke Bay for processing, although in recent years Canada has processed its own marked-fish recoveries (Margolis 1985a; LeBrasseur *et al.* 1987; Margolis *et al.* 1989).

(3) Tagging Data Sources

In this report, the tag recovery information through 1989 for both inshore and offshore tagging programs was derived principally from published and unpublished data records of the tag-coordinating agencies mentioned previously. The NMFS data base was the principal source of information on offshore recoveries of adipose-clipped steelhead. Most adipose-clipped fish that also carried a CWT were previously reported in INPFC documents (Dahlberg 1981, 1982; Wertheimer and Dahlberg 1983, 1984; Dahlberg and Fowler 1985; Margolis 1985a; Dahlberg *et al.* 1986, 1987, 1988, 1989; Margolis *et al.* 1989). The data base includes fin-clipped and coded-wire-tagged steelhead recovered during Canadian experimental squid fishing operations in 1985-1987 off the North American coast (Margolis *et al.* 1989). Steelhead caught during 1987-1989 fishing operations of Japan's landbased salmon fishery and recovered during the Japanese port sampling program were not included because precise recovery locations were not available (Unpublished data presented at the 1988 and 1989 annual meetings of INPFC Sub-Committee on Salmon; Fisheries Agency of Japan 1988b, 1989b). Two steelhead carrying CWTs recovered by commercial fisheries off southeastern Alaska were also not included because of a lack of specific recovery data (Karen Crandall, Alaska Department of Fish and Game, personal communication). Information on recoveries of steelhead with clipped fins, other than adipose, or clipped maxillary bones were obtained from Margolis (1985a) and Margolis *et al.* (1989). Information on the numbers of fish tagged and released offshore and the subsequent recoveries of these fish were obtained from FRI and FAJ data. Some high-seas tagging information has been previously reported (Sutherland 1973; French *et al.* 1975). Only inshore and offshore releases through 1988 and recoveries through 1989 are reported in the present publication.

4. Description of Parasite Studies

The concept of using parasites acquired by salmonids in fresh water as naturally occurring "biological tags" to determine the ocean distribution of specific stocks or stock groups of anadromous Pacific salmonids was introduced by Margolis (1963) some 35 years ago. More recently, Margolis (1984, 1985b, 1990) described the application of this technique of stock identification to steelhead trout. He used two freshwater trematodes, adult *Plagioporus shawi* in the intestine and *Nanophyetus salmincola* metacercariae in the kidney, to define the ocean distribution of steelhead from the U.S. Pacific Northwest (Washington, Oregon, northern California, and Idaho). These two trematodes occur in juvenile steelhead trout from this region only and survive in the fish host for all or part of its marine life. The freshwater area of origin of steelhead trout harbouring *P. shawi* and *N. salmincola* is determined by the distribution of the obligatory first intermediate snail hosts. Only in the U.S. Pacific Northwest do steelhead and the obligatory snail hosts co-occur in the same river systems (Margolis 1984, 1990).

Dalton (1989a, 1989b) extended Margolis' (1984, 1985b) studies to cover additional years of high-seas sampling. He concentrated on using *N. salmincola* as a stock-identifying marker and also examined (Dalton 1989a) the possibility of using prevalence data for this parasite to estimate the proportion of U.S. Pacific Northwest steelhead among high-seas samples. Most recently, Myers *et al.* (1991) examined the kidneys of steelhead caught west of 165°E and demonstrated the presence of U.S. Pacific Northwest origin fish in these far western waters. Margolis and McDonald (Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. unpublished data) applied the parasite stock identification methodology to 714 steelhead caught in the northeastern Pacific Ocean off British Columbia, Washington, and Oregon.

5. Information on Artificial Production

Information on the number of smolts released by North American hatcheries between 1960 and 1976 was obtained from Wahle and Smith (1979). All other information was obtained from records of state or provincial fish management agencies (Alaska Dept. of Fish and Game [ADFG] 1978-1988, British Columbia Ministry of Environment [BCMOE] unpublished data, California Dept. of Fish and Game [CDFG] 1978-1988, Idaho Dept. of Fish and Game [IDFG] unpublished data, Oregon Dept. of Fish and Wildlife [ODFW] 1978-1988, Washington Dept. of Wildlife [WDW] 1978-1988), or from individual hatchery records (federal and state, unpublished).

IV. OCEAN LIFE HISTORY

1. Age and Growth at Sea

(1) Age Composition

Scales from 10,668 immature and maturing steelhead collected offshore by research vessels during 1955-1985 were examined for life history information. Total ages were determined for only 3,475 (32.6%), principally because of regeneration of the freshwater portions of the scales (ocean ages were determined for 92.4% of the total sample). In the subsample of scales with complete freshwater and ocean ages, there were 24 age groups (Table 2). Of these, ages 3.1, 2.1, 3.2, and 1.1 collectively constituted 65.7% of the sample and were the only age groups that individually contributed more than 10% of the sample. The total age of most fish was less than 6 years; approximately 6% of the fish were 6 years or older. The oldest fish had lived ten years (age 5.5), and the youngest was caught before completing its second year of growth (age 1.0).

This same general age structure was found for pelagic steelhead in studies by Sutherland (1973) and Okazaki (1984a). The majority of fish in all three studies belonged to age groups 3.1, 2.1, and 3.2 however, the range of total ages in our study (1-10) was broader than in Sutherland's (2-8) or Okazaki's (1-6) studies. The number of distinct combinations of total freshwater and ocean ages (24) was also greater than in previous reports (Sutherland, 19; Okazaki, 15). A notable difference between this and the other two studies was in the number of age 1.1 fish. In our sample there were 10.8% age 1.1 fish, versus 0.6% in Sutherland's, and 2.0% in Okazaki's samples.

The freshwater age composition of offshore samples was dominated by age 3. fish (42.3%). Similar findings were reported by Sutherland (1973) and Okazaki (1984a). However, the proportion of freshwater age 1. fish in our sample was large relative to the other two studies. Sutherland (1973) found only 3 (0.9%) age 1. fish in his sample of 323 steelhead. Okazaki (1984a) found 90 (3.6%) age 1. fish in his larger data set of 2,336 fish. In our analysis, 17.0% of the readable scales showed a single freshwater annulus. These differences may be explained partially by trends in production of hatchery fish over the 30-year period when high-seas samples were collected. Most hatchery smolts are released as yearlings, whereas wild fish are almost entirely age 2. or older. In the 1950s and 1960s hatchery programs were not as successful and widespread as they are today, and the relative abundance of hatchery fish offshore was undoubtedly much lower. Some scale samples used in our analysis were collected in these early years, and trends in proportion of age 1. fish in our samples over time reflect this (Fig. 7). This would also be true for Sutherland's study because his samples were collected in the 1950s and 1960s.

Table 2. Age composition of high-seas steelhead. Data from Japanese, Canadian, U.S., and U.S.S.R. research vessel samples, 1955-1985. Repeat spawning fish included.

Age Group[1]	No. of Fish	Percent
1.0	7	0.2
2.0	47	1.3
3.0	63	1.8
4.0	6	0.2
1.1	377	10.8
2.1	560	16.1
3.1	926	26.6
4.1	324	9.3
5.1	23	0.7
6.1	1	<0.1
1.2	201	5.8
2.2	306	8.8
3.2	424	12.2
4.2	93	2.7
5.2	6	0.2
1.3	7	0.2
2.3	25	0.7
3.3	47	1.3
4.3	10	0.3
2.4	7	0.2
3.4	11	0.3
4.4	2	<0.1
2.5	1	<0.1
5.5	1	<0.1
	3,475	100.0

Freshwater Age	No. of Fish	Percent
1	592	17.0
2	946	27.2
3	1,471	42.3
4	435	12.5
5	30	0.9
6	1	<0.1
	3,475	100.0

Ocean Age	No. of Fish	Percent
0	251	2.5
1	6,108	61.9
2	3,095	31.4
3	330	3.4
4	65	0.7
5	12	0.1
6	2	<0.1
	9,863	100.0

Total Age	No. of Fish	Percent
1	7	0.2
2	424	12.2
3	824	23.7
4	1,245	35.8
5	773	22.2
6	170	4.9
7	29	0.8
8	2	0.1
10	1	<0.1
	3,475	100.0

[1]Freshwater age precedes dot, ocean age follows dot.

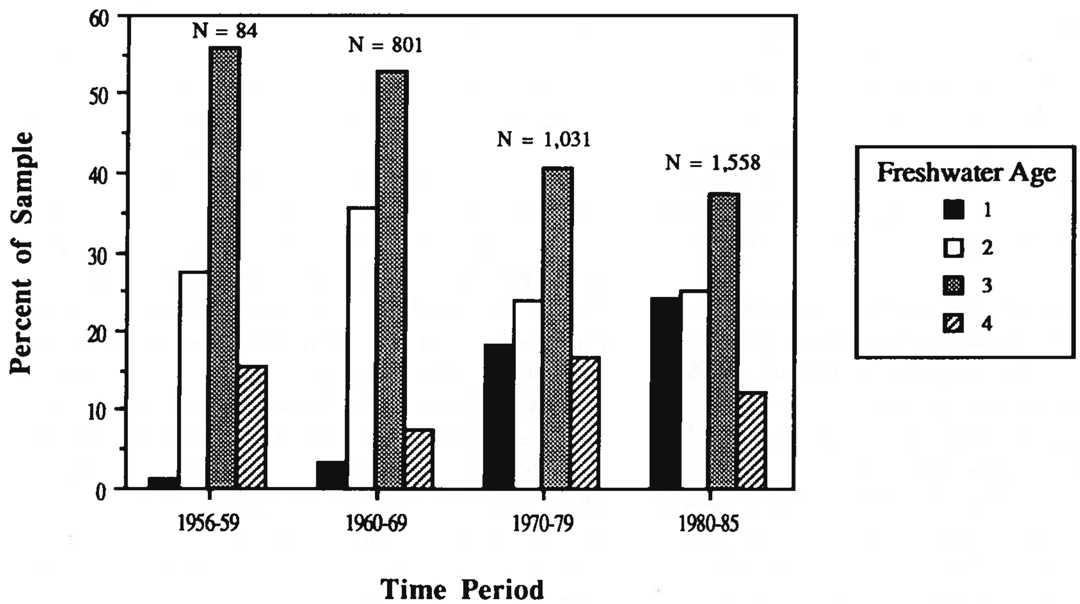


Figure 7. Trends in freshwater age composition of high-seas steelhead samples, 1956-1985.

Okazaki's samples were collected between 1972-1982, when hatchery fish were more abundant. However, there may have been differences in age interpretations because many age 1. fish can be quite easily misinterpreted as age 2. fish (Davis and Light 1985).

The observed occurrence of age 1. fish in our samples was low relative to the percentage of hatchery fish thought to contribute to the total North American adult steelhead population. Of the average number of adults returning to the North American coast each year, about half are estimated to be of hatchery origin (see section, *Abundance of North American Steelhead*). Clearly this estimate is not reflected in the proportions of freshwater age 1. fish in our offshore samples, even among recent samples (Fig. 7). However, because only a fraction of the total scales sampled offered freshwater age information, it is difficult to say with certainty what the actual freshwater age composition of the offshore steelhead population is, especially if there are differences in scale regeneration frequencies between hatchery and wild fish.

Most steelhead caught offshore were in their second (age .1, 61.9%) or third (age .2, 31.4%) summer at sea (Table 2). Relatively few age .0 fish were present (2.5%), suggesting that gear selectivity and/or distribution of sampling effort resulted in low catches of this age group (Sutherland 1973). Because sampling was widespread, the most likely explanation is sampling gear bias. The high-seas steelhead population is composed predominantly of maiden fish. Of the 9,863 fish with readable ocean life history records on their scales, only 709 (7.2%) had spawned previously. Within the subsample of 3,475 fish with complete freshwater and ocean ages, 3,280 (94%) were maidens, representing twenty age groups (Table 3), and 195 were kelts, representing 17 age groups (Table 4). Thirteen age groups were common to both maidens and kelts, but some age groups were exclusive to each group. By freshwater age, more age 1. fish (possibly hatchery fish) were found among maidens than kelts, but ages 2. and 3. predominated for both groups. By ocean age, 68.9% of maidens with readable ocean age were in their first (age .0) or second (age .1) summer growth seasons, and only 1.6% were age .3 or older. In contrast, among kelts only 6.6% were age .1, and 38.4% were age .3 or older. The over-all age composition of maiden fish resembles that of the combined sample (maidens and repeat-spawners combined) because of the low abundance of kelts.

Table 3. Age composition of maiden steelhead from high-seas catches. Data from Japanese, Canadian, U.S., and U.S.S.R. research vessel samples, 1955-1985. See text for details of age designation terminology. Asterisks denote age groups not found among repeat-spawning fish in the sample.

Age Group[1]	No. of Fish	Percent
1.0*	7	0.2
2.0*	47	1.4
3.0*	63	1.9
4.0*	6	0.2
1.1	375	11.4
2.1	554	16.9
3.1	918	28.0
4.1	322	9.8
5.1*	23	0.7
6.1*	1	<0.1
1.2	194	5.9
2.2	266	8.1
3.2	371	11.3
4.2	83	2.5
5.2*	6	0.2
1.3	4	0.1
2.3	10	0.3
3.3	24	0.7
4.3	4	0.1
3.4	2	0.1
	3,280	100.0

Freshwater Age	No. of Fish	Percent
1	580	17.7
2	877	26.7
3	1,378	42.0
4	415	12.7
5	29	0.9
6	1	<0.1
	3,280	100.0

Ocean Age	No. of Fish	Percent
0	251	2.7
1	6,061	66.2
2	2,705	29.6
3	125	1.4
4	11	0.1
5	1	<0.1
	9,154	100.0

Total Age	No. of Fish	Percent
1	7	0.2
2	424	12.2
3	824	23.7
4	1,245	35.8
5	773	22.2
6	170	4.9
7	29	0.8
8	2	0.1
10	1	<0.1
	3,280	100.0

[1]Freshwater age precedes dot, ocean age follows dot.

The frequency of repeat spawning was recorded in a subsample of 251 kelts in the total sample of 709 kelts. Seventy-one percent had spawned once, 21% twice, 8% three times, and one fish, four times. Eleven percent spawned initially after their first summer of ocean growth, 69% after two summers, 19% after three summers, and one fish spent four summers at sea before spawning.

Okazaki (1984a) concluded from limited data on Kamchatkan stocks (Maksimov 1972, 1976; Savvaitova and Maksimov 1969) that Asian steelhead tend to remain longer both in fresh water and at sea than North American forms. He suggested that, like sockeye salmon (*Oncorhynchus nerka*), as reported by Mosher (1963), this age composition difference might be useful in separating Asian from North American steelhead. However, additional age composition data for adult Asian steelhead (Savvaitova *et al.* 1973) indicate considerable overlap in age composition with North American populations, particularly with Alaskan and British Columbia stocks. Because of this variability, age composition does not now appear to be a useful means of separating North American from Asian steelhead in high-seas samples.

(2) Growth

The growth of steelhead during their marine residence was examined using length and weight data for steelhead caught by research vessels during 1955-85. Okazaki (1984a) suggested a tendency for average fork lengths of males to be greater than those of females in offshore waters. Other researchers observed similar tendencies among adults sampled in streams (Shapovalov and Taft 1954; Narver and

Table 4. Age composition of steelhead kelts in high-seas catches. Data from Japanese, Canadian, U.S., and U.S.S.R. research vessel samples, 1955-1985. See text for details of age designation terminology. Asterisks denote age groups not found among maiden fish in the sample.

Age Group[1]	No. of Fish	Percent
1.1	2	1.0
2.1	6	3.1
3.1	8	4.1
4.1	2	1.0
1.2	7	3.6
2.2	40	20.6
3.2	53	27.2
4.2	10	5.1
1.3	3	1.5
2.3	15	7.7
3.3	23	11.8
4.3	6	3.1
2.4*	7	3.6
3.4	9	4.6
4.4*	2	1.0
2.5*	1	0.5
5.5*	1	0.5
	195	100.0

Freshwater Age	No. of Fish	Percent
1	12	6.1
2	69	35.4
3	93	47.7
4	20	10.3
5	1	0.5
	195	100.0

Ocean Age	No. of Fish	Percent
0	—	—
1	47	6.6
2	390	55.0
3	205	28.9
4	54	7.6
5	11	1.6
6	2	0.3
	709	100.0

Total Age	No. of Fish	Percent
1	—	—
2	2	1.0
3	13	6.7
4	51	26.2
5	70	35.9
6	40	20.5
7	16	8.2
8	2	1.0
10	1	0.5
	195	100.0

[1]Freshwater age precedes dot, ocean age follows dot.

Withler 1971; Leggett and Narver 1976; Hooton *et al.* 1987). Sutherland (1973) suggested that the opposite tendency occurred in weights of steelhead sampled offshore; females were heavier than males in all age categories. Sutherland also suggested sampling gear bias might lead to non-representative samples of steelhead size ranges.

To resolve these issues, preliminary analyses were used to assess whether mean lengths and weights of male and female steelhead were different, and whether different gear types influenced mean lengths and weights. In a gross analysis by ocean age group, age .1 males (570 mm) were found to be significantly longer than age .1 females (565 mm) (t-test, $P=.0005$). However, the sample was large ($N = 7{,}135$) and the absolute size difference was small (5 mm), leading us to conclude that the difference was not particularly significant biologically. The effect of sex on mean steelhead weights was similar to that for lengths, except that males were significantly heavier than females for both age .1 ($\Delta=46$ g, $P=.006$) and age .3 fish ($\Delta=435$ g, $P=.013$). Again, the weight difference for age .1 fish was small and the sample size was large ($N = 7{,}131$). In the case of age .3 fish, the weight differences may have been biologically significant, but because the sample was relatively small ($N = 200$) for this age group, these weight differences were ignored, and male and female data were pooled.

Analysis of variance procedures were used to test for differences in mean lengths and weights among gears. By age group, purse seine-caught fish were significantly shorter than gillnet-caught steelhead of all age groups, and significantly shorter than longline-caught fish for ages .0, .1, and .3 fish. Gillnet-caught steelhead were also longer than longline-caught fish for age groups .1 and .2. Purse seine-caught steelhead also generally weighed less than fish caught with gillnets or longlines. No significant weight differences were found between gillnet- and longline-caught fish.

Despite the statistical length and weight differences among gear types, a full range of lengths and weights was desired for the growth analysis, and because length- and weight-frequency histograms showed incomplete overlap in size-class contributions for each gear type, all three gear types were pooled prior to further analyses. Readers should realize, however, that smaller fish (typically age .0) are not well represented in the high-seas samples. The following analysis of steelhead ocean growth makes use of all available length and weight data, ignoring sex and gear type.

Fork length data were available for 9,824 fish, and body weight data were available for 6,944 fish. The mean, standard deviation, and other descriptive statistics for lengths and weights of these fish are presentedby ocean age in Table 5. Monthly size data for ocean-caught steelhead are presented in Figs. 8 (for length) and 9 (for weight). The curves suggest rapid growth of steelhead during their pelagic existence, particularly in the first and second years of ocean life. Mean length of age .1 steelhead was 227 mm (67%) greater than that of age .0 and mean length of age .2 was 125 mm (22%) greater than that of age .1 (Table 5). Mean weight of age .1 was 1,601 g (409%) greater than that of age .0, and mean weight of age .2 steelhead was 1,489 g (75%) greater than age .1. Weight increased by approximately 21% per year between ages .2 to .3 and .3 to .4. Samples of older age categories (.4 and .5) were too small to yield reliable average lengths and weights, but they indicate that growth continues at a substantial rate in later years. The apparent drop in length between ocean age .1 and .2, age .2 and .3, and possibly .3 and .4, may reflect the departure of larger, mature fish from the ocean population by late fall or early winter (Fig. 8); in February or March average lengths appear to be less than those of the next youngest age group a few months before.

Table 5. Descriptive statistics for lengths and weights of ocean-caught steelhead. Length and weight data are from samples collected by research vessels on the high seas, 1955-1985. Data sources: Fisheries and Oceans Canada, Fisheries Agency of Japan, Fisheries Research Institute.

Length (mm)					
Ocean Age	Mean	Sample Size	Std. Dev.	Minimum	Maximum
0	337	245	57.6	171	482
1	564	6079	50.8	352	748
2	689	3095	62.1	450	929
3	749	328	65.3	513	964
4	802	65	55.8	676	954
5	817	12	46.6	700	892
Combined	606	9824	95.7	171	964

Weight (g)					
Ocean Age	Mean	Sample Size	Std. Dev.	Minimum	Maximum
0	391	53	237.1	105	1300
1	1992	4313	513.2	650	4950
2	3481	2331	983.8	1050	7400
3	4206	202	1250.8	1320	8000
4	5119	40	1351.6	2690	8550
5	4490	5	692.2	3500	5220
Combined	2566	6944	1092.7	105	8550

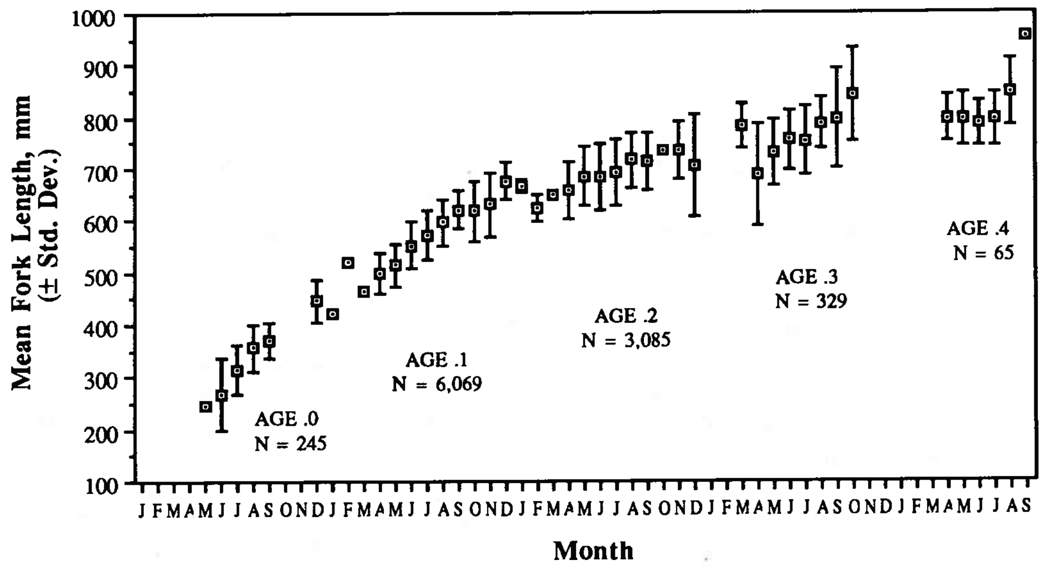


Figure 8. Mean monthly lengths of ocean-caught steelhead, 1956-1985.

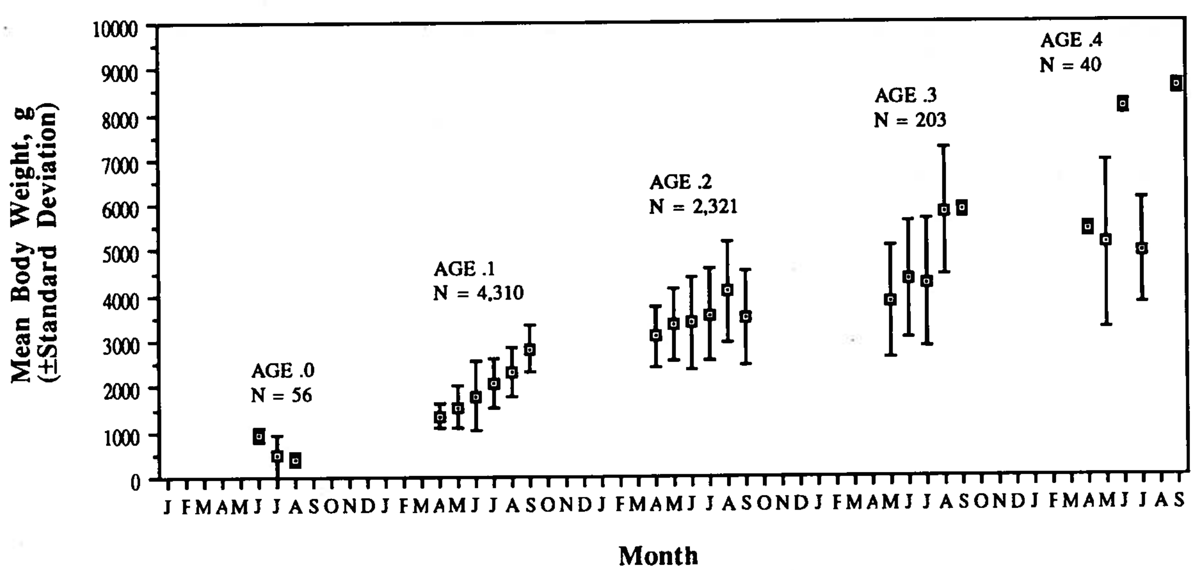


Figure 9. Mean monthly weights of ocean-caught steelhead, 1956-1985.

The relationship between weight and length of steelhead at sea is described by the following equation, calculated from a standard regression of Log(Weight) on Log(Length):

$$\text{Weight} = .000028\ (\text{Length})^{2.846}$$
$$r^2 = .92$$
$$N = 6{,}955$$

This relationship is presented graphically in Fig. 10. Hooton *et al.* (1987) found similar length-weight relationships for wild summer- and winter-run steelhead in streams of Vancouver Island, B.C. They derived their relationships from back calculated lengths at ocean age determined from scale features. Growth of Vancouver Island steelhead were described by the equations:

Weight = .0000133 $(\text{Length})^{2.946}$
for summer-run fish, and

Weight = .0000415 $(\text{Length})^{2.785}$
for winter-run fish

When plotted, these curves do not differ visibly from the curve in Fig. 10.

(3) Sex ratio

Overall, female steelhead (54.1%) were more abundant than males in high-seas samples. Sex ratio data examined are from the combined Canadian and U.S. sampling, 1956-1985, Japanese sampling, 1981-1985, and U.S.S.R. sampling, 1983-1985, and includes maturing and immature fish sampled during the spring (March-May), summer (June-August), and fall (September-November) periods. In the spring sample, 52.4% of 741 steelhead were females, in the summer sample 54.2% of 7,376 were females, and in the fall sample 57.8% of 225 were females. Sample sizes by area and season are shown in Appendix Figs. 10 to 12.

Sex ratios of steelhead in research vessel catches are displayed by area in Figs. 11 and 12 for the spring and summer seasons (March-May and June-August) for areas in which total sample size exceeded 20 steelhead. Fall period sample sizes were too small to examine sex ratio by area. Although the spring predominance of females is not apparent in Fig. 11, the higher proportion of females in summer is evident in Fig. 12. There appears to be no evidence of a sex ratio cline from east to west in the North Pacific. Of steelhead sampled in summer west of 175°W, 54.4% were females, and of those sampled east of 175°W, 53.5% were females. Of a sub-sample of 250 kelts captured in summer, 56.4% were females, indicating a sex ratio similar to the total sample of age groups combined.

In an analysis of steelhead catches by month and area in gillnets and longlines of Japanese research vessels from 1972 through 1982, Okazaki (1984a) also found females to predominate, averaging 57.5% of the total catch. He concluded that the proportion was not uniform across all research areas, and that females tended to predominate in western and northern waters in all months. The present analysis of combined data does not indicate a cline in steelhead sex ratio across the North Pacific.

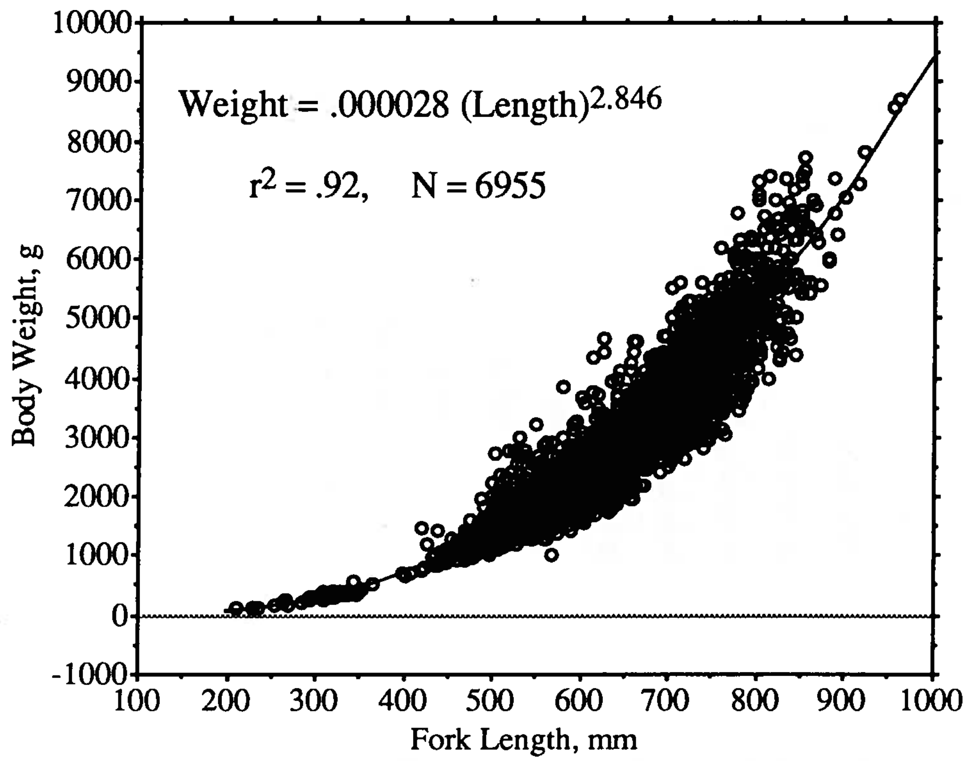


Figure 10. Length-weight relationship for ocean-caught steelhead.

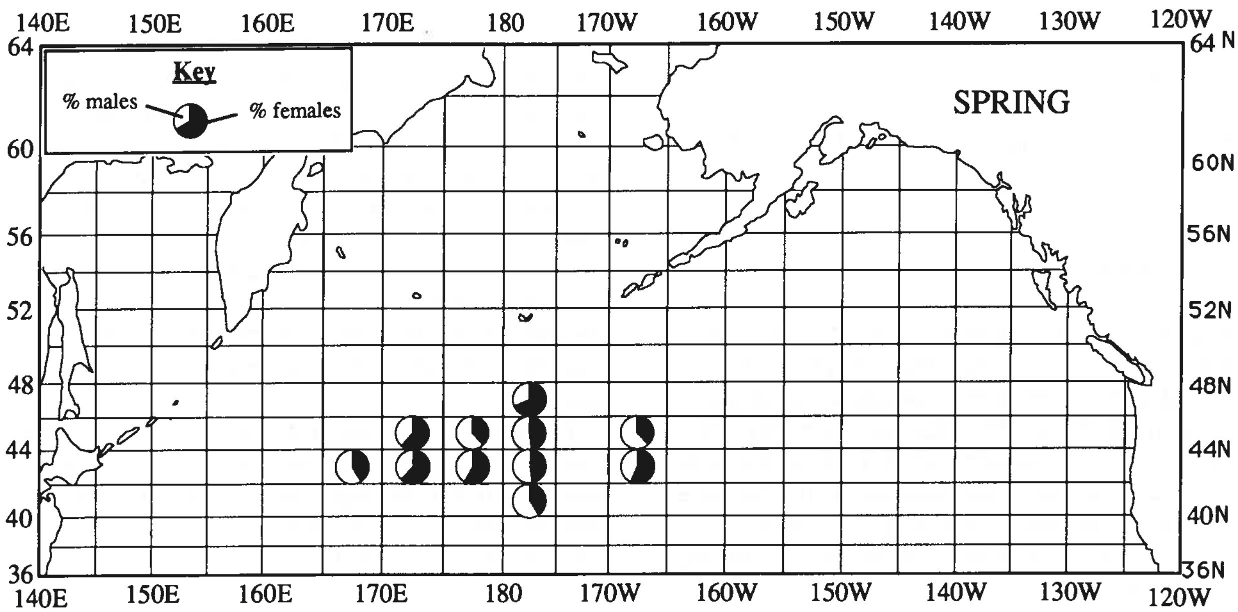


Figure 11. Percent composition of female and male steelhead in offshore catches, March-May. Data from U.S. and Canadian (1955-1982), Japanese (1981-1985), and U.S.S.R. (1983-1985) research vessels operating in the North Pacific Ocean.

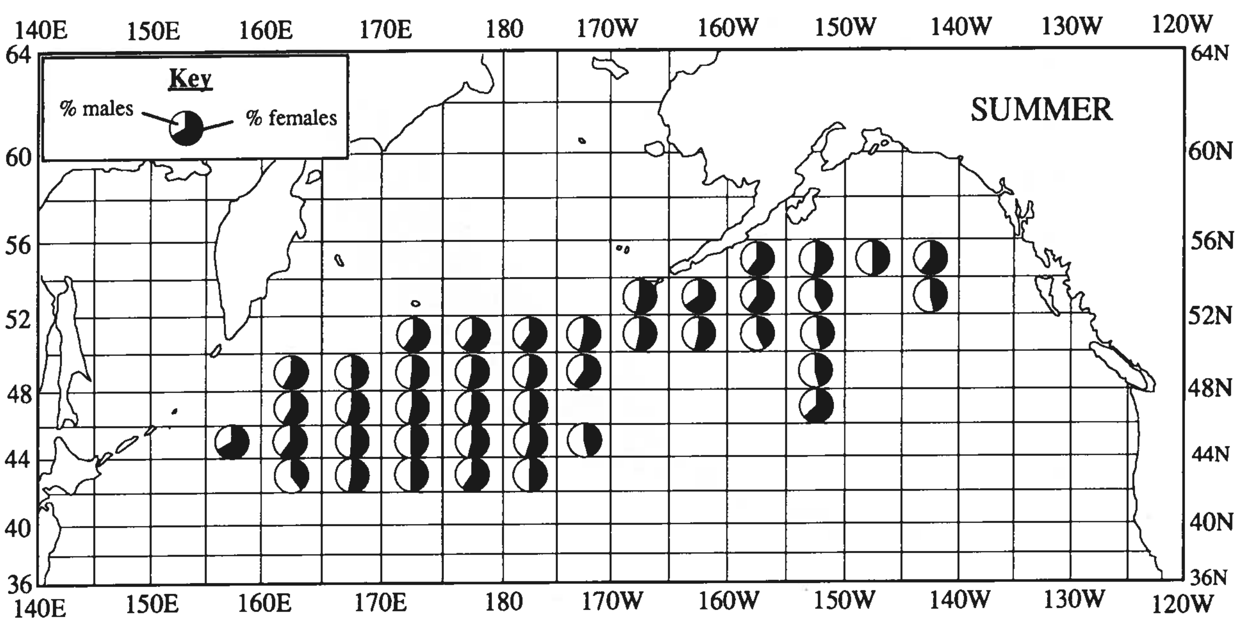


Figure 12. Percent composition of female and male steelhead in offshore catches, June-August. Data from U.S. and Canadian (1955-1982), Japanese (1981-1985), and U.S.S.R. (1983-1985) research vessels operating in the North Pacific Ocean.

There may be a difference in anadromy by sex between North American and Kamchatkan steelhead (Okazaki 1984a). In many North American rivers, female steelhead outnumber males by 1.3:1 to 3.2:1 in sports catches (Maher and Larkin 1955; Withler 1966; Narver 1969). However, trapping of upstream migrating fish indicates that females and males are present in nearly equal numbers (Pautzke and Meigs 1940; Shapovalov and Taft 1954). This indicates that angling may selectively take females (Withler 1966). Although a slightly greater number of females may be present in a population due to greater survival following spawning, it is presumed that the sex ratio of North American steelhead is essentially 1:1 (Withler 1966). No pattern of differences was found in the sex ratio of steelhead populations from the southern to northern portions of their North American range (Sheppard 1972).

Females may predominate in the anadromous forms of Kamchatkan steelhead (Okazaki 1984a). Maksimov (1976) observed that 65-70% of downstream migrants of smolts in the Bol'shaya River were females. After completion of downstream migration, males predominated in the population remaining in the river in June and July. In Kamchatkan steelhead stocks more closely connected with life in fresh water, males mature in the river, and anadromous females have been observed spawning with these precocious river males (Savvaitova 1975). Maksimov (1972) reported that the ratio of male to female spawners in the Utkholok River was 1:1.63 when precocious males were not counted.

2. Seasonal Distribution and Migratory Behavior

Soon after steelhead smolts enter the ocean they begin a directed movement into offshore waters. Although details of routes taken or movements made by individual fish remain obscure when using simple catch and biological data, the collective movements of fish at sea are readily discernable. In the following description of seasonal movements of steelhead in the ocean, initial emphasis will be placed on the entire high-seas population, followed by emphasis on individual age and spawning history groups.

In spring, steelhead are found in their greatest concentrations between 42°N and 52°N from the North American coastline westward to 155°W in the Gulf of Alaska (Fig. 13). To the westward, their distribution in this season extends nearly to 150°E and becomes more southerly from east to west. Steelhead were essentially absent in research vessel hauls in a wide band extending from the northern Gulf of Alaska and south of the Aleutian Island chain to the Asian coast. In earlier years, no steelhead were reported caught in spring by Japanese research vessels sampling during 1972-1976 in the southeastern Sea of Okhotsk.

By summer, the distribution of steelhead has spread distinctly north and west in the eastern North Pacific and northward south of the central and western Aleutians. Lower densities were encountered west of 175°E and north of 42°N in the North Pacific Ocean. Low abundance was indicated west of 165°E and in the Bering Sea (Fig. 13). The southern limit of distribution in summer has moved somewhat north from 38°N to near 40°N. Nearshore abundance in the North American Pacific Northwest region in summer is substantially less than in spring but remains strong in a few areas. Japanese research vessels sampling during 1972-1976 encountered a few steelhead in summer in the southeastern Sea of Okhotsk and Kuril Islands area.

In autumn, sampling was not widespread enough to get a complete indication of where steelhead occur, but catches did show the main body of steelhead concentrated along the southern side of the Aleutian Island chain and into the central Gulf of Alaska, roughly from 170°E to 140°W and north of 48°N (Fig. 14). A few steelhead were taken in earlier years by Japanese research vessels off the west coast of Kamchatka south of 56°N.

In winter, the main group of steelhead in the North Pacific had apparently moved further south and east across the Gulf of Alaska to the area south of 58°N, primarily south of 52°N (Fig. 14). No winter sampling was conducted south of 44°N except for one longline set in area 3042, or west of 165°E , or in the Okhotsk Sea. Steelhead abundance in waters relatively close to shore (east of 135°W) was higher in winter than in summer or autumn and had returned to levels near those found in spring. The general pattern of seasonal movement for the bulk of migrating steelhead appears to be northward and westward from spring through summer, followed by southward and eastward from autumn through winter. This annual pattern of movement is also portrayed by individual age or spawning history groups.

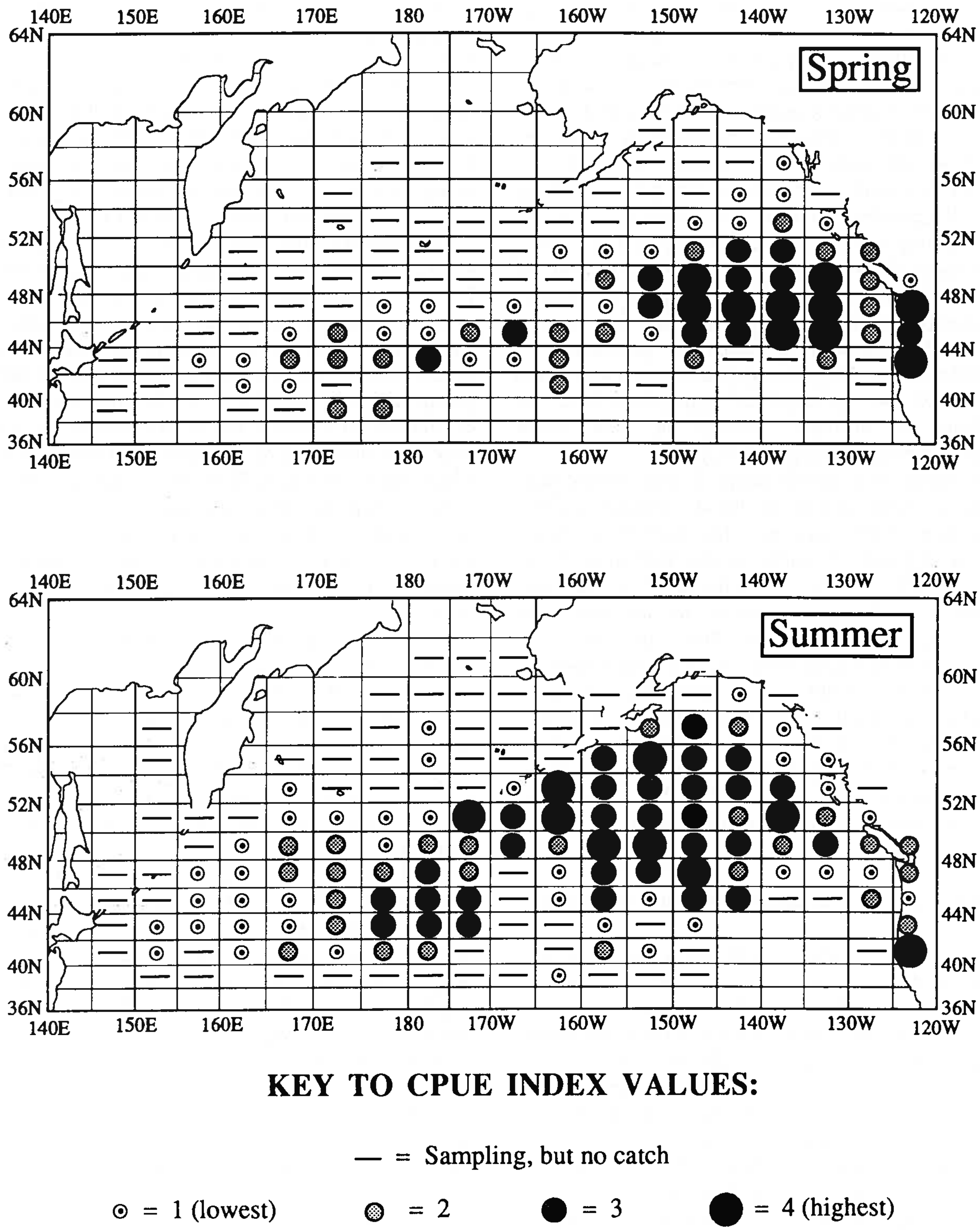
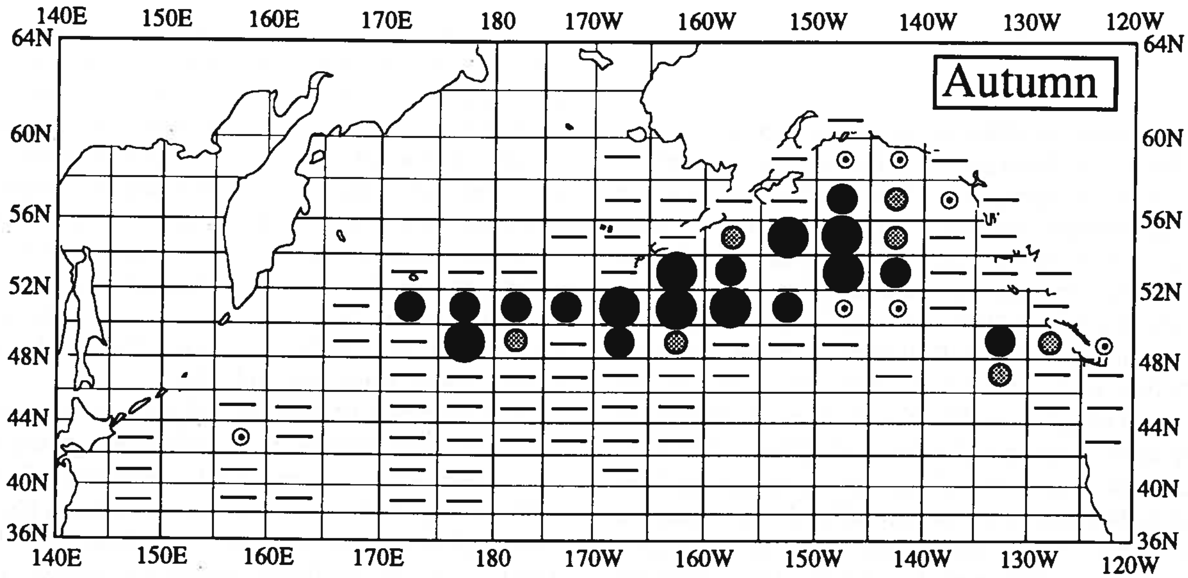
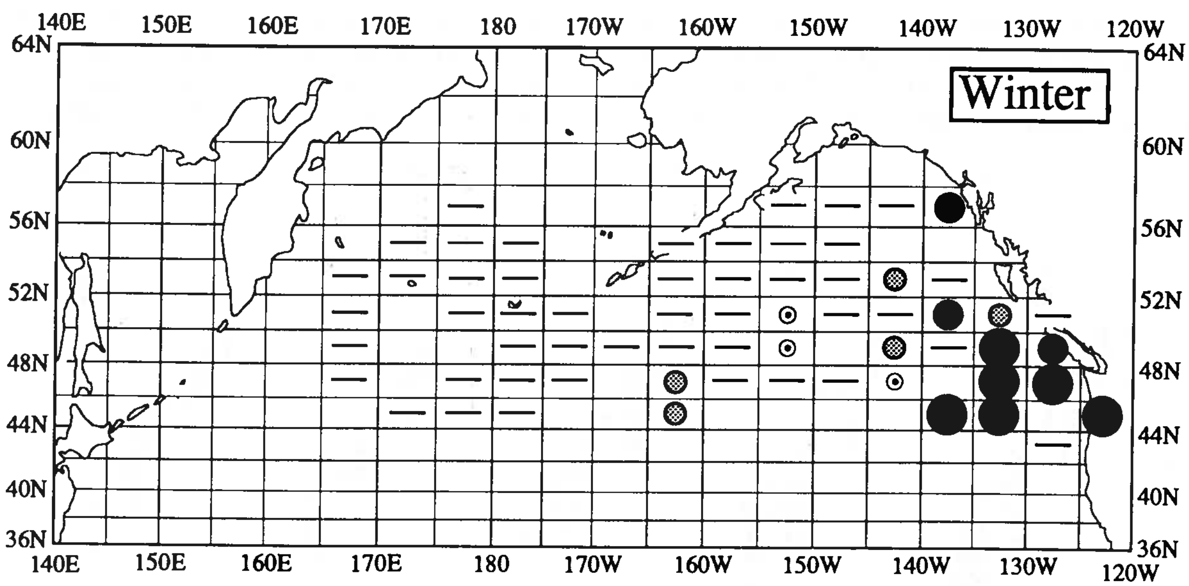


Figure 13. Ocean distribution of steelhead in spring (March-May) and summer (June-August) based on weighted average catch per-unit-effort (CPUE) data from U.S. and Canadian (1955-1990), U.S.S.R. (1983-1990), and Japanese (1981-1989) research vessels fishing with purse seines, gillnets, and longlines.





KEY TO CPUE INDEX VALUES:

— = Sampling, but no catch

⊙ = 1 (lowest) ◍ = 2 ● = 3 ⬤ = 4 (highest)

Figure 14. Ocean distribution of steelhead in autumn (September-November) and winter (December-February) based on weighted average catch per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1989) research vessels fishing with purse seines, gillnets, and longlines.

(1) **Ocean Age .0**

The seasonal shifts in ocean distribution of age .0 steelhead are portrayed in Append. Figs. 13 and 14. Nearshore sampling with fine-mesh purse seines in spring through autumn along the North American coast from northern California to Alaska reveals that soon after ocean entry, juvenile steelhead move quickly offshore (Hartt 1980; Wakefield *et al.* 1981; Miller *et al.* 1983; Hartt and Dell 1986). Purse seine set-direction data also indicate that age .0 fish off the coasts of Oregon and Washington move northward as they move westward (Miller *et al.* 1983). Details of nearshore abundance of this ocean-age group from May to September are presented for North American fish in Fig. 15. In May, which is the peak of smolt outmigration, high inshore concentrations reflect the influx of age .0 fish into coastal waters, especially in waters off Washington and Oregon adjacent to the mouth of the Columbia River. Inshore catch rates decrease markedly from June to July and only a few age .0 fish are found near the coast in July except for the area off northern California. The four juvenile steelhead caught in eight seine sets in this area (Fisher and Pearcy 1985a) are probably members of half-pounder populations lingering in the area prior to their return to streams in late summer. Elsewhere along the coast, juveniles are probably late-migrating smolts. In August, juveniles are scarce inshore. No age .0 fish were caught in sets off southern Oregon or Northern California in August, suggesting that by this time half-pounders have exited coastal waters and returned to nearby streams. In September, ocean age .0 steel-head are rare or absent in nearshore areas (Miller *et al.* 1983; Fisher *et al.* 1983, 1984; Fisher and Pearcy 1985a; Hartt and Dell 1986).

The decrease in numbers of juveniles in coastal waters of North America from spring through summer is accompanied by increased abundance farther offshore, especially in the central and western Gulf of Alaska (Pearcy and Masuda 1982; Hartt and Dell 1986). Age .0 steelhead apparently achieve their western-most extension in summer, as evidenced by the fish caught in the central North Pacific (Append. Fig. 13). In autumn, juveniles are concentrated in the western Gulf of Alaska north of 50°N and are found between 165°W and 125°W (Append. Fig. 14). Only three age .0 steelhead were taken in winter, during longline operations in area W4050 (Append. Fig. 14).

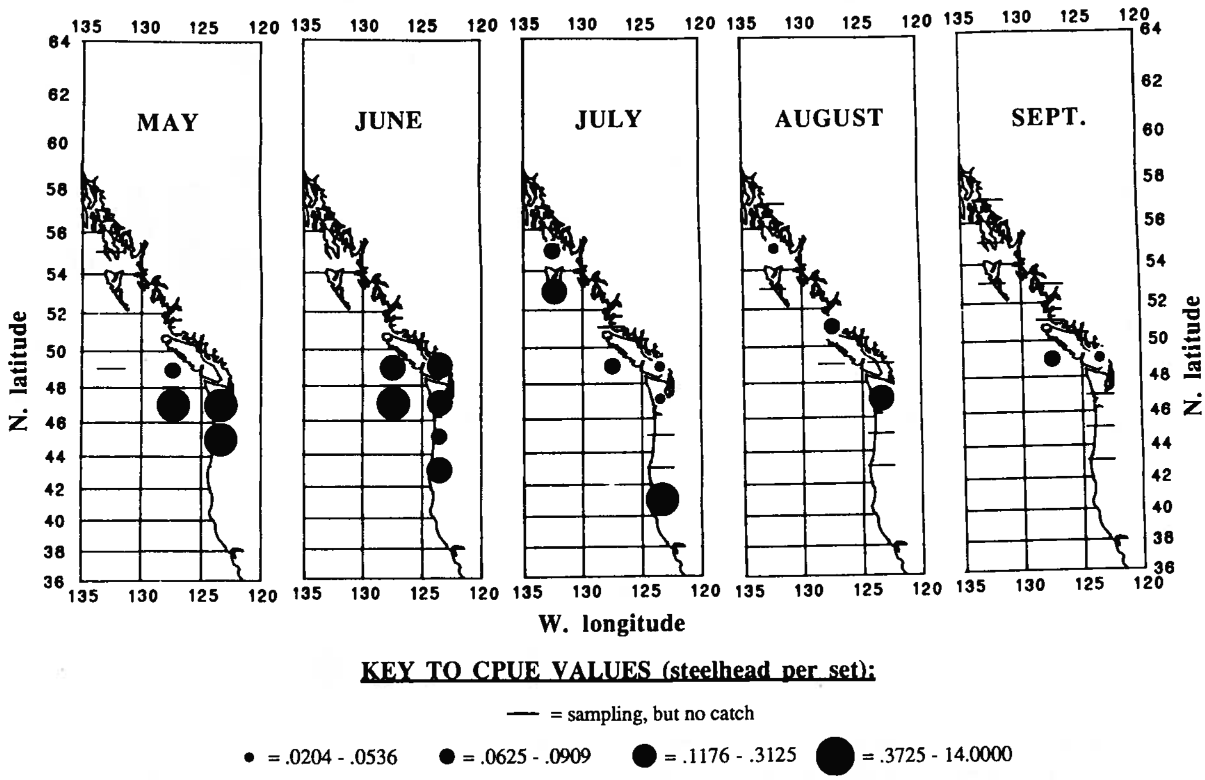


Figure 15. Nearshore distribution of age .0 steelhead from May to September based on U.S. (1955-1982) purse seine catch-per-unit-effort data.

Sampling was not conducted by Japanese research vessels near the Kamchatka Peninsula after 1976, but in earlier years a few age .0 steelhead were captured in summer along the southwest coast of Kamchatka (data from Japan Fisheries Agency). These catches indicated the presence of age .0 steelhead from Asian streams. None were reported in this area in spring or fall sampling.

(2) Ocean Age .1

Large-scale movements of age .0 fish probably continue during winter months and account for a broader dispersal of these fish, now age .1, in the spring. By the end of their first winter at sea juvenile steelhead have grown considerably larger (ca 450-580 mm; Fig. 8) and are more vulnerable to gillnet and longline sampling gear. Age .1 fish are concentrated offshore in the Gulf of Alaska, especially between 165°W and 130°W, and 44°N and 50°N. They extend westward to about 155°E in a band of much lower abundance (Append. Fig. 15). Distribution west of 160°W is more southerly than in the Gulf of Alaska. Age .1 steelhead are absent in more northern waters of the North Pacific from Yakutat, Alaska, westward along the Alaska Peninsula and Aleutian Island chain. Sampling was not conducted in waters near the Kamchatka Peninsula.

Interestingly, a small concentration of age .1 juveniles appears in the spring off the coast of southern Oregon and northern California (INPFC area W2542, see Append. Fig. 15). These fish are separated from the main mass of age .1 steelhead and are likely half-pounders returning to sea after their initial (non-spawning) migration into fresh water (Everest 1973). The low abundance of age .1 fish in other nearshore areas along the coast suggests age .1 fish do not migrate into coastal waters in March through May.

By summer, the center of abundance of age .1 steelhead has shifted north and west to areas north of 46°N and 42°N in the eastern and western North Pacific, respectively (Append. Fig. 15). Their overall distribution in summer has expanded considerably from spring and stretches from the North American coast around Vancouver Island (48°N) westward nearly to 150°E. However they are relatively scarce west of 165°E. They are most abundant in waters roughly between 175°W and 140°W.

In autumn, age .1 steelhead catches were irregular but still showed concentrations in areas immediately south of the Alaska Peninsula and Aleutian Islands (Append. Fig. 16). Small groups of age .1 fish were also found in the Gulf of Alaska and offshore from Vancouver Island, B.C. In winter (December-February), age .1 steelhead were caught only east of 155°W between 50°N and 54°N.

(3) Ocean Age .2 or Older

This group of fish is composed of both maidens and kelts. In contrast to the spring distribution of age .1 fish, age .2 and older (.2+) fish are fairly abundant in nearshore waters in spring (Append. Fig. 17). Elsewhere, the general distribution of .2+ fish is similar to age .1 fish in spring, except that the older fish appear to be slightly more abundant in waters west of 165°W. Also, the center of abundance of age .2+ fish appears to be somewhat farther north than younger fish at this time of year. As with the age .1 fish, the age .2+ steelhead distribution is more southerly in the central and western North Pacific in spring.

Virtually the same pattern of northwestward movement from spring through summer is seen for age .2+ steelhead as was found for age .1 fish (Append. Fig. 17). In summer, age .2+ fish were concentrated mostly in waters north of 46°N in the Gulf of Alaska or north of 42°N in the west-central North Pacific, and were rarely encountered in the Bering Sea. The only notable differences between age .2+ and age .1 fish in summer is that age .2+ fish are less prevalent, except near the North American coast.

Autumn and winter distributions for age .2+ steelhead show the same general features as for age .1 fish (Append. Fig. 18).

(4) Immature Fish (Pre-Spawning "Maidens")

The general migration pattern of maidens (all age groups combined) largely resembles the seasonal movements of age .1 fish, because few or no fish within the age .1 group have spawned. As such, the pattern of distribution for maidens can be described as a northwesterly movement from spring through summer (Append. Fig. 19), then southeasterly between late fall and winter (Append. Fig. 20). As with age .1 fish, maidens of all ages remain fairly distant from the shores of either continent throughout their oceanic life except for summer months when they are abundant in nearshore waters immediately south of the Alaska Peninsula and Aleutian Islands. Their annual migratory cycle repeats itself until the season when the fish mature and move inshore to seek spawning streams. This final inshore movement of maturing fish was not plainly visible for fish returning in autumn, and only somewhat more evident, if visible at all, for fish moving shoreward in winter (Append. Fig. 20).

(5) Mature Fish (Post-Spawning "Kelts")

The migration of kelts differs, principally in extent, from the seasonal movements of maidens. In contrast to the continuous and extensive presence of maidens offshore in spring, kelts are most plentiful in coastal and nearshore waters (Append. Fig. 21). The center of abundance of kelts occurs in the area between 44°N and 52°N and from the North American coast westward to 145°W. A scattering of kelts occurs in other localities within the Gulf of Alaska or westward to 165°E between 42° and 48°N. Like maidens, kelts move farther offshore in summer but lag behind maiden fish in the westward extent of their distribution. The abundance of maidens is highest in waters from the Gulf of Alaska to 165°E, whereas kelts are less broadly dispersed and are found in greatest numbers east of 175°W. Also apparent is the lower overall abundance of kelts by comparison with maiden fish, because of the generally small fraction of most populations that survive spawning and return to the sea. The pattern of southward and eastward movement from autumn into winter exhibited by other groups of steelhead is hinted for kelts (Append. Fig. 22).

(6) Distribution Based on Gonadal Analysis of Maturity

Okazaki (1984a) analyzed data on gonad weights to distinguish movement patterns of immature and maturing fish. He detected small developmental differences in fish of the western and central North Pacific over the course of the summer but they were insufficient to enable him to define the distribution of the two maturity groups.

3. Distribution by Area of Origin

For many species of Pacific salmon a wealth of stock-specific information has accumulated from scale pattern analyses and other work that enables researchers to study the distribution of various stocks at sea. Such detailed insight into the distribution of steelhead, however, is elusive and suffers from both a lack of research and an apparent inability to clearly distinguish various stocks or groups using standard stock-separation techniques. For example, summer and winter races of steelhead are known to be genetically distinct on the basis of life-history observations (Everest 1973; Leider *et al.* 1984) and breeding experiments (Neave 1944), yet no morphological or biochemical evidence has been uncovered that allows reliable identification of individuals of the two races (Light 1987b). Without reliable stock separation methods, all clues to the differential distribution of stocks and groups must come from direct evidence from recoveries of tagged fish or from parasitological studies.

(1) Information from Tagging Studies

(a) Coastal Returns from Steelhead Tagged at Sea

From 1956 to 1988, 1,722 steelhead trout were tagged with external tags and released during INPFC high-seas tagging experiments (Fig. 6). Of these tagged steelhead, 77 were recovered in North American coastal areas or spawning streams (Fig. 16).

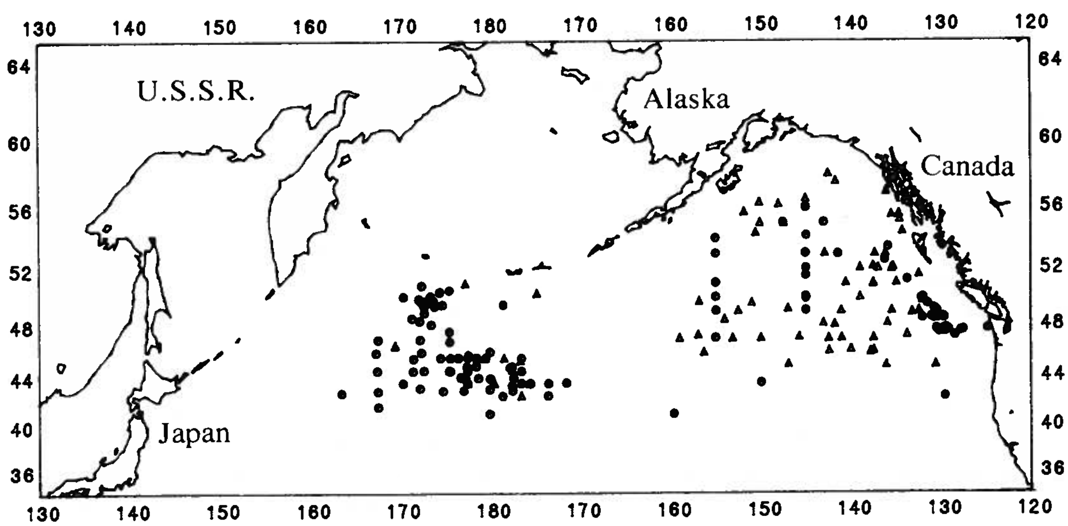


Figure 16. Ocean distribution of North American steelhead trout as evidenced by recoveries through 1989 of fish that carried a disk tag or spaghetti tag (▲, n=77), or a coded-wire tag (●, n=166). Duplicate recoveries at the same 1°x1° location are not shown.

Sixty-five of the recoveries were from the Canadian and United States tagging operations conducted prior to 1971 and almost entirely in the Gulf of Alaska. Only one of the sixty-five recovered fish was released west of 175°W. Because hatchery releases were compara-tively low during this period, probably most of the steelhead captured for tagging were wild-origin fish. The remaining 12 recoveries of the 77 total were from releases after 1978 from tagging primarily by Japan west of 175°W. For both time periods of release combined, the approximate ocean age composition of recovered fish at time of release was 1% age .0, 48% age .1, 31% age .2, and 20% age .3. Seventy-nine percent of the recovered fish returned within a year of release without spending an additional growing season at sea.

Of the 22 steelhead returning to British Columbia streams (Fig. 17), only 3 spent an additional year in the ocean. Nineteen were recovered between June and October, indicating summer run fish, and most were recaptured in inshore salmon fisheries. All 22 had been tagged in the 1960s east of 155°W. Of the 15 fish returning to coastal Washington and Puget Sound streams (Fig. 17), all returned within 12 months of tagging. In contrast to British Columbia recoveries, 14 of the 15 steelhead were recaptured between December and May, suggesting winter-run fish; about half were taken in salmon fisheries. Five of the 15 were tagged after 1978 and west of 175°W. Of the 19 recoveries in the Columbia River and tributaries (Fig. 18), most returned within a year of tagging, about half were recaptured between June and October, and about 1/3 were taken in river salmon fisheries. Seven of the 19 were tagged post-1978 and five of them were tagged west of 175°W. Of the 12 coastal Oregon and nine California recoveries (Fig. 18), all had been tagged in the 1960s and east of 160°W, and all but four were recovered in streams between December and February. There were no commercial net fisheries for salmon along the Oregon-California coasts.

No tags from high-seas releases have as yet been returned from Kamchatkan or Alaskan streams, although there has been an unconfirmed report of recoveries of tagged steelhead in west Kamchatka. Because of the suspected low abundance of Kamchatkan steelhead (Harris 1988) and the low recovery effort, the chance of recovering a disk-tagged steelhead in Asia is likely to be small. The relative abundance of steelhead in Alaskan streams is also small (Light 1987a).

(b) High-seas Recoveries of Steelhead Tagged or Marked and Released as Smolts

Over 138 million steelhead were marked or tagged and released during inshore experiments at North American hatchery facilities between 1978 and 1989 (Table 1). More than 1,200 fish whose marks or tags indicate or confirm release from these facilities were recovered offshore by research and commercial fishing vessels. Eight hundred and forty-two were missing the adipose fin and presumed to be adipose-clipped fish. Among the latter group, 166 were also found to carry a CWT. These recoveries greatly extended the information on high-seas distribution of North American steelhead (Fig. 16). The clustering of recoveries west of 170°W resulted from sampling on Japanese research and mothership vessels, whereas most of the recoveries in the Gulf of Alaska resulted from sampling by the University of Hokkaido research vessel *Oshoro maru* and the Canadian experimental fishery for squid.

Steelhead from British Columbia, Washington, and the Columbia River Basin (Figs. 17 and 18) were well dispersed throughout the areas sampled from approximately 41°N northward to the Aleutian Islands in the central North Pacific, and from 163° 32' E eastward to the North American coastline. Three tagged fish from Alaska were recovered in the west-central North Pacific in the same general areas as fish from other regions (Fig. 17). No CWT fish from California have been recovered at sea, although on average approximately 200,000 tagged fish were released yearly between 1980 and 1985 (Johnson and Longwill 1988). Oregon fisheries agencies have not released any CWT fish from coastal streams.

The confirmed western-most limit of North American steelhead distribution on the high seas based on a tagged fish recovery is defined by a recovered coded-wire tagged fish from the Quinault River, Washington. This fish was captured in June 1989 by a Japanese research vessel at 42°44'N, 163°32'E, which is approximately 5,370 km from the mouth of its natal stream (Dahlberg *et al.* 1989). The southern-most limit for North American steelhead is identified by three adipose-clipped, coded-wire tagged fish from tributaries of the Snake River (Columbia River Basin) that were captured by a Canadian research vessel in 1987 at 40°58'N, 159°39'W (LeBrasseur *et al.* 1987).

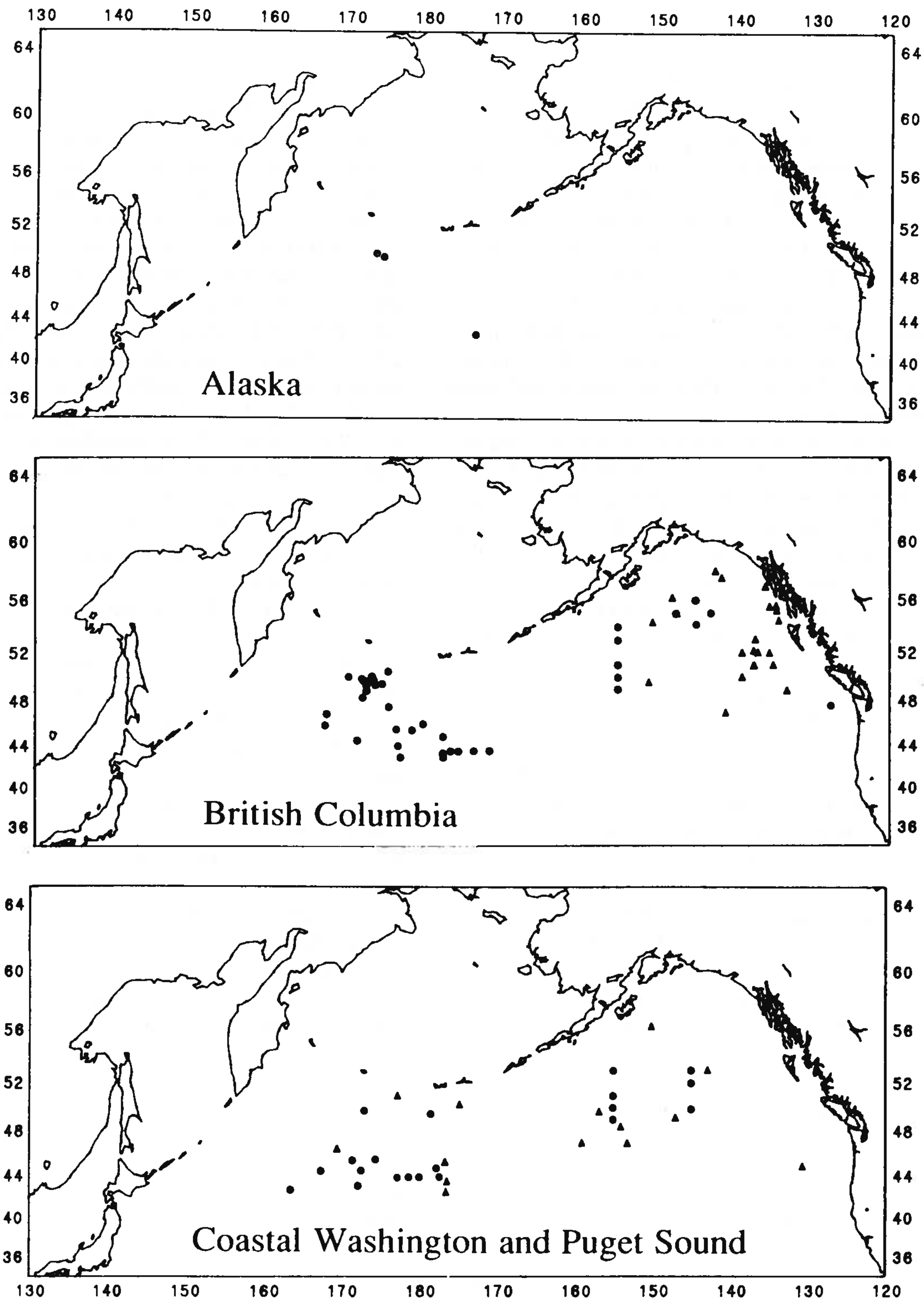


Figure 17. Ocean distribution of steelhead trout from Alaska, British Columbia, and Coastal Washington and Puget Sound, as evidenced by recoveries of disk tags (▲) and coded-wire tags (•) during INPFC-related research,1956-1989. Duplicate recoveries at the same 1°x1° location are not shown.

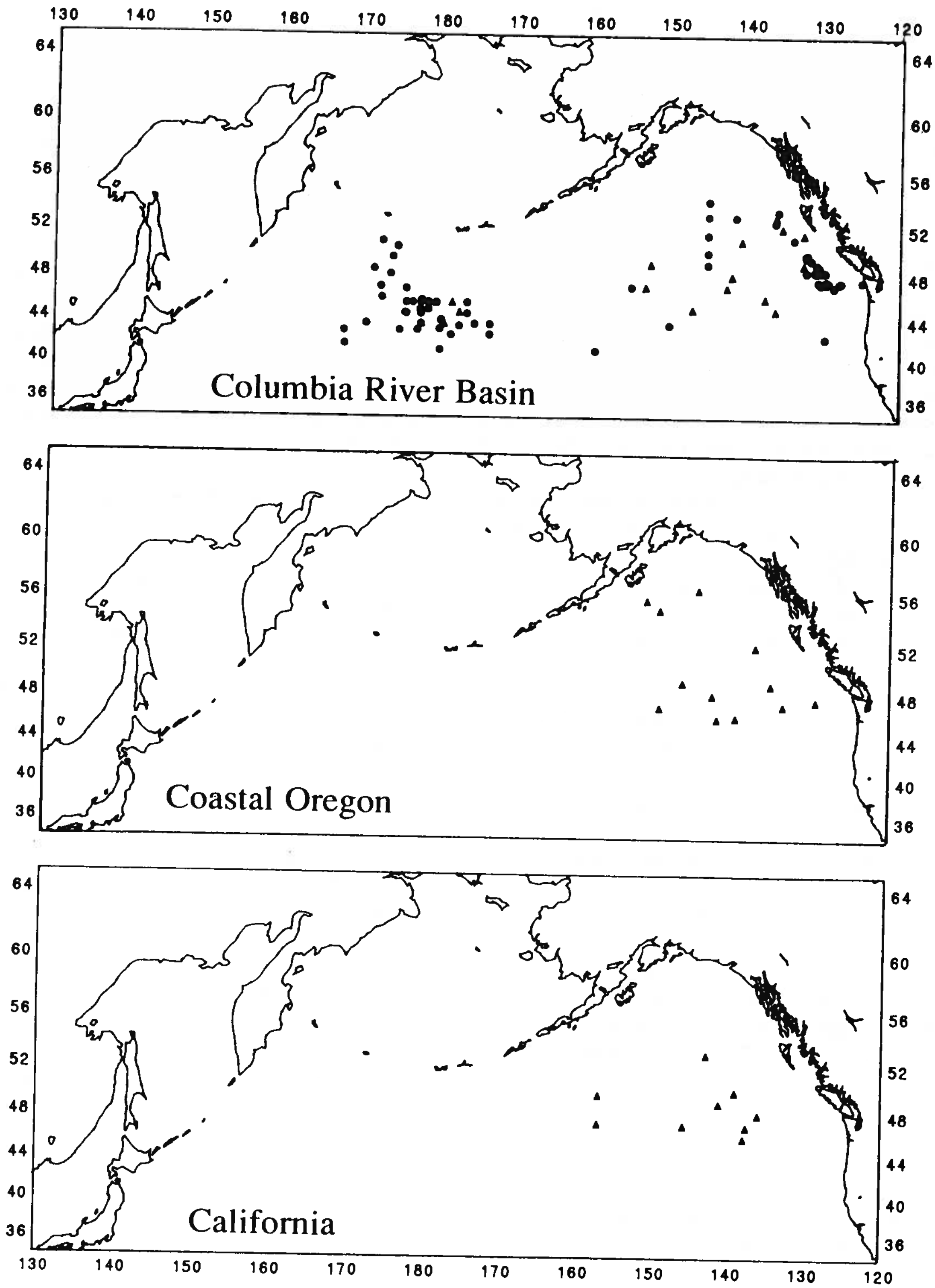


Figure 18. Ocean distribution of steelhead trout from the Columbia River Basin, coastal Oregon, and California, as evidenced by recoveries of disk tags (▲) and coded-wire tags (•) during INPFC-related research, 1956-1989. Duplicate recoveries at the same 1°x1° location are not shown.

Data on rate of recovery of coded-wire tagged steelhead by coastal area of release, Alaska to California, show relatively uniform high-seas recovery rates except for California (Table 6). Because examination of high-seas research vessel catches for steelhead with missing adipose fins was limited prior to 1981, only data on tagged steelhead smolts released in 1980 and subsequent years are included in Table 6. For this period, total offshore recovery rates of CWT steelhead varied between 3.9 and 11 per million tagged smolts released for areas other than California. (A disproportionate number of CWT steelhead (37 of 39) taken in the Canadian experimental squid driftnet fishery were of Columbia River drainage origin, boosting total recoveries from Columbia River releases.) For CWT recoveries made west of 170°W, recovery rates among release areas north of California ranged between 3.9 and 6.0 per million released.

Extensive marking of North American steelhead smolts has been conducted in addition to that utilizing coded-wire tags (Table 1). Examination for and recording of all fin- and maxillary-clipped steelhead in high-seas sampling has not been as consistent as for coded-wire tagged fish. However, the pattern of recoveries of steelhead with missing fins is further indication of the distribution of North American steelhead (Fig. 19). Three fin-clipped steelhead of unconfirmed North American origin were recovered at 159°50'E, 162°09'E, and 162°28'E, beyond the western range determined from tagging.

(c) Distribution of Regional Groups

Information obtained from disk tags and CWT recoveries was combined to compare the oceanic distributions of North American regional groups (i.e., inland and coastal forms). Coded-wire tagged fish provide the best evidence of the offshore distribution of regional groups. Data on disk-tagged fish were included for those steelhead whose time and area of inshore recovery allowed classification as to coastal or inland.

Inland and coastal groups of North American steelhead are defined on the basis of LDH-4 and SOD allelic frequencies (Utter and Allendorf 1977; Parkinson 1984). Inland steelhead occur in tributaries of the Columbia and Fraser rivers east of the Cascade mountain range. In the Columbia River watershed inland steelhead occur in and upstream from the Klickitat and Deschutes rivers and are summer steelhead. In the Fraser River watershed inland steelhead occur above the junction of the Fraser and Thompson rivers. To date, coded-wire- or disk-tagged fish from the Columbia River basin are the only inland stocks recovered from high-seas sampling or tagging. A comparison of the offshore distribution of the Columbia River basin steelhead with that of coastal summer steelhead stocks indicates that, although they occupy the same areas in the central and western North Pacific during their marine migrations, there are apparent differences in distribution in the Gulf of Alaska (Fig. 20). The generally more northern distribution shown for summer coastal steelhead is due in large part to the presence of British Columbia fish, whereas the cluster of Columbia River basin steelhead shown off Vancouver Island and Washington were recoveries made during the offshore Canadian experimental driftnet fishery for squid during the months of June, July, and August.

(2) Information from Parasitological Studies

More than 3,000 steelhead taken over a broad range of the North Pacific Ocean from 1983-1987 and in 1990 were examined for parasites in the combined studies of Margolis (1984, 1985b), Dalton (1989b), Myers *et al.* (1991), and Margolis and McDonald (unpublished data). Many of the steelhead sampled by Dalton (1989b) in 1984 and 1985 were examined for *P. shawi* only and all of those sampled by him in 1986 and 1987 were examined for *N. salmincola* only. Of the total number of steelhead sampled in all parasite tag studies noted above, 1,528 were examined for both *N. salmincola* and *P. shawi*, 865 for *P. shawi* only, and 798 for *N. salmincola* only. The annual prevalence of *N. salmincola* in the aforementioned studies varied from 10.2% to 54%, and that for *P. shawi* varied from 0.9% to 5.9%, for high-seas samples taken west of 140°W. Thus, *N. salmincola* is a more powerful stock marker, and accounts for the concentration of Dalton (1989a, 1989b) and Myers *et al.* (1991) on this parasite.

In the samples taken off the coast of North America (east of 140°W) (Fig. 21) from 1985 to 1987 (Margolis and McDonald, unpublished data), the annual prevalence of *N. salmincola* (32.8%-52.4%) was similar to that (36.1%-54%) in samples taken during the same years west of 140°W (Dalton 1989a, 1989b). However, the annual prevalence (26.6%-30.5%) of *P. shawi* in the samples from along the North American coast was much higher than in the samples from high-seas areas west of 140°W (0.9%-5.9%), but the data from the two regions were obtained largely in different years (1985-1987 versus 1983-1985).

Table 6. Release and high-seas recoveries of coded-wire tagged steelhead, 1980-1988, by area of release.

Area of release	CWT released (thousands)	Total recoveries		Recoveries west of 170°W	
		No.	Percent	No.	Percent
Alaska	776	3	3.9×10^{-6}	3	3.9×10^{-6}
British Columbia	4848	48	9.9×10^{-6}	29	6.0×10^{-6}
Wash. coast and Puget Sound	2336	22	9.4×10^{-6}	13	5.6×10^{-6}
Columbia River watershed	7945	87	11.0×10^{-6}	44	5.5×10^{-6}
California	1211	0	0.0	0	0.0

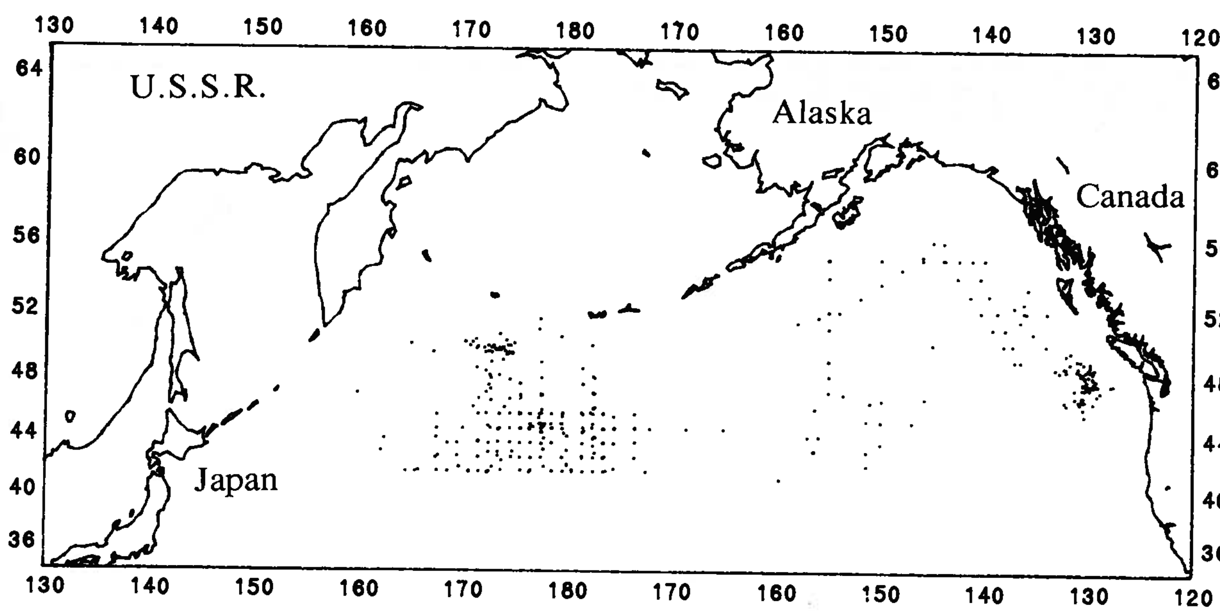


Figure 19. Ocean distribution of recovered steelhead trout with missing fins or clipped maxillary bones but without coded-wire tags. Duplicate recoveries at the same 1°x1° location are not shown.

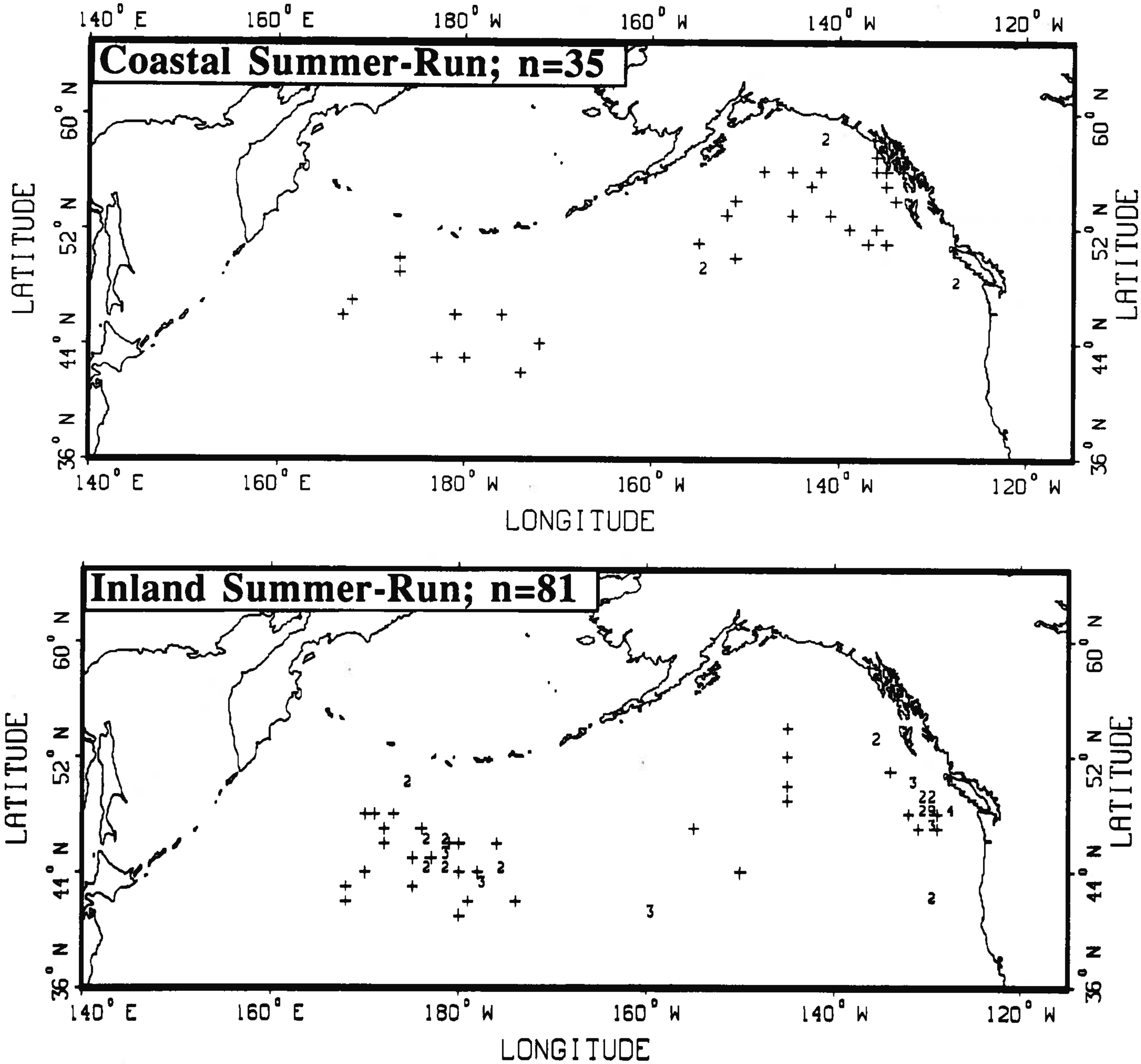


Figure 20. Comparison of ocean distributions of North American summer steelhead of inland versus coastal origin, as evidenced by recoveries of disk tags and coded-wire tags. A plus (+) sign denotes a single fish. Numbers from 2 to 9 denote multiple fish at the same (1° latitude by 1° longitude) location.

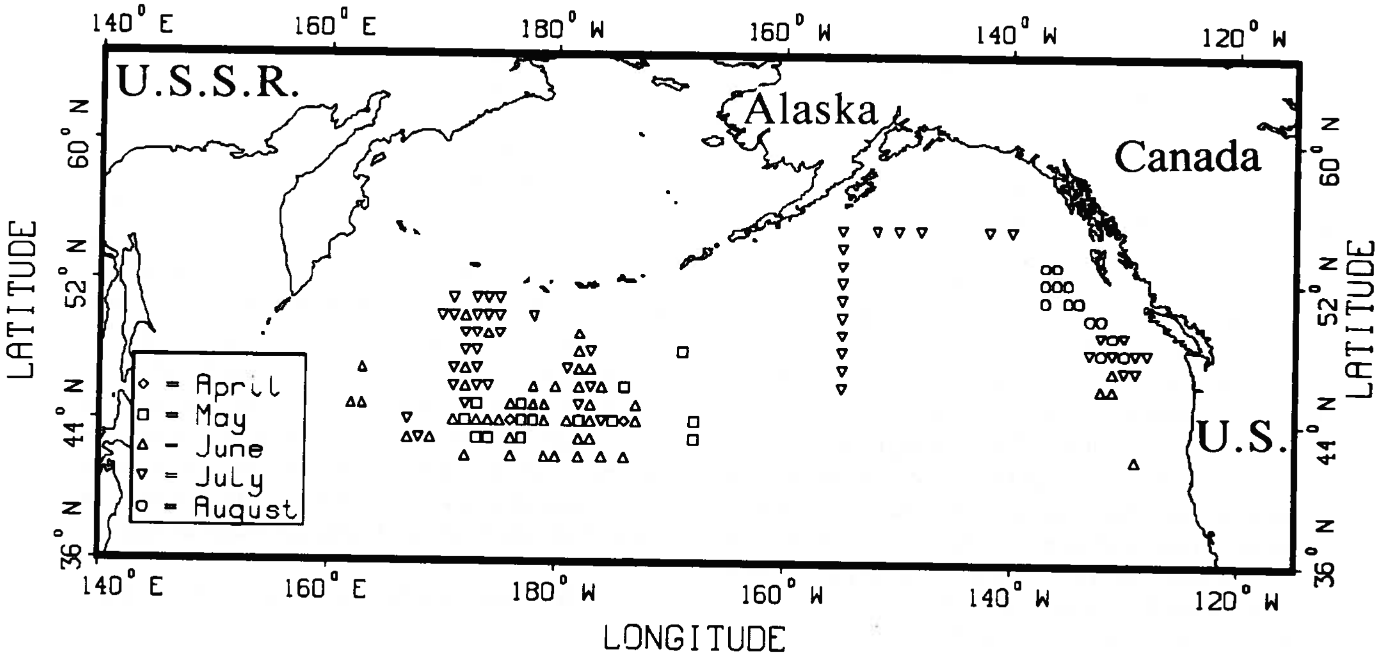


Figure 21. Ocean distribution of U.S. Pacific Northwest steelhead as determined by the presence of N. salmincola and P. shawi in samples from the North Pacific Ocean during the months of April to August 1983-1987 and 1990 combined. (Based on data from Margolis (1984, 1985b), Dalton (1989b), Myers et al. (1991), and Margolis and McDonald (unpublished).)

Nevertheless, comparison of the data for 1985 (30% versus 0.9% for the two regions) suggests that many *P. shawi* are lost as steelhead move far offshore or that the specific stock composition in the two regions differs markedly.

Of the 3,191 steelhead sampled, 921 (28.9%) carried one or both of the parasite tags. The parasite-marked fish were widely distributed across the North Pacific Ocean, indicating a westward ocean distribution of U.S. Pacific Northwest steelhead trout to at least 162°29'E (at 44°56'N) (Fig. 21), which is slightly beyond the westward distribution identified by CWT recoveries. The latitudinal range in waters west of about 167°W extended from about 41°N to 50°N, and eastward from 155°W the latitudinal range extended from approximately 42°N to 55°N. Apart from the sampling in the region approximately 200 miles (320 km) off the North American coast, sampling in the eastern Pacific Ocean was confined to a series of stations along 55°N (from 155°W to 140°W) and along 155°W (from 45°N to 55°N). No samples were examined from between 167°W and 155°W.

The spatial and temporal distribution of the U.S. Pacific Northwest origin steelhead trout shown in Fig. 21 reflects the sampling effort by month and area. A broad ocean distribution of U.S. Pacific Northwest steelhead trout was found from April to July. There appeared to be no significant difference in the distributional range between males and females, between maturing and immature fish, and between 1-ocean winter and 2-ocean winter fish of this stock group (Margolis 1985b).

The possibility of using prevalence data on *P. shawi* and *N. salmincola* for estimating proportions of steelhead trout of U.S. Pacific Northwest origin in high-seas samples was alluded to by Margolis (1984, 1985b), but adequate data to attempt such quantitative analyses were not available. However, from a comparison of parasite-tag prevalences among spring and summer samples from the central and western North Pacific Ocean, Margolis (1985b) speculated that the proportion of U.S. Pacific Northwest steelhead trout within each 5° band of longitude between 175°W and 170°E was similar within each of the years 1983 and 1984. Similar comparisons by Dalton (1989a), using chi-square analysis, led to the following conclusions: (1) In 1985, prevalence of *N. salmincola* was significantly greater east of 180° than west of this longitude ($p = 0.003$). (2) In 1986, prevalence also tended to be greater east of 180° than west of this longitude, but this difference was not significant at the $p = 0.05$ level. Prevalence, however, was significantly greater north of 46°N than south of this latitude ($p = 0.26$). (3) In 1987, there were no apparent east-west or north-south trends in *N. salmincola* prevalence in the central and western North Pacific Ocean.

By combining data on *N. salmincola* prevalence in steelhead trout smolts from a large number of streams and rearing areas sampled in 1987 and 1988 with data on the relative abundance of steelhead in these areas, Dalton (1989a) estimated the proportion of steelhead trout that were infected with *N. salmincola* within the enzootic area for this parasite. He then compared the prevalences in samples of steelhead trout taken in 1986 and 1987 in the central and western North Pacific Ocean with the estimated overall prevalence for the enzootic area, to estimate proportions of U.S. Pacific Northwest steelhead trout in the sampled high-seas areas. Dalton (1989a) recognized the existence of biases and unsatisfied assumptions in this procedure; nevertheless, from the high prevalences observed in the high-seas samples, he concluded that a large majority of the steelhead trout sampled in the central (actually, central and western) Pacific Ocean were from the U.S. Pacific Northwest.

(3) Information from Genetic Studies

Okazaki (1985) used biochemical genetic information to distinguish North American from Asian steelhead and to estimate their distributions on the high seas. His results showed Asian fish to be highly abundant in the central and western North Pacific or even farther east in most months. A critical review of Okazaki's work by Mulligan *et al.* (1988), coupled with the knowledge of the overwhelming numerical superiority of North American relative to Asian steelhead (Light 1987a; Harris 1988), failed to support his conclusions. Harris (1988) provisionally concluded that North American stocks predominate in waters east of 165°E, and current evidence from tagging and parasite studies offers little to dispute this.

On the basis of genetic analysis, Okazaki (1985) suggested that inland and coastal groups of steelhead migrate to different areas of the North Pacific, with inland steelhead being more abundant in the central and western North Pacific and also in more southerly regions than coastal steelhead. This conclusion cannot be readily evaluated from the above tagging analyses, since inland steelhead recoveries were represented only by Columbia River basin fish, and coastal steelhead recoveries were a combination of summer and winter fish, which showed different distributions.

(4) Summary of Distribution by Area of Origin

In the absence of other direct evidence, tag-recovery and parasitological information continue to provide the strongest clues on the distribution of different stocks or groups, and indicates that steelhead from most areas along the coast of North America are widely dispersed and heavily intermixed. In the absence of similar information for Asian steelhead, the extent of their ocean distribution and migrations remains obscure.

The results of tagging experiments and parasite studies show that North American steelhead are distributed throughout a large part of the marine areas known to be travelled by migrating steelhead (Fig. 22).

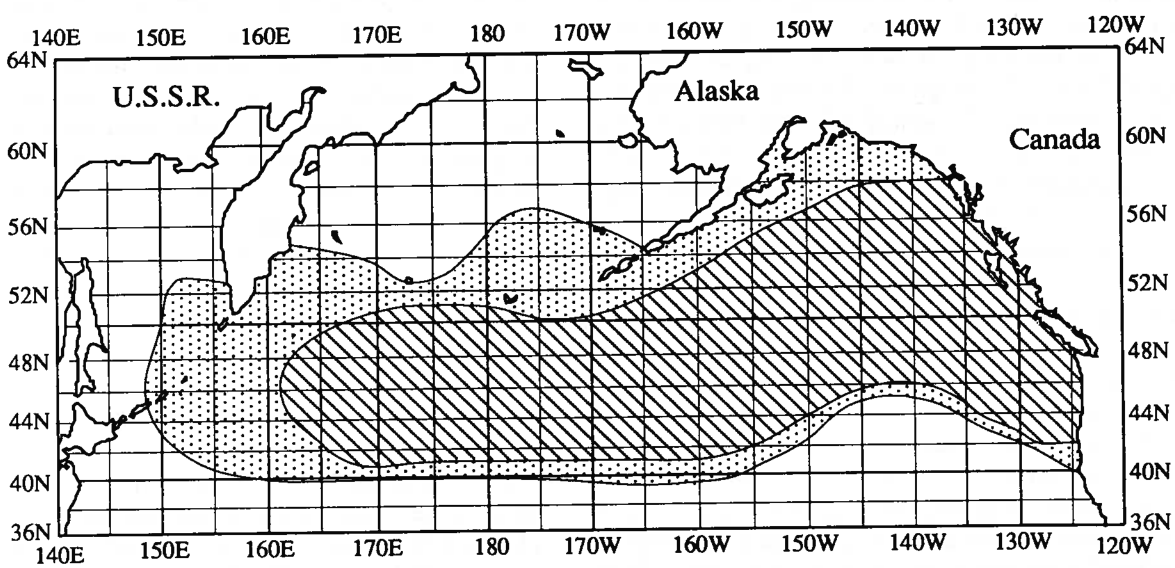


Figure 22. Known ocean distribution of North American steelhead as determined by recoveries of tagged fish (1956-1989) or fish infected with North American origin indicating parasites (1983-1987 and 1990) within the larger distribution of steelhead determined from U.S. and Canadian (1955-1990), U.S.S.R. (1983-1990), and Japanese (1972-1989) research vessel catch data.

The general extent of steelhead marine distribution covers a broad area from the North American continent to the southeastern waters of the Sea of Okhotsk. A few fish have been caught in the Bering Sea (Sutherland 1973; Okazaki 1983) and in the northwestern Sea of Okhotsk (Okazaki 1983). The southern boundary of steelhead distribution extends as far south as 39°N, but generally lies between 40°N and 44°N. North American steelhead have been found throughout most of this area except in waters west of 162°E, in the Bering Sea, and along the southern fringe of the distribution, where the abundance of steelhead is relatively low.

The tagging results suggest that steelhead from most streams along the North American Pacific coast have similar distributions offshore. However, differences between Columbia River inland steelhead and summer coastal stocks were noted in the Gulf of Alaska. In addition, steelhead from coastal Oregon and California may have more restricted westward migrations than do the more northern stocks (Fig. 18). Although these results may be an artifact of the lack of coded-wire tagged smolt releases from coastal Oregon and the relatively low number of releases from California, there may well be a true difference in ocean distribution of these stocks.

4. Distribution of Seasonal Races

The marine distributions of summer and winter steelhead determined from the tag recovery data base are shown in Fig. 23. Although the two groups show broadly overlapping distributions, some differences in detail of distribution are apparent. These are: (1) a higher proportion of winter steelhead was found south of the central and western Aleutians, (2) the northwest extent of distribution (i.e., south of Attu) was stronger for winter steelhead, and (3) there were no winter steelhead represented in eastern Gulf of Alaska waters. These results support the hypothesis that summer and winter steelhead have different seasonal patterns of marine distribution to accommodate the wide difference in time of return to fresh water exhibited by the two races. Because sampling in the eastern Gulf of Alaska was conducted primarily in the months June-August, the gear was much more likely to encounter homeward-bound summer steelhead.

The CWT recoveries give some inference as to migration routes of summer steelhead returning to spawn. The group of steelhead taken in the Canadian experimental squid fishery that were identified as Columbia River summer steelhead were captured generally northwest of the river mouth and presumably were en route to the river. This would imply a rather direct route of migration from this offshore area. Other evidence, from inshore recoveries of CWT steelhead in coastal salmon fisheries of southeastern Alaska operating from late June to mid-September indicated a southward movement of summer steelhead along the coast. Of 184 CWT steelhead recovered in southeastern Alaska commercial fisheries during 1980-90, 169 originated from release sites in British Columbia, primarily Vancouver Island systems, six from southeastern Alaska releases, three from Washington, three from Idaho, and one from California (Didier 1990). The relatively fewer Columbia River origin steelhead taken in the inshore southeastern Alaska fishery versus the Canadian offshore experimental squid fishery may indicate a difference in path of approach to home streams between summer steelhead stocks of British Columbia and the Columbia River.

Light (1986, 1987b) used otolith microstructure differences between summer and winter steelhead sampled in coastal areas in an attempt to identify racial origins of several hundred steelhead sampled from the west-central and eastern North Pacific in 1983 and 1984. Some race-specific differences in otolith microstructure were detected, but when his results were applied to high-seas samples, no obvious differences in distribution of the two seasonal races were found, except for a slight predominance of summer steelhead in most areas. A high degree of overlap in the measurements between the two races limited the utility of the technique.

5. Distribution Relative to Sea Surface Temperature

In contrast to the broad east-west distribution of steelhead, the north-south distribution is more confined. From analysis of sea surface water temperatures at the point of capture of steelhead trout by salmon research vessels of Canada, United States, and Japan during the period 1953-1967, Sutherland (1973) determined that catches were made in areas with surface water that ranged in temperature from 5° to 14.9°C. The majority (61%) were caught in areas with surface waters of 8° to 11.4°C. The data suggested to him that the limits of steelhead trout distribution conform closely to the 5° isotherm on the north and the 15° isotherm on the south. Results differed considerably among vessels of the three nations, apparently reflecting season and area of sampling.

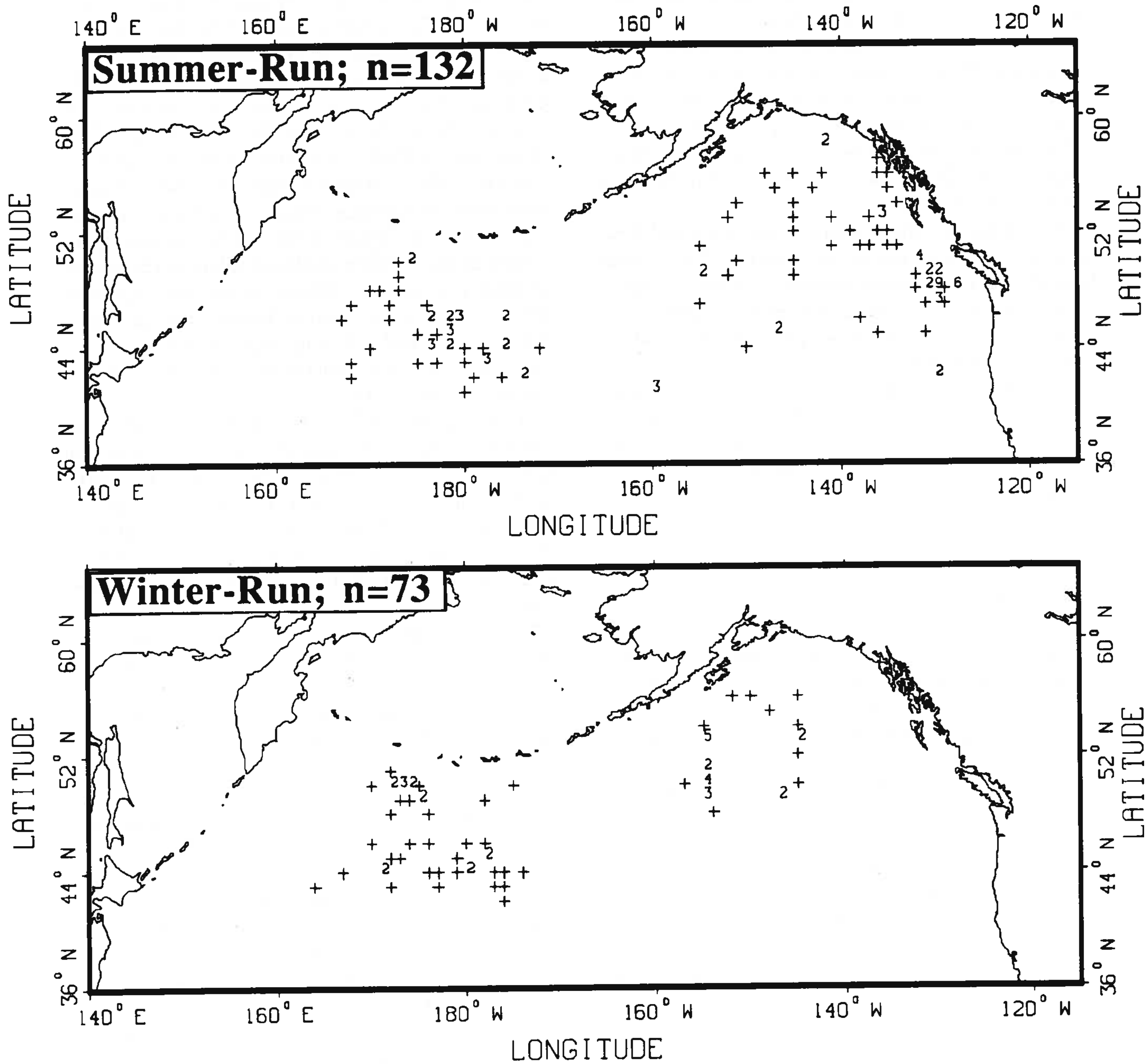


Figure 23. Comparison of ocean distributions of North American summer and winter steelhead trout, as evidenced by recoveries of disk tags and coded-wire tags. A plus (+) sign denotes a single fish. Numbers from 2 to 9 denote multiple fish at the same (1° latitude by 1° longitude) location.

From similar tabulations of Japanese salmon research vessel data, 1972-1982, Okazaki (1983) reported that the range of surface temperatures associated with presence of steelhead trout extended from 2.8° to 15.2°C, with greatest overall frequencies of catch within the range of 6° to 10°C.

Because temperature boundaries are important in determining the exposure of steelhead to offshore salmon or squid driftnet fisheries, especially in the southern limits of their range, a new analysis was conducted using steelhead CPUE of Japanese salmon research vessels. The analysis was restricted to the North Pacific-Bering Sea area between 170°E and 145°W. There were no northern or southern boundaries for exclusion of data. Data encompassed the years 1981-1989 and the months of May, June, and July, when research vessel sampling was most extensive. It is apparent from this analysis that there is a seasonal shift in distribution of steelhead with respect to sea surface temperature as ocean temperatures increase from late spring to summer (Fig. 24). Catches averaging over 0.04 steelhead per tan occurred in the one-degree temperature intervals between 6.0° and 8.9°C in May, between 7.0 and 9.9°C in June, and between 8.0° and 11.9°C in July. Peak CPUEs occurred in the interval 7.0-7.9°C in May, 8.0-8.9°C in June, and 9.0-9.9°C in July. No steelhead were caught at surface temperatures above 9.9°C in May, 12.9°C in June, or 13.9°C in July, or at surface temperatures below 4.0°C in May and June or 6.0°C in July (Table 7). As a result of this changing seasonal distribution with respect to temperature, the main body of feeding-migrating steelhead remain well north of the subtropical-subarctic boundary in the North Pacific, yet south of the Aleutian chain at least during this period of the year.

Although the main body of feeding steelhead is in North Pacific waters of 12°C or less, a contingent of summer steelhead returning to coastal streams must migrate through warmer waters. This was shown by steelhead catch data of the two principal vessels utilized during the 1985-87 Canadian experimental squid driftnet fishery conducted in international waters just off the coasts of Vancouver Island, Washington, and Oregon. Surface water temperatures ranged from 12.6° to 14.7°C at the beginning of sets in which 30 steelhead were caught in June; from 12.8° to 15.8°C for sets in which 625 steelhead were caught in July; and from 13.9° to 15.7°C for sets in which 148 steelhead were caught in August. CWT data from the catches indicated a high proportion of the steelhead were summer-run fish, many apparently en route to the Columbia River basin.

6. Vertical Distribution

The vertical distribution of steelhead is poorly known but circumstantial evidence suggests a preference for surface waters. Vertical distribution experiments by U.S. scientists using sunken gillnets in the eastern North Pacific showed that nine of ten steelhead were taken in the top seven meters of the water column (Godfrey *et al.* 1975). However, a single steelhead was taken in a sub-surface net set at 15-23 m, revealing that steelhead do occur in deeper waters. Steelhead are also found near the surface as they approach coastal streams. Six summer steelhead fitted with depth-sensitive sonic transmitters spent 72% of their time within 1 m of the surface as they moved through a coastal fjord en route to the Dean River, B.C. (Ruggerone *et al.* 1990).

For juvenile steelhead in coastal waters, the occurrence of insects, barnacle larvae, and some fish taxa associated with the neustonic layer in their diet suggested to Brodeur (1989) that juvenile steelhead forage to some extent in the surface layer on large or heavily-pigmented organisms. Because the diets of steelhead trout caught in open waters of the North Pacific more closely resembled the composition of neuston rather than of fauna sampled in oblique mid-water trawls, Pearcy *et al.* (1988) suggested that steelhead forage at the surface at night.

7. Rates of Travel at Sea

The limited information on movements of steelhead in offshore waters is derived from tagging studies. Steelhead tagged offshore with external tags and then recovered in spawning streams provide the best evidence of net rates of movement for steelhead at sea. Because the data are most useful for estimates of swimming speeds over approximate straight-line distances between release and recovery, fish recovered within 50 days of tagging were arbitrarily chosen as the most likely to have moved directly from the site of release to the point of recovery. Of the 78 steelhead tagged offshore that were recovered in North American streams or inshore fisheries (Appendix Table 2), 13 were recovered within this time frame. The average straight-line distance travel rate for these fish was 50 km/day. The fastest fish swam from the eastern Gulf of Alaska to the Columbia River, a distance of approximately 1,438 km, in 17 days at a rate of 85 km/day. The slowest fish took 50 days to travel 762 km at a rate of 15.2 km/day.

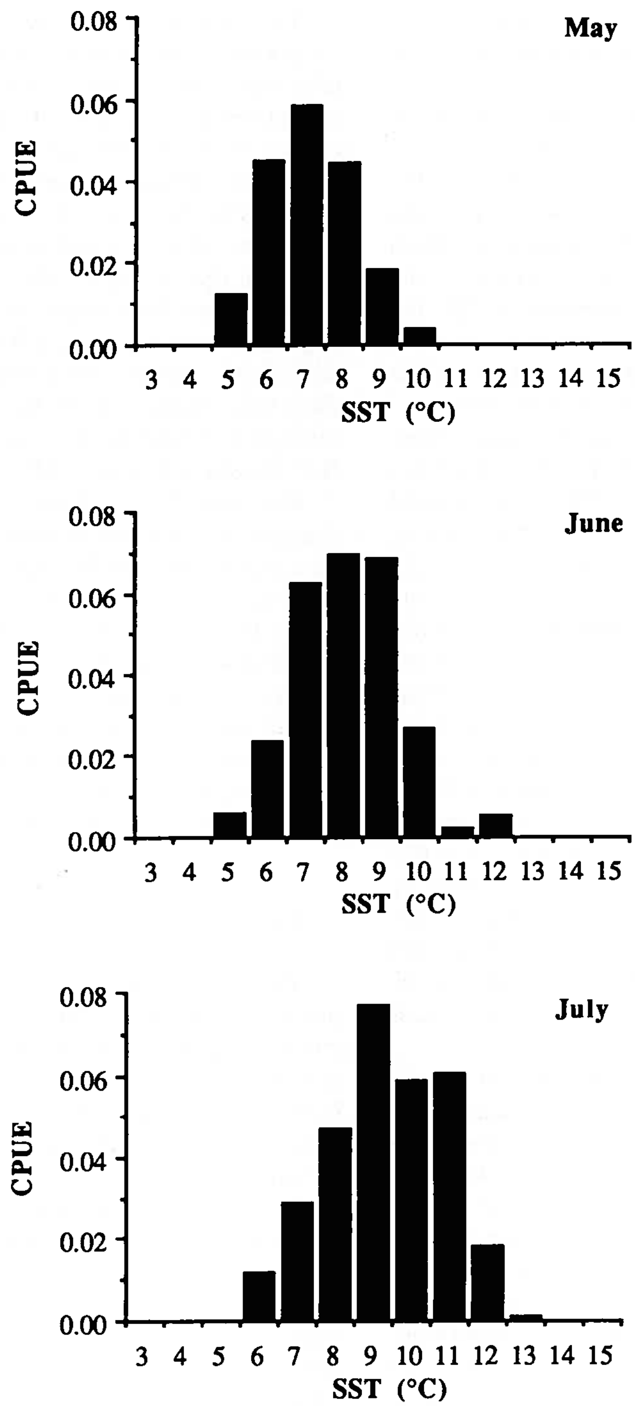


Figure 24. Distribution of steelhead catches by sea surface water temperature, May-July, based on mean catch per tan by Japanese salmon research vessels, 1981-1989, in the North Pacific-Bering Sea area between 170°W and 145°E.

Table 7. Steelhead mean catch per tan (CPUE) stratified by sea surface temperature in months May-July obtained in sampling by Japanese salmon research vessels in the North Pacific-Bering Sea area between 170°E-145°W, 1981-1989. (Temperature intervals are: 3=3.0-3.9, 4=4.0-4.9, etc.)

Month	SST (°C)	Catch (No. of fish)	Effort (tans)	CPUE
May	3	0	3,424	0.0000
May	4	2	9,274	0.0002
May	5	132	10,559	0.0125
May	6	154	3,424	0.0450
May	7	115	1,987	0.0579
May	8	58	1,314	0.0441
May	9	12	658	0.0182
May	10	1	262	0.0038
May	11	0	264	0.0000
June	3	0	640	0.0000
June	4	1	5,498	0.0002
June	5	53	8,757	0.0061
June	6	299	12,745	0.0235
June	7	436	6,966	0.0626
June	8	292	4,201	0.0695
June	9	138	2,017	0.0684
June	10	31	1,176	0.0264
June	11	2	939	0.0021
June	12	1	194	0.0052
June	13	0	383	0.0000
June	14	0	693	0.0000
June	15	0	788	0.0000
June	16	0	228	0.0000
June	20	0	228	0.0000
July	3	0	61	0.0000
July	5	0	3,001	0.0000
July	6	154	13,261	0.0116
July	7	603	21,002	0.0287
July	8	739	15,744	0.0469
July	9	840	10,919	0.0769
July	10	250	4,248	0.0589
July	11	157	2,604	0.0603
July	12	35	1,941	0.0180
July	13	2	1,662	0.0012
July	14	0	1,228	0.0000
July	15	0	1,291	0.0000
July	16	0	1,265	0.0000
July	17	0	203	0.0000
July	18	0	1,086	0.0000
July	19	0	689	0.0000
July	20	0	686	0.0000
July	21	0	362	0.0000
July	22	0	100	0.0000

Once steelhead reach coastal waters on their homeward migration, a combination of radio and sonic tagging studies provide insight into several important aspects of their inshore migratory behavior such as: how fast do the fish swim, what are their net travel rates, at what depth do they swim, are there differences in activity over the diel cycle, and what responses do the fish show to shorelines and tidal currents. In 1987, maturing steelhead were caught by purse seine in a British Columbia fjord, fitted with radio transmitters, and released 96.4 km from the mouth of the Dean River. Their mean travel rate to a receiving station at the river mouth was 17.2 km/d (N=19, range 6.5-42.0) (Ruggerone *et al.* 1990).

To provide detailed information on the movements in these coastal waters, in 1988 six steelhead were fitted with depth-sensitive ultrasonic transmitters and were followed for 1-2 d after release in the area where the radio transmitter study had been conducted. The six fish averaged 2.0 km/h but their net travel rates averaged only 0.8 km/h. The difference between swimming speeds and net travel rates reflects 1) changes in direction during active swimming, both in open water and after encountering land, 2) the effects of current velocities, and 3) a tendency to slow or stop at night. Nocturnal movement was reported to result primarily from drift with the tidal currents. These data suggested that daytime cues such as the sun and polarized light might be used in orientation and swimming activity (Ruggerone *et al.* 1990).

Little can be generalized about coastal migrations of steelhead from the single study cited above. However, the swimming speed (about 1 body length/second) and imperfect orientation are consistent with similar studies on salmon (pink: Stasko *et al.* 1973; sockeye: Madison *et al.* 1972; Quinn *et al.* 1989; chum: Ichihara and Nakamura 1982). Net travel rates of maturing salmon and steelhead seem to be slower in coastal waters than at sea. This difference may be related to physiological adjustment to fresh water and to the difficulties of negotiating the complex islands and inlets that typify coastal waters in British Columbia and southeastern Alaska.

8. Food and Feeding

In the only detailed study to date of the marine food of juvenile steelhead (age .0), Pearcy *et al.* (1990) found many types of fishes (mainly juvenile rockfishes) and euphausiids to be important prey by weight in steelhead sampled off the Oregon-Washington coasts, although decapod and barnacle larvae and hyperiid amphipods were important numerically (Brodeur 1990a). Euphausiids tended to dominate the diet of juvenile steelhead when abundant (such as in strong upwelling years) whereas fishes tended to dominate in other years (Brodeur 1990b). As noted earlier, juvenile steelhead apparently spend little time feeding in coastal waters and migrate directly offshore to the open ocean.

Studies of stomach contents and feeding habits of age .1 and older steelhead trout in epipelagic waters of the North Pacific Ocean have been confined primarily to the northeast Pacific Ocean (Taylor and LeBrasseur 1957; LeBrasseur 1966; Manzer 1968; Pearcy *et al.* 1988). In the most detailed study of steelhead food habits, Light (1985) examined 639 stomachs of steelhead collected in April-July 1983 by Japanese research vessels in the western North Pacific and Gulf of Alaska and in June-July 1984 by the mothership fishery in the western North Pacific. Although some investigators stratified analyses according to oceanic domains (LeBrasseur 1966; Light 1985; Pearcy *et al.* 1988), the definitions of these domains and boundaries at time of collecting are in some cases uncertain. Therefore, in the discussion to follow, reference to specific oceanic domains will be minimized.

In general, steelhead trout consume mainly large nekton, such as fish and squid, but they also utilize euphausiids, amphipods, pteropods, and pelagic polychaetes (Brodeur 1990a). Taylor and LeBrasseur (1957) found stomachs of steelhead collected primarily in the eastern half of the Gulf of Alaska contained mostly fish (63% by volume) and squid (31%), with shrimp and amphipods of minor importance. LeBrasseur (1966) also found fish to be the dominant food in coastal domain waters, but squid were more important in subarctic waters, and the diet was more mixed in transitional waters to the south. Pearcy *et al.* (1988) examined steelhead stomachs taken in driftnet collections from three years of north-south transects in the Gulf of Alaska. Major foods were fish, squid, euphausiids, amphipods, and polychaetes. In general, squid increased and fish and polychaetes decreased in importance with decreasing latitude along one transect.

In the more comprehensive study by Light (1985), steelhead were found to consume prey from five major taxonomic groups: fish, squid, polychaetes, crustaceans, and a group that contained miscellaneous taxa and unidentifiable contents (mostly pteropods). Fish were the most significant numerical component of the diet, accounting for 29% of the total prey abundance (all samples combined), and provided nearly half (47%) of the total biomass. Juvenile Atka mackerel (*Pleurogrammus monopterygius*) were the most important fish in the diet. Threespine sticklebacks (*Gasterosteus aculeatus*) were present in 8% of the samples. Fish of the family Myctophidae (lanternfishes) were also common in the diet. *Stenobrachius leucopsarus* was the most abundant representative of this family. *Tarletonbeania crenularis* and *Protomyctophum thompsoni* occurred in the samples infrequently.

Gonatid squids were the second most common prey category in the total sample. *Berryteuthis magister* was the most abundant species in this taxon (14% occurrence overall; 50% in the 1983 Western Subarctic), and was the largest squid found in the diet. This species represented 39% of the overall mean biomass of the stomach contents (83% of the 1983 Western Subarctic total). *Gonatus middendorfii* represented 7.5% of the overall mean biomass, and occurred in 3% of the stomachs. None of the other squid species were identified in more than 2% of the stomachs.

Fish and squid collectively contributed 98% of the total prey biomass, and accounted for 38% of prey abundance. The remaining biomass was distributed among taxa that consist of numerous individuals that exhibit low average biomass per individual, such as crustaceans and pelagic polychaetes. Crustaceans (mainly hyperiid amphipods) were found in 28% of the stomachs, and individual species of this taxon contributed between 2% and 46% of total prey numbers. In terms of biomass, however, crustaceans were not an important contributor to the diet (less than 1% overall). *Parathemisto pacifica* and *Hyperia medusarum* dominated the crustacean fraction of the diet. Other hyperiid amphipods and euphausiids were noticeable in the diet, but the majority of other crustacean taxa were rare. Pelagic polychaetes (family Alciopidae) were another prey category with high abundance and low biomass.

The results of comparisons between and within domains showed that steelhead feed on a variety of organisms, of which only a few are represented in the stomach of any one steelhead. The occasional superabundance or absence of prey in stomachs of steelhead taken together in the same haul suggests either that prey are evenly distributed and are selectively consumed by individual fish, or that prey are patchily distributed and steelhead feed opportunistically. Major between-year differences in food composition, probably reflecting food availability, also were noted by Light (1985) in western subarctic area samples. Squid were predominant (92% by weight) the first year of sampling, whereas fishes made up the bulk (>68%) of the steelhead diet the second year. Differences in time and locality of sampling may have contributed to these differences in food composition.

Steelhead were found to feed on the same types of organisms as the five species of co-occurring Pacific salmon. The principal difference between the diets of steelhead and salmon is the relative importance of different taxonomic groups. Some taxa, such as euphausiids, are known to be principal components of salmon diets (Allen and Aron 1958; Ito 1964; LeBrasseur 1966), yet are of minor importance to steelhead. In addition, steelhead were found to feed on pelagic polychaetes and threespine sticklebacks, whereas pelagic polychaetes are uncommon in the diet of Pacific salmon (Brodeur 1990a), and threespine sticklebacks have been reported only in coho salmon stomachs (Davis 1990).

In an examination of adult steelhead diets in coastal waters, Fresh *et al.* (1981) found that fish, including northern anchovy, juvenile chinook salmon, and smelt, comprised almost all the food items identified. Crab larvae were the only invertebrate prey identified.

9. Model of Ocean Migration of North American Steelhead

A composite picture of movements of North American steelhead during their marine residence can be created from the life history information presented earlier. Most steelhead smolts enter the sea in spring through early summer and move directly offshore. A small contingent comprised of age .0 juvenile half-pounders makes a brief foray into coastal marine waters off southern Oregon and northern California in late spring and early summer. However, by late summer of this first year at sea, most North American fish have moved well offshore and are concentrated in the western Gulf of Alaska. As fall approaches, they turn south and east toward the North American coastline. Half-pounders return to fresh water at this time.

The center of abundance and details of steelhead movements in winter are currently unknown. However, westward movement is apparently renewed during winter months, and by summer of their second year at sea, young steelhead are widely distributed over a large area of the North Pacific. Most are found between 165°W-130°W and 44°N-50°N. Except for half-pounders re-entering coastal waters, age .1 fish are probably relatively scarce near shore in spring. By late July of their second ocean year, the main group of age .1 steelhead has moved a considerable distance west and north and are more abundant south of the eastern Aleutian Islands and western Gulf of Alaska. In mid- to late-summer a reverse movement begins from west to east, although a portion of summer run steelhead returning to spawn at ocean age .1 must either remain near the coast or begin their reverse migration by late spring or early summer in advance of the main group of immature fish. The bulk of the high-seas population shifts south and east through fall and into winter. Winter-run fish bound for North American streams probably move with the main group of southeasterly travelling steelhead. This movement would place age .1 winter-run fish inshore along the coast on schedule to enter spawning streams in December-April.

The shoreward movement of maturing fish is not clearly shown by CPUE data, but is indicated by CWT data. At some point during the spring or summer of their second year at sea, many maturing summer steelhead depart the main group of migrating fish and move shoreward to arrive at and enter their home streams between May and November. To arrive on schedule, they must move opposite the direction of the main group of immature fish travelling north and west. Some summer-run fish may simply remain in eastern waters after the main group of fish departs. Half-pounders that begin to mature in their second summer at sea probably do not travel far before turning back toward spawning streams.

By the spring of their third year at sea, steelhead are once again broadly distributed across the North Pacific. A notable feature of this season is the appearance of post-spawning fish that are beginning to move offshore. The seasonal pattern of northwest to southeast movements of immature fish in their third and later years at sea resemble those of age .1 fish. Kelts lag behind maidens in their westward distribution but still travel a considerable distance offshore before returning to spawn again. Fish that spawn consecutively probably never return to the distant waters they may have travelled as maidens. South-eastward movements from late autumn into winter include the shoreward movement of maturing winter-run fish. This same seasonal cycle begins again for fish in the spring of their fourth year at sea and each year thereafter, although far fewer fish participate each additional year.

10. Comparison of Migratory Behavior with that of Pacific Salmons

Steelhead trout differ in their ocean migrations in several respects from the five Pacific salmon species common to North America and Asia, including behavior upon entry into the ocean, paths of migration, and distances travelled. Because the center of abundance of North American steelhead stocks is roughly from the Columbia River to the Skeena River, and the ocean distribution of these stocks is better known, it is convenient to compare their migration behavior with salmon stocks originating in the same general area.

Upon entry into the ocean, juvenile steelhead apparently move more directly offshore than do juvenile salmon. This has been indicated by the purse seine sampling conducted off the Columbia River and the Oregon and Washington coasts and from the Straits of Juan de Fuca northward into the Gulf of Alaska. In the former sampling area the juvenile steelhead were found to have moved farther offshore than juvenile chinook and coho in May-June, and were relatively much less abundant in the same areas in July and September. Miller *et al.* (1983) reported over 90% of the juvenile steelhead taken in late May-early June of 1980 to be 15-32 km offshore, whereas few of the juvenile coho and chinook were found at distances greater than 20 km offshore during this time or in early July and late August-early September. From sampling conducted in 1981, Wakefield *et al.* (1981) observed: "With the exception of steelhead, salmonids were characteristically absent from collections in clear, 'blue' oceanic water (Secchi disk reading >15 m). During May and June steelhead were most common in seine sets in clear water, 20 to 25 miles offshore in areas adjacent to the Columbia River. Steelhead were consistently found farther offshore than the other six salmonid species collected."

In sampling farther to the north, juvenile salmon have been found to move northward in a narrow belt close to shore (less than 37 km wide off the coast of southeastern Alaska), whereas steelhead trout were relatively rare in the coastal belt but occurred in a number of areas far offshore (Hartt and Dell 1986). Sockeye, chum, and pink salmon typically remained within the coastal belt during summer, some coho and chinook salmon migrated offshore early in their first summer at sea, and steelhead trout apparently migrated directly off-shore. A certain proportion of juvenile coho, chinook, and chum salmon are known to remain in Puget Sound or nearby coastal waters through the summer, but there is little evidence that juvenile steelhead remain inshore. By mid-summer, age .0 steelhead are found widely distributed in offshore waters north of 50°N, whereas the juvenile sockeye, chum, and pink salmon in particular are still restricted to the coastal band (Hartt and Dell 1986).

The marked change in overall high-seas distribution of age .0 steelhead from the March-May period to the June-August period indicates a much more rapid dispersal in a northwesterly direction than is indicated for age .0 salmon originating in the same coastal areas. Although age .0 steelhead were caught in summer as far west as 175°W-180° between 44°N and the Aleutians, we cannot be sure that these were North American steelhead, and the main concentration was still east of 165°W in summer and fall. Information is scant on distribution of steelhead during their first winter in the ocean, but it can be inferred from spring distribution of age .1 fish that they have moved generally southeastward toward the North American coast; hence, winter distributions of age .0 salmon and steelhead originating in the same coastal area may be similar.

There is a major difference between the extent of ocean migration of age .1 steelhead and that of the Pacific salmon species originating in the U.S. Pacific Northwest and British Columbia streams. Whereas age .1 steelhead of U.S. Pacific Northwest and Canadian origins are found in a band across the North Pacific nearly to 160°E, age .1 salmon remain in more easterly waters. Age .1 pink and coho salmon from Washington-British Columbia are distributed in Gulf of Alaska waters essentially east of 150°W (Godfrey *et al.* 1975; Takagi *et al.* 1981). Similarly, tag returns have shown that immature Washington-British Columbia chum (ages .1 and .2) are restricted primarily to Gulf of Alaska waters east of 156°W (Neave *et al.* 1976). Immature sockeye from British Columbia were more broadly distributed in the North Pacific, but extended only as far west as 177°E (French *et al.* 1976). Columbia River chinook salmon have been identified from tagging as far west as 176°W (Major *et al.* 1978), but there are indications from tagging and trawl sampling that age .1 immature chinooks from the U.S. Pacific Northwest-British Columbia area are less widely distributed, tending to remain in more inshore Gulf of Alaska waters and frequenting greater depths than do age .1 steelhead.

Age .1 pink and coho salmon mature and return to fresh water to spawn following their second summer at sea. A substantial portion of the steelhead population also spawns following their second summer at sea. It has not been determined with certainty whether these steelhead undergo the same extensive westward migration as the remainder of the age .1 steelhead population, or whether they may show more restricted migration. However, provisional maturity studies of steelhead sampled by Japanese research vessels on the high seas, primarily in the central and western North Pacific, indicated a substantial proportion of the age .1 steelhead taken in the summer samples were maturing (56% of males, 26% of females) (Okazaki 1984a). This suggests that even maturing age .1 steelhead exhibit the wide-ranging migration pattern of this species.

As with age .2 sockeye and chum salmon, which usually spend at least another year at sea, the seasonal distribution and migration of age .2 steelhead mirrors closely that of age .1 fish, except that kelt steelhead returning to the ocean have a more restricted distribution.

Size and growth rate may play a role in the migration rate and ultimate ocean distribution of age .0 salmonids. Steelhead smolts generally average about 160 mm in length, compared to coho and chinook, which are less than 100 mm. By time of the late May-early June coastal sampling in 1980, when the juvenile steelhead were found farther off the Columbia River mouth than the salmon, juvenile steelhead averaged 212 mm in length, compared with 166 mm for chinook and 172 mm for coho (Miller *et al.* 1983). By summer, sockeye, chum, and pink salmon sampled in the northeastern Gulf of Alaska were similar in length, and sockeye and pink salmon appeared to have similar rates of daily growth. Age .0 coho and chinook averaged considerably larger in length, as did the limited number of age .0 steelhead sampled (Hartt and Dell 1986: Fig. 43).

The initial large size at entry into the ocean and rapid growth rate probably are factors in the generally more extensive ocean migrations of steelhead trout. Examination of growth curves for sockeye, chum, pink, and coho salmon (Lander *et al.* 1966), chinook salmon (Major *et al.* 1978), and steelhead trout (Okazaki 1984a) indicate that by July 1 of the second summer at sea, steelhead trout average considerably longer than sockeye, chum, pink, and chinook, and about the same as coho salmon (Table 8). Okazaki (1984a) suggested that such rapid growth may be related to piscivorous feeding habits as indicated for coho and chinook salmon.

Ocean distributions of salmon and steelhead relative to sea surface temperature are comparable, but show some specific differences. In the central North Pacific, steelhead appear to move from south to north from May through July in a seasonal pattern that resembles the south to north movement of coho salmon.

Table 8. Approximate average size of age .1 salmonids as of July 1 of their second summer at sea.

Species	Length (mm)	Weight (g)	Reference
Sockeye	340	450	Lander et al. (1966, Figs. 27-28)
Chum	340	450	" " " "
Pink	475	1350	" " " "
Chinook	450	--	Major et al. (1978, Fig. 2, ocean type)
Coho	560	2400	Lander et al. (1966, Figs. 27-28)
Steelhead	580	2570	Length: Okazaki (1984a, Fig. 5) Weight: calculated from Margolis et al. (1989) for steelhead 575-585 mm. long

Distributions of chinook salmon and occasionally chum salmon originating in streams of the U.S. Pacific Northwest and British Columbia extend farther into Bering Sea waters than do steelhead. Distributions of sockeye, chum, chinook, and pink salmon from other areas also are more widespread in the Bering Sea than steelhead trout. In the central North Pacific, sockeye salmon tend to remain in cooler waters than do steelhead trout.

V. ABUNDANCE OF NORTH AMERICAN AND ASIAN STOCKS

1. Abundance of North American Steelhead

Sheppard (1972) estimated that 1.5 million adult steelhead were present along the North American coast (excluding Alaska). His results were based on catch estimates and the assumption that the combined annual sport and commercial harvest represented 50% of the total average run.

Light (1987a) estimated the average number of adult steelhead of both hatchery and wild origins that return annually to coastal streams (measured before harvest by inshore commercial and sport fisheries) from sport harvest data, counts at dams, and other run size information collected by resource agencies from 1970 through 1986. The estimates were rough because of the imprecise nature of the data and the wide interannual variability that is apparently typical of many steelhead populations, but they were based on the best information available and provided a general view of the magnitude of steelhead abundance. The total annual abundance of all North American stocks was estimated to be 1.6 million fish (Table 9). The Columbia River Basin is the center of abundance and produces an estimated 28% of the total coastwide population, followed by coastal Oregon (21%), California (17%), British Columbia (16%), coastal Washington and Puget Sound (13%), and Alaska (5%). The proportion of hatchery fish was estimated at 50% overall, and ranged from 3% in Alaskan populations to 73% in populations from the Columbia River Basin.

The similarity of estimates by Sheppard (1972) and Light (1987a) might indicate that there was little change or even an increase in the coastwide abundance of North American steelhead over the intervening 15 years. However, because the estimates are imprecise and based on different methods and data, to assess changes in the status of steelhead stocks through a direct comparison of these two studies is inadvisable. Sheppard (1972) predicted that the abundance of many steelhead stocks would decline over the years from increased fishing pressures, mortality at hydroelectric projects, or habitat degradation, but existing information is inadequate to fully determine the extent or direction of possible changes. Changes may not be reflected in overall numerical abundance, but may instead be manifested through localized shifts in abundance or through qualitative changes (e.g., shifts in the proportion of hatchery and wild fish) in certain populations.

(1) Artificial Production in North America

Artificial propagation is an integral part of the management of steelhead along the Pacific coast of North America. Production facilities first began rearing and releasing steelhead in the late 1800s, and are at present operating throughout the Pacific coast region from California to Alaska. Propagation programs are now designed primarily for the benefit of the recreational fishery to enhance natural production or to mitigate for losses resulting from habitat destruction or fish passage obstructions such as hydroelectric dams.

Table 9. Estimated average annual abundance of adult North American steelhead (hatchery and wild stocks) (from Light 1987a, with update of British Columbia data).

Region	Number of Adults (nearest 1,000)[2]		
	Hatchery (%)	Wild (%)	Total
Alaska	2,000 (3)	73,000 (97)	75,000
British Columbia[1]	34,000 (13)	225,000 (87)	259,000
Coastal Washington and Puget Sound	151,000 (70)	64,000 (30)	215,000
Columbia River Basin (Wash., Oregon, Idaho)	330,000 (73)	122,000 (27)	452,000
Coastal Oregon	222,000 (67)	108,000 (33)	330,000
California[3]	60,000 (22)	215,000 (78)	275,000
Total	799,000 (50)	807,000 (50)	1,606,000

1 Estimate from British Columbia Ministry of Environment, subject to revision as additional inventory information becomes available.
2 Rounding to the nearest 1,000 was for convenience only, and was not intended to reflect the precision of the estimates (i.e., the estimates could have as easily been rounded to the nearest 10,000). The figures shown could fluctuate by more than one-third from year to year. See text for discussion.
3 Does not include age .0 fish (half-pounders).

A comprehensive discussion of the history of North American salmonid artificial propagation from its beginnings in the last century through 1976 is provided by Wahle and Smith (1979).

Steelhead production facilities along the coast are operated by state, provincial, federal, and private groups. In larger facilities, typical operations include artificial spawning, incubation, and rearing to produce smolt-sized fish (approximately 160 mm) within one year. In smaller facilities, eggs or juveniles may be obtained from larger public hatcheries and then reared in small ponds, net pens, or raceways. Many facilities use broodstock derived from populations native to the stream on which the hatchery was built, but some use stocks derived from other systems (Crawford 1979). Some hatcheries, especially in British Columbia, routinely take eggs from naturally-produced "wild" broodstock.

In 1987 there were 84 hatcheries and at least 25 rearing, imprinting, or acclimation ponds involved in the propagation of steelhead along the Pacific coast of North America (4 in Alaska, 22 in British Columbia, 44 in Washington, 26 in Oregon, 4 in Idaho, and 9 in California). In Washington, Oregon, and Idaho, rearing facilities are concentrated within the Columbia River basin. Alaska's steelhead-producing hatcheries are located in the south-central and southeastern portions of the state (Van Hulle 1985). California's hatcheries are found no farther south than the San Francisco Bay area, and in British Columbia, steelhead hatcheries are concentrated in the southern part of the province and on Vancouver Island (Wahle and Smith 1979).

A measure of the magnitude of artificial production of steelhead is the number of migrant-sized juveniles produced by hatcheries each year. The number of steelhead smolts released annually from production facilities along the Pacific coast of North America increased from approximately 2.8 million in 1960 to 30 million in 1987, and averaged 24.6 million in the decade 1978-1987 (Fig. 25, Table 10). States or provinces contributed to this average production as follows: Idaho (41.9%), Washington (27.6%), Oregon (18.4%), California (9.4%), British Columbia (2.5%), and Alaska (0.2%). Facilities in the Columbia River basin accounted for nearly two-thirds of the average coastwide production. Approximately 738,000 adults would be produced annually from these smolt releases, assuming a 3% smolt-to-adult survival rate for hatchery-reared fish. This figure is close to an earlier estimate (Light 1987a) of the coastwide abundance of adult hatchery fish (approximately 750,000), and indicates that artificially-produced steelhead contribute substantially to the total North American steelhead population.

In their examination of escapements for 85 populations of naturally-produced steelhead along the Pacific coast of North America, Konkel and McIntyre (1987) concluded that most were declining. The future demand for steelhead as a gamefish will likely increase rather than diminish (Billings 1987), and unless habitat enhancement or other measures result in increased wild production, the reliance on hatchery-produced steelhead to enhance natural production will similarly increase (Northwest Power Planning Council 1986).

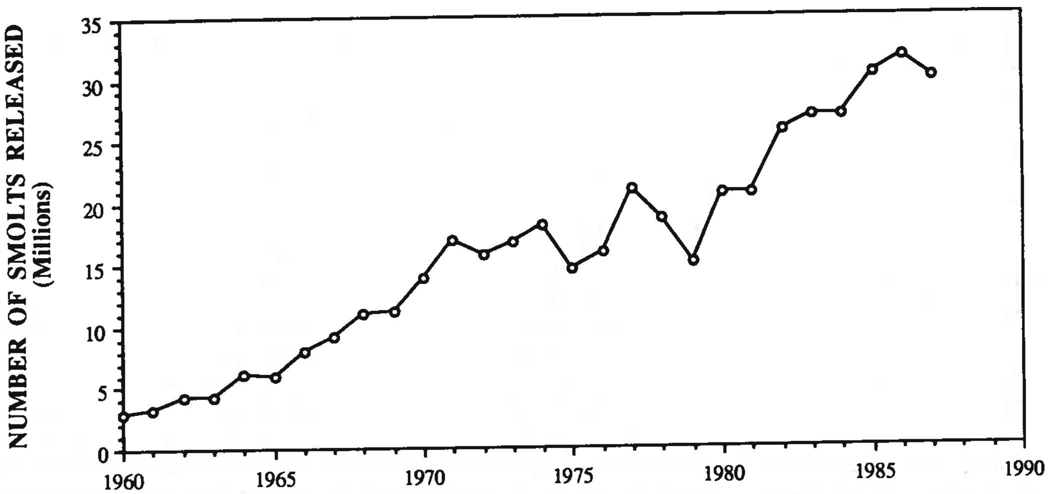


Figure 25. Number of steelhead smolts released annually by production facilities along the Pacific coast of North America (*from* Light 1989b).

Table 10. Thousands of steelhead smolts released annually by production facilities along the Pacific Coast of North America.

Year	Alaska	British Columbia	Coastal Washington	Coastal Oregon	Columbia River Basin: Washington	Columbia River Basin: Oregon	Columbia River Basin: Idaho	Total Columbia River Basin	California	Coastwide Total
1960	0	0	1128.2	295.5	681.5	406.2	0	1087.7	315.1	2,826.5
1961	0	0	867.4	436.9	1004.1	370.8	0	1374.9	518.1	3,197.3
1962	0	0	1215.3	662.4	1071.0	1096.9	0	2167.9	187.3	4,232.9
1963	0	0	1442.6	591.8	1335.9	752.8	0	2088.7	72.3	4,195.4
1964	0	0	1326.8	845.9	1839.6	831.0	0	2670.6	1163.1	6,006.4
1965	0	0	1336.7	841.5	2120.4	817.2	24.1	2961.7	736.7	5,876.6
1966	0	0	1477.2	823.0	2054.6	1007.0	138.8	3200.4	2436.2	7,936.8
1967	0	0	1230.2	905.7	2453.1	1119.8	1364.8	4937.7	2027.0	9,100.6
1968	0	0	1498.2	1206.6	2697.1	1371.2	2034.2	6102.5	2129.7	10,937.0
1969	0	0	2084.9	1412.8	2731.5	1413.6	1732.5	5877.6	1818.8	11,194.1
1970	0	0	1932.0	1742.6	3692.2	1168.7	3173.3	8034.2	2188.5	13,897.3
1971	0	0	1945.7	1750.1	3306.8	1189.8	4932.0	9428.6	3752.5	16,876.9
1972	0	0	1847.3	1839.1	3176.1	1646.8	2585.1	7408.0	4552.8	15,647.2
1973	0	41.7	2217.8	1731.1	3394.5	1833.5	4619.6	9847.6	2953.8	16,792.0
1974	0	23.0	2061.5	1609.0	2805.2	2047.3	6340.0	11192.5	3222.7	18,108.7
1975	17.5	25.8	2146.8	1662.0	2888.5	1726.5	3511.6	8126.6	2524.3	14,503.0
1976	16.5	80.5	2696.4	1597.2	2786.7	1960.9	3774.4	8522.0	3026.3	15,938.9
1977	0.6	61.5	6031.4	2212.2	3235.3	1749.7	5609.0	10594.0	2064.0	20,963.7
1978	10.7	143.3	2861.2	2785.4	3155.7	3007.2	4706.1	10869.0	1903.6	18,573.3
1979	0	466.4	2927.8	317.0	3333.8	287.7	5141.7	8763.2	2512.7	14,987.1
1980	5.4	415.1	3388.1	2397.3	3248.3	1885.3	7606.9	12740.5	1761.3	20,707.7
1981	10.4	482.7	3316.7	2163.3	3555.2	1989.4	6824.5	12369.2	2336.6	20,678.9
1982	52.1	708.1	3112.7	2345.5	2579.1	1850.5	12865.3	17295.0	2180.4	25,693.8
1983	45.3	693.9	2729.2	2298.1	3972.2	2394.0	11972.3	18338.5	2724.6	26,829.6
1984	22.2	863.7	3238.3	2219.5	4628.3	2704.0	10797.6	18129.9	2422.1	26,895.8
1985	195.0	866.9	2850.0	2425.5	4046.5	2775.2	14215.6	21037.3	2889.9	30,264.7
1986	105.8	724.6	3143.3	2360.0	4281.2	2639.2	16059.8	22980.3	2276.8	31,590.8
1987	171.4	790.9	2662.9	2520.6	4785.1	4003.3	13008.4	21796.8	2036.1	29,978.8
Production Average:	50.2	425.9	2311.3	1571.4	2887.8	1644.5	6219.0	9640.8	2455.5	15,872.6
1978-87 Average:	61.8	615.6	3023.0	2183.2	3758.6	2353.6	10319.8	16432.0	2304.4	24,620.1
Percent:	0.2	2.5	12.3	8.9	15.3	9.5	41.9	66.7	9.4	100.0

2. Abundance of Asian Steelhead

Limited information (Savvaitova *et al.* 1973 U.S.S.R. fishery research agency TINRO, pers. comm.) suggests that the Asian population of steelhead consists of small runs to a few river systems, and is smaller than the combined North American population by orders of magnitude (Harris 1988). No artificial rearing of Asian steelhead is known to occur.

VI. CATCH OF STEELHEAD

1. Inshore Catch of Steelhead

(1) North American Catch

(a) Recreational Catch

Recreational fishing is the primary means by which steelhead are caught in North America. Virtually all of the steelhead caught by recreational anglers are taken in fresh water, with only a small fraction being caught in marine waters, and these are usually caught incidentally during fisheries for Pacific salmon (Berry 1980). Fisheries management agencies in Alaska, British Columbia, Washington, Idaho, and Oregon monitor the annual catch of steelhead using some form of a punchcard, creel census, or survey questionnaire. A substantial number of steelhead are caught each year in California, but this state currently has no monitoring program for steelhead. A punchcard is basically a record of an angler's catch that is maintained by the angler and returned to the local management agency at the conclusion of a fishing season. Numbers derived from the returned punchcards are then corrected for a non-response bias and an overall catch estimate is produced. A creel census is a direct survey of a sample of anglers during the fishing season. The numbers obtained from the survey(s) are expanded by the total number of anglers in an area over the fishing season to estimate the total catch for that area. Creel census information is often used to supplement or refine estimates derived by other methods. A mailed questionnaire solicits fishing effort and catch information from a sample of steelhead license owners (Billings 1987). A combination of a questionnaire and a creel census is used in Alaska (Mills 1987) and British Columbia (Billings 1987). A punchcard system and creel censuses are used in Washington (Washington Department Wildlife 1988a) and Oregon (Eden and Swartz 1987), and a creel census is used in Idaho (Hall-Griswold and Cochnauer 1987; McArthur 1988).

Based on the above methods, estimates of recreational catches of steelhead in North America for run years 1980-81 to 1987-88 (where data were available) ranged from approximately 235,000 to 449,000 fish (Table 11).

Table 11. Estimated annual steelhead catch[1] (number of fish) by recreational fisheries along the Pacific coast of North America[2], 1980-81 through 1987-88 run-years. Data sources: Alaska Dept. Fish and Game, British Columbia Ministry of Environment and Parks, Washington Dept. of Wildlife, Idaho Dept. of Fish and Game, Oregon Dept. of Fish and Wildlife.

	Region					
Run-Year[3]	Alaska[4]	British Columbia	Washington	Idaho[4]	Oregon	Combined
1980-81	4,832	10,941	117,182	9,000	159,116	301,071
1981-82	3,264	9,965	115,756	13,000	147,365	289,350
1982-83	3,673	13,483	96,091	20,500	101,393	235,140
1983-84	5,364	15,084	105,781	32,000	121,291	279,520
1984-85	6,539	18,909	175,371	25,000	223,548	449,367
1985-86	4,723	19,426	137,121	34,364	153,288	348,922
1986-87	5,850	24,777	171,813	39,893	163,737	406,070
1987-88	5,914	16,725	127,136	30,102	162,908	342,785

1 Includes only fish caught and killed.
2 Alaska to Oregon only California catch data not available.
3 A run-year includes summer-run fish caught in a single calendar year and winter-run fish caught in adjacent calendar years (e.g., the 1980-81 run-year includes the 1980 summer-run catch and the 1980-81 winter-run catch).
4 Calendar year totals for the first year in the sequence only (e.g., in run-year 1980-81, only 1980 calendar year totals are included).

These data represent the fish caught and killed by recreational fishermen. A growing number of steelhead anglers are adopting the strategy of releasing fish unharmed rather than killing them, regardless of whether or not the fish are legally harvestable. Recent estimates for the Idaho sport fishery (McArthur 1988) indicate that up to 50% of the fish that are caught are released. In British Columbia, over 80% of the catch is released (Billings 1987). No information is available that allows an estimation of what percentage of these released fish are recaptured or how frequently, but Billings (1987) speculated that this pattern of fishing was responsible for recent increases in total catch. These data suggest that the value of the North American recreational steelhead fishery should be based on the total fish hooked and landed, rather than simply on fish that were caught and killed. For this reason, the recreational catch figures used in this report likely represent an underestimation of the true fishery value.

(b) Commercial/Tribal Catch

The only inshore commercial fisheries that are directed toward steelhead are those of the native North American Indian tribes in Washington and the Columbia River basin. Most of these tribal-caught steelhead are taken in fresh water or in river estuaries using gillnets (Bijsterveld and James 1986; Columbia River Inter-Tribal Fish Commission unpublished report; Washington Department of Wildlife 1988b). Other commercially-caught steelhead are taken incidentally during fisheries for Pacific salmon (Berry 1980; Alaska Department Fish and Game unpublished data; Maureen Kostner, Canada Department Fisheries and Oceans, personal communication). This incidental catch occurs both in rivers (e.g., the lower Columbia River) and in inshore marine areas (e.g., Puget Sound and southeastern Alaska). The majority of the incidental harvest occurs in Alaska, British Columbia, coastal Washington and Puget Sound, and the Columbia River basin; however, steelhead are probably also caught incidentally during most of the coastal marine salmon fisheries. Estimated commercial and tribal catches of steelhead in North America for run-years 1980-81 to 1987-88 ranged from approximately 91,000 to 275,000 (Table 12).

The estimated total annual inshore catch of North American steelhead (both recreational and commercial) ranged from 331,000 to 703,000 for run-years 1980-81 to 1987-88.

(2) Asian Catch

No data on inshore commercial or recreational catch are available.

2. High-Seas Catch of Steelhead

(1) Japanese High-Seas Salmon Fisheries

The extensive intermingling of North American and Asian steelhead trout with Pacific salmons in the North Pacific Ocean has rendered them vulnerable to incidental capture by the high-seas salmon driftnet fisheries of Japan operating in the western North Pacific. Because of the seasonal changes in the high-seas distribution pattern of steelhead, interception rates in the driftnet fisheries vary with time and area of fishing effort. CPUE records from salmon research vessel operations have shown that during the historic May-July commercial fishing season, steelhead have been more abundant in the area of the landbased driftnet fishery operating south of 46°N than in the mothership fishery area to the north. The overall distribution of steelhead tends to shift northward during this period, such that the latitudinal center of distribution in waters west of 175°W shifts from about 44°N in May to about 49°N in August (Harris 1988, estimated from charts in Okazaki 1983).

Records of steelhead catch in Japan's landbased and mothership driftnet salmon fisheries were not available prior to the 1980s, and can only be estimated based on CPUE data from research vessels fishing commercial-type driftnets coupled with effort data records from the commercial salmon vessels fishing in the same time-area zones. Since 1981, however, at the request of INPFC member nations, statistics of steelhead trout catches by the landbased fleet have been reported annually. For the mothership fishery, operating in the North Pacific largely in the U.S. EEZ, Japan acceded to the request by the United States that incidentally-caught steelhead not be retained for commercial processing. In 1983, however, the United States requested that for research purposes all steelhead caught incidental to salmon during fishing operations of the mothership salmon fleets within the U.S. EEZ be returned to the motherships for collection or sampling by U.S. foreign fishery observers. From 1984 through 1986 all steelhead returned to the motherships were frozen whole and later shipped to the United States for detailed biological sampling.

Table 12. Estimated commercial and subsistence harvest (number of fish) of steelhead along the Pacific coast of North America[1], 1980-81 through 1987-88 run-years. Washington catches include fish caught by tribal fisheries in the Columbia River Basin. Data sources: Alaska Dept. Fish and Game, Department of Fisheries and Oceans Canada, Washington Dept. of Wildlife, Columbia River Intertribal Fish Commission.

Region (fishery)	Run-Year[2]							
	1980-81	1981-82	1982-83	1983-84	1984-85	1985-86	1986-87	1987-88
Alaska[3] (comm.)[4]	1,530	898	1,989	5,429	7,080	9,530	53,127	3,620
British Columbia[3]								
(comm.)	12,306	17,532	21,129	13,245	30,848	46,775	35,340	16,587
(tribal)	6,221	7,203	12,911	18,228	31,469	12,998	14,058	9,802
(combined)	18,527	24,735	34,040	31,473	62,317	59,773	49,398	26,389
Washington								
(tribal)	75,317	65,198	60,281	80,224	184,307	173,223	172,104	177,425
Coastwide Total	95,374	90,831	96,310	117,126	253,704	242,526	274,629	207,434

1 Alaska to Oregon only California catch data not available.
2 A run-year includes summer-run fish caught in a single calendar year and winter-run fish caught in adjacent calendar years (e.g., the 1980-81 run-year includes the 1980 summer-run catch and the 1980-81 winter-run catch).
3 Calendar year totals only.
4 Conservative estimates.

(a) Japanese Landbased Driftnet Salmon Fishery

The reported catch by the landbased fishery for the years 1981-1989 is given in Table 13 by 10-day reporting period. Catches declined in recent years with the decline in total fishing effort. Catches ranged from a high of about 29,000 steelhead in 1983 to 3,000 in 1989.

Steelhead catches in the landbased driftnet fishery were concentrated between 42°N and 46°N, 165°E and 175°E. Fifty percent of the steelhead catch in these years was taken in area E7042, followed by areas E6542 (22%) and E7044 (17%). The latter area was closed after mid-June each year, which reduced the potential catch there.

Table 13. Reported catch of steelhead trout (numbers of fish) and fishing effort (tans x 1000) by the Japanese landbased driftnet salmon fishery by period, 1981-1989. Source of statistics: Fisheries Agency of Japan (1982-1990).

Year	May			June			July		Total Catch	Total Effort
	Early	Mid	Late	Early	Mid	Late	Early	Mid		
1981[1]	6	19	18	272	4,991	3,635	3,635		15,470	3,234
1982	350	997	3,492	1,135	3,888	8,674	8,167		26,703	2,962
1983	541	3,330	4,971	606	7,710	5,819	4,568	1,366	28,911	3,114
1984		1,872	4,623	4,226	1,978	1,314	879		14,892	2,824
1985				141	3,324	4,701	3,856	2,050	14,072	2,442
1986				757	3,439	3,131	922		8,249	1,436
1987			0	2,360	4,099	1,044	215		7,718	1,156
1988			42	2,253	2,747	209			5,251	793
1989			275	1,588	1,189				3,052	781

1 Data were collected from 139 of the 209 vessels fishing in 1981. Harris (1989) estimated a total catch of 23,000 steelhead in 1981.

Light (1989a) compared steelhead catches by the landbased fishery (1981-1986) with estimated catches for the fishery derived from a combination of CPUE data (fish catch per tan of commercial-mesh gillnet) from Japanese research vessels operating in the same areas as the commercial fleet and the known effort expended by the commercial fleet in each year steelhead catch data were available. The average reported catch by the Japanese landbased driftnet salmon fishery for the entire 6-year period (19,311) was approximately 10% less than the estimate. Reported catches exceeded estimates in 1982, 1983, and 1984 by as much as 163% (range = 108% to 163%), but in 1981, 1985, and 1986, the reported catches were only 51% to 70% of the estimated catches. The disparities between estimated catches based on research vessel catches and catches reported by the commercial fleet suggest that the research and commercial catch statistics were not directly comparable (Light 1989a).

(b) Japanese Mothership Salmon Fishery

Without direct catch records of steelhead trout for the mothership fishery, one alternative was to use the records of return of steelhead taken by catcherboats to the motherships for examination by U.S. observers as probable minimal estimates of catch. A second alternative was to base catch estimates on average 1981-1985 CPUE data from Japanese research vessels. These comparisons were made for the years 1984-1986 (Table 14). In June of each year, few steelhead were returned to the motherships, and little catch was expected because the steelhead were still in more southern waters. In July, the observed catch represented between 10% and 55% of the expected landings (28% overall). The mothership fleets expended greater effort than research vessels in most times and areas, and as a result, the commercial fleets often landed fish where research vessel CPUE was zero.

A second comparison was made using the data for times and areas within years where both research vessel data and catch returned to the motherships were available. Results of the mothership catcherboat effort data applied to research vessel CPUE data in 1984 and 1986 indicated that in 1984 a catch of approximately 3,000 steelhead would have been expected (Table 15). This is considered a minimum estimate, because mothership catcherboats landed steelhead in areas where there was no research vessel effort for comparison. The reported catch was 214 steelhead. In the two strata where both commercial and research vessels operated in 1986, no steelhead were caught by research vessels, whereas 41 steelhead were caught by the mothership fleet. The small number of strata (8) available precluded a statistical comparison of the mean CPUE between commercial and research vessels in 1984, but the large differences between estimated and reported catches in strata where steelhead were landed suggest that in this year some steelhead were overlooked in the mothership catcher-boat catches.

Although the data on recent incidental catches of steelhead by catcherboats of the mothership driftnet salmon fishery are scant, it is apparent that the mothership fishery interception of steelhead has been of a much lower magnitude than the landed catch in the landbased salmon fishery.

(2) Flying Squid Fishery

The extensive high-seas driftnet fishery for flying squid (*Ommastrephes bartrami*) is conducted by vessels of Japan, Taiwan, and South Korea in the central North Pacific generally south of the main concentration of salmonids. However, because the driftnet mesh sizes used are similar to those in Japan's directed salmon fisheries, because distributions of salmonids and flying squid overlap to some extent, particularly in the northern portion of the squid fishing area (the degree of overlap depends on ocean temperatures), and because of the very large combined driftnet effort in the squid fishery, there is concern over the potential magnitude of incidental interceptions of salmon and steelhead trout in the squid driftnet fishery. The Japanese fishery and history of regulations are described by Yatsu (1990). During the June-December fishing season the northern boundary of the fishery shifts seasonally between 40°N and 46°N, approximately in accord with summer warming and autumn cooling of surface waters.

Harris and Kautsky (1987) analyzed salmonid catch data and flying squid incidental catch by Japanese research vessels in the area of the northern boundary of the authorized Japanese squid driftnet fishery area at that time (July and August northern boundaries were the same as October and November boundaries until 1989). Steelhead were not encountered by the research vessels within the squid fishery area in any month from June to August 1981-1985, but were caught near the northern border in all three months. When salmonid species co-occurred with flying squid, both the salmonid species and the squid were in low abundance.

Table 14. Comparison of estimated[1] catch with reported[2] catch for steelhead taken by Japanese commercial salmon mothership fleets, 1984-1986 (*from* Light 1989a).

Year	Month	Total Catch: Estimated	Total Catch: Reported
1984	June	0	6
	July	1,332	390
		1,332	396
1985	June	0	2
	July	699	381
		699	383
1986	June	0	13
	July	1,137	103
		1,137	116
	Grand Total	3,168	895

[1] Estimated from mothership effort and average (1981-1985, unweighted) steelhead CPUE data (fish per tan of commercial-mesh gillnet) from Japanese research vessels operating in the same time-area strata as the mothership fleets.
[2] "Reported" catch refers to the number of steelhead taken during fishing operations within the U.S. 200-mile limit that were returned to the motherships for sampling by U.S. foreign fishery observers. The mothership fishery does not officially record or report the numbers of steelhead caught in U.S. waters.

Table 15. Comparison of reported and estimated steelhead catches for times and areas where both motherships and research vessels operated in July, 1984 and 1986 (*from* Light 1989a).

Year	Month	10-day period	INPFC 1°X5° area	Total Catch: Estimated[1]	Total Catch: Reported[2]
1984	July	1	E7052	0	0
			7051	0	0
			6552	0	0
			6551	0	0
			6550	0	0
		2	7050	1,253	83
			7049	1,657	130
			7048	181	1
				3,091	214
1986	July	1	7050	0	11
			7049	0	30
				0	41

[1] Estimated from Japanese research vessel CPUE (fish/tan of commercial-mesh gillnet) multiplied by mothership effort (tans).
[2] "Reported" catch refers to the number of steelhead taken during fishing operations within the U.S. 200-mile limit that were returned to the motherships for sampling by U.S. foreign fishery observers. The mothership fishery does not officially record or report the numbers of steelhead caught within U.S. waters.

The authors concluded that the (pre-1989) northern boundary of the Japanese squid driftnet fishery area was effective in limiting the incidental catch of salmonids, including steelhead, to fairly low levels. These conclusions reflect the views of Takagi (1983) and Ogura and Takagi (1987), as confirmed by Ito and Murata (1989). Harris and Kautsky (1987) suggested, however, that some catch could occur in the area, particularly in cold years when water cooler than 15°C extends into the fishery area.

Walker and Burgner (1985), in an analysis of steelhead distribution with respect to surface temperature, concluded that historic temperature records indicate that steelhead are unlikely to be encountered along the northern border of the squid fishery zone in June and August, that they may be encountered in very low densities in July, and that there is the potential for more significant incidental catches in September. They cautioned that October-December temperatures do not preclude the presence of steelhead in the squid fishery area, but information on the distribution of steelhead during those months was scant.

Ignell (1988) reported on 36 research vessel operations fishing in the northernmost 0.5° latitude of the squid regulatory area. These research cruises included Canadian, Japanese, Taiwanese, and Republic of Korea vessels. They covered primarily the years 1986 and 1987, when cool waters extended farther south than in average years, increasing the potential for encounter of salmonids within the squid fishery boundary. In the 36 operations a total of 170 km of gillnet was fished. One steelhead and 428 salmon were caught. Eighty two percent of the gillnet operations occurred in sea surface temperatures less than 15°C. West of 175°W the salmonid catch per tan was 22 times that east of 175°W. The steelhead was caught in early June 1987 in 11.9°C water. The 1987 June surface temperatures were about 3°C colder than average.

Table 16 is a compilation of the combined effort in tans and steelhead catch/100 tans of the Japanese salmon research vessels (1981-1987) and squid research vessels (1984-1989), west and east of 170°W by latitude and month, June through November. One steelhead was captured in the area of the squid driftnet fishery east of 170°W in August, but latitudes of highest CPUE were consistently well north of the monthly northern boundaries of the fishery in June-August. No steelhead were taken in the limited sampling in September-November.

The above results are in accord with expected distribution based on sea surface temperature, which indicates that in June and July few steelhead would be expected in waters above 12°C. Multi-year means and range of the 12°C sea surface isotherm positions between 170°E and 145°W for the months of June and July, 1972-1980, fell north of the northern boundary of the squid fishery. (See Figs. 2 and 4, Burgner and Meyer 1983).

Additional data are being collected by observers aboard vessels of the commercial squid driftnet fleets. No steelhead were reported in monitored catches in 1989, but the time-area coverage of the fleet was limited. Observer coverage of the squid driftnet fishery is continuing and is expected to provide sufficient data to quantify potential incidental take of steelhead trout. Because of the more northern center of distribution of steelhead trout, catches within the designated boundary of the squid fishery are expected to be minimal in normal years, despite the very large quantity of gear fished, but could occur in cold water years when salmonids, including steelhead, would have a more southerly distribution that would extend south of the northern squid fishery boundary and would overlap with the northern area of squid distribution.

3. Effects of Regulatory Changes on High-Seas Catches of North American Steelhead

Harris (1988) provided a history of the Japanese high-seas salmon fisheries, a review of changes in the INPFC and U.S.S.R.-Japan treaties and how they have affected the fisheries and catches, and a qualitative analysis of how the level of high-seas catch of salmonids of North American origin has changed. Based on evidence from tagging and parasite data he concluded that "North American steelhead range across the present mothership fishery area and across some of the most heavily fished sectors of the landbased fishery area, as far west as about 167°E." The more recent evidence from tagging and parasite studies shows that North American steelhead occur as far west as about 162°E. Harris (1988) concluded that closure of the area east of 175°E in 1978 served well to protect North American steelhead from high-seas capture (because abundance of steelhead in this area is generally higher than west of 175°E), but that there was potential for increased steelhead catches in the areas remaining open to the mothership and land-based fisheries.

Beginning in 1989, Japan shifted the northern boundary of the squid driftnet fishery northward in

July and August. Although this change increases the probability of incidental interception of steelhead trout, there are insufficient data on steelhead CPUE in these areas to quantify the effect of the regulatory change. Increased regulatory control to minimize out-of-area fishing by squid vessels of the nations engaged in the fishery probably is of greater consequence.

Table 16. Driftnet effort in tans and mean catch of steelhead per 100 tans in combined research vessel sampling of Japanese salmon research vessels, 1981-1989, and squid research vessels, 1984-1989, between 40°N and 54°N, 170°E and 145°W. (Catch and effort data were provided by the Fisheries Agency of Japan.) A = total tans fished B = catch/100 tans. Horizontal bars denote monthly northern fishery boundary.

	June		July		August		September		October		November	
N.	A	B	A	B	A	B	A	B	A	B	A	B
170°E - 170°W												
54	1064	0.00	2083	0.10								
53	1216	0.00	264	0.00								
52	920	0.00	132	0.00								
51	1613	0.00	4334	0.39								
50	3234	0.00	8832	1.25								
49	2782	0.04	2581	1.74								
48	2469	0.61	3023	7.61	1648	5.40						
47	2751	2.73	3837	7.92	652	4.14						
46	2502	4.92	5176	8.64	310	2.90	180	0.00				
45	3801	7.60	5147	8.00	565	1.95	60	0.00			184	0.00
44	3419	9.04	3865	4.01	397	0.00	120	0.00			200	0.00
43	3600	8.22	4764	0.65	526	0.00	120	0.00	—		84	0.00
42	2419	5.70	2651	0.19	690	0.00	220	0.00	100	0.00	184	0.00
41	1160	0.43	2855	0.00	591	0.00			100	0.00	100	0.00
40	574	0.00	2308	0.00	591	0.00			100	0.00	184	0.00
170°W - 145°W												
54	220	0.00	645	9.92								
53	110	0.00	557	9.69								
52			637	13.19								
51			872	19.50								
50			742	35.98								
49			346	32.08								
48			345	9.86								
47			219	19.18	392	0.51						
46			300	7.33	897	0.22				180	0.00	
45	100	8.00	319	2.82	797	0.13	159	0.00	59	0.00		
44			675	1.19	699	0.00	159	0.00				
43	200	1.00	500	0.00	496	0.00	60	0.00				
42			1075	0.00	598	0.00	338	0.00				
41	100	0.00	774	0.00	298	0.00	60	0.00				
40	100	0.00	399	0.00	200	0.00						

VII. SUMMARY

Steelhead trout, the anadromous form of rainbow trout (*Oncorhynchus mykiss*), originate in Pacific coast streams of North America and Asia (USSR). Their spawning range in North America extends from Santa Monica Bay, California to the north side of the Alaska Peninsula and Unimak Island. They have not been reported in Bristol Bay drainages. Their center of abundance is the Columbia River basin and adjacent rivers to the north and south. In Asia, steelhead trout are reported in scattered streams along the northern Okhotsk Sea coast, in western Kamchatka, and in rivers of east Kamchatka south of the Ozernaya River. They possibly occur in the Commander Islands. They are most abundant in streams of western Kamchatka between the Penzhina and Bol'shaya Rivers.

Seasonal races are defined by the timing of adult returns to spawning streams and by the state of sexual maturity upon entry into fresh water. The gonads of summer steelhead (including fall run fish) are only slightly developed when they enter fresh water, whereas winter steelhead (including spring run fish) have well developed gonads when they enter fresh water. All seasonal races spawn at approximately the same time (principally January to May). Although both races are widespread, summer and winter steelhead spawning distributions do not completely coincide.

In North America, two major genetic groups, inland and coastal, have been defined on the basis of allele frequencies. Inland populations are exclusively summer-run and are found only in the Fraser and Columbia River drainages east of a line approximately coinciding with the crest of the Cascade Mountains.

Two subgroups with restricted ocean migration patterns are the "half-pounders" of southern Oregon and northern California, which return to fresh water initially only a few months after entry into the ocean as smolts, and western Kamchatka coastal populations that appear to undertake only brief, localized marine migrations.

Steelhead typically remain at sea for two to four summer growing seasons (one to three winters) before returning to fresh water to spawn. Unlike the Pacific salmons, they may return to spawn more than once. Prior to their first spawning migration, immature steelhead of all age groups and both sexes are referred to as "maiden" fish. If maiden steelhead survive their spawning and successfully return to the sea, they are called "kelts". Kelts are predominantly female. The frequency of repeat spawning varies greatly among populations.

Steelhead exhibit homing behavior characteristic of salmonids, but considerable straying of hatchery fish is known to occur. Once in their spawning stream, steelhead hold in specific sections before spawning. Spawning occurs primarily in late winter and spring, with some regional variation produced by stream temperature or flow regimes. Spawning behavior is similar to that of Pacific salmons except female steelhead do not guard their nests after spawning.

The numbers of degree days required for embryonic development of steelhead to the emergence stage are considerably fewer than for the Pacific salmons, and alevin size at emergence is smaller. Egg development generally occurs on an increasing stream temperature schedule. Stream residence of juvenile steelhead lasts from one to five or more years, with the majority spending two to three years in fresh water; hatchery fish are normally released as smolts after one year. Freshwater age generally increases from south to north. Size more than age is the critical determinant in initiation of smolt outmigration. Fork length of most wild smolts is near 160 mm. Smolt migration occurs for the most part from mid-March to mid-July.

Scales of steelhead collected offshore by research vessels of Canada, Japan, and the United States during 1955-1985 were examined for life history information. In the subsample of 3,475 scales with readable freshwater and ocean ages (32.6% of the total sample) there were 24 age groups, of which ages 3.1, 2.1, 3.2, and 1.1 each contributed more than 10% of the sample. Age 3. was the most common freshwater age. The observed occurrence of freshwater age 1. fish was low considering the percentage of hatchery fish expected to be present, since most hatchery fish are released as yearlings and wild fish normally are two or more years old upon smoltification. This apparent age composition anomaly may result from errors in determination of freshwater ages from scales.

Most steelhead caught offshore were in their second (age .1, 61.9%) or third (age .2, 31.4%) summer at sea. Of the 9,863 fish with readable ocean life history on their scales, only 7.2% had spawned previously. In a subsample of 251 kelts, 71% had spawned once, 21% twice, 8% three times, and one fish, four times.

From fish with readable ocean ages, fork length data were available for 9,824 fish, and body weight for 6,944 fish. The growth curves suggest rapid growth of steelhead during their pelagic existence, particularly in the first and second years of ocean life.

Overall, female steelhead (54.1%) were more abundant than males in high-seas samples. No evidence of a sex ratio cline from east to west was found in the North Pacific. Whereas the sex ratio of North American steelhead is near 1:1, females may predominate in the anadromous forms of Kamchatkan steelhead.

Seasonal movements of steelhead in the ocean were analyzed utilizing available research vessel catch data from purse seines, gillnets, and longlines. Soon after steelhead smolts enter the ocean they begin a directed movement into offshore waters. In spring, steelhead are found in greatest concentrations between 42°N and 52°N from the North American coastline westward to 155°W in the Gulf of Alaska, but their range extends nearly to 150°E. By summer, the distribution has spread north and west in the eastern North Pacific and northward south of the central and western Aleutians. Lower densities occurred west of 175°E, and abundance was low west of 165°E and in the Bering Sea. By summer the southern limit of distribution has shifted north from 38°N to near 40°N.

From limited autumn sampling, catches indicated the main body of steelhead was concentrated along the southern side of the Aleutian Islands and into the central Gulf of Alaska, roughly from 170°E to 140°W and north of 48°N. In winter, the main group of steelhead had apparently moved further south and east. Thus the general pattern of seasonal movement for the bulk of migrating steelhead appears to be northward and westward from spring through summer, followed by southward and eastward from autumn through winter.

A few steelhead were taken in summer and autumn in the southeastern Sea of Okhotsk and Kuril Islands area by Japanese research vessels fishing in 1972-1976.

Additional analyses of steelhead catch data from research vessels were conducted by ocean age and spawning history groups. The annual pattern of movement described above is also portrayed in general by the individual groups, with some modifications as noted below.

Along the North American coast, juvenile steelhead (age .0) move quickly offshore soon after ocean entry. Off the coasts of Oregon and Washington they move northward as they move westward. By July few age .0 fish are found near the coast. A decrease in juveniles in coastal waters from spring through summer is accompanied by increased abundance farther offshore in the Gulf of Alaska.

In contrast to the spring distribution of age .1 steelhead, age .2 and older fish (maidens and kelts) are relatively more abundant in nearshore Gulf of Alaska waters in spring and their center of abundance is farther north. In contrast to maidens, kelts are more plentiful in coastal and nearshore waters, and lag behind maiden fish in the westward extent of their distribution.

The marine distribution of steelhead trout covers a broad area from the North American continent to the southeastern waters of the Sea of Okhotsk. A few fish have been caught in the Bering Sea and in the northwestern Sea of Okhotsk. The southern boundary of steelhead distribution extends as far south as 39°N, but generally lies between 40°N and 44°N.

Ocean distributions of steelhead trout by area of origin were determined from direct evidence from coastal recoveries of fish tagged at sea, from high-seas recoveries of fish that were coded-wire tagged (CWT) or marked as smolts, and from parasitological examination of high-seas samples using *Nanophyetus salmincola* and *Plagioporus shawi* as indicators of U.S. Pacific Northwest origin steelhead. North American steelhead have been found throughout most of the general distribution area except in North Pacific waters west of 162°E, in the Bering Sea, and along the southern fringe of the distribution, where the abundance of steelhead is relatively low. No tags from high-seas releases have as yet been returned from Kamchatkan or Alaskan streams, but high seas recoveries have been made of CWT steelhead from Alaskan streams. Tagging results indicate that steelhead from coastal Oregon and California have more restricted westward migrations than do the more northern North American stocks.

The western-most limit of North American steelhead distribution on the high seas based on tagged fish recovery is 163°32'E for a CWT fish from the Quinault River, Washington, a distance approximately 5,370 km from the river mouth. The western-most limit based on parasite tags is 162°29'E, approximately one degree longitude farther west, for a U.S. Pacific Northwest steelhead. Three fin-clipped steelhead of unconfirmed North American origin were recovered at 159°50'E, 162°09'E, and 162°28'E, beyond the western range determined from tagging and parasite identification.

The southern-most limit for North American steelhead is identified by three CWT fish from Snake River (Columbia River basin) tributaries that were captured at 40°58'N, 159°39'W.

Although tag recovery data showed that summer and winter steelhead had broadly overlapping marine distributions, differences in detail of distribution support the hypothesis that summer and winter steelhead have different seasonal patterns of marine distribution to accommodate the wide difference in time of return to fresh water. For summer steelhead, the CWT recoveries suggested a difference between stocks of British Columbia and Columbia River in path of approach to home streams. Regarding inland versus coastal groups, a comparison of the offshore distribution of Columbia River basin steelhead (inland group) and coastal group summer steelhead indicate that, while they occupy the same areas in the central and western North Pacific during their marine migrations, they differ in distribution in the Gulf of Alaska.

A steelhead CPUE analysis of Japanese salmon research vessels sampling between 170°E and 145°W showed a seasonal shift in distribution of steelhead with respect to sea surface temperature as ocean temperatures increase from late spring to summer. Peak CPUEs occurred in the interval 7.0-7.9°C in May, 8.0-8.9°C in June, and 9.0-9.9°C in July. No steelhead were caught at surface temperatures above 9.9°C in May, 12.9°C in June, or 13.9° C in July, or at surface temperatures below 4.0°C in May and June or 6.0°C in July. Whereas the main body of feeding steelhead is in North Pacific waters of 12°C or less, driftnet sampling in international waters just off the coasts of Vancouver Island, Washington, and Oregon in 1985-1987 demonstrated that summer steelhead returning to coastal streams may migrate through warmer waters. Steelhead catches were made in sets where surface water temperatures ranged from 12.6°C to 15.8°C in June-August.

The vertical distribution of steelhead in the ocean is poorly known, but available evidence suggests a preference for near-surface waters.

Rates of travel at sea were calculated for 13 steelhead tagged offshore and recovered in North American streams or inshore fisheries within 50 days. The average travel rate calculated over approximate straight-line distances between release and recovery points was 50 km/day and the fastest fish averaged 85 km/day for 17 days. Radio transmitter studies in coastal waters indicate that as steelhead approach their home streams they move more slowly.

In general, steelhead trout feed mainly on fish and squid, but also utilize euphausiids, amphipods, pteropods, and pelagic polychaetes. In the most comprehensive study, fish provided nearly half of the total diet biomass. Juvenile Atka mackerel were the most important fish in the diet. Gonatid squids were the second most common prey category. The principal difference between the diets of steelhead and salmon is the relative importance of different taxonomic groups. Euphausiids, often the principal components of salmon diets, were of minor importance to steelhead, whereas steelhead fed on pelagic polychaetes and threespine sticklebacks, uncommon items in salmon diets.

A model of ocean migration of North American steelhead is described and comparisons of migratory behavior with that of Pacific salmons are drawn. Upon entry into the ocean, juvenile steelhead are larger and move more directly offshore than do juvenile salmon. Age .0 steelhead disperse more rapidly in a northwesterly direction than age .0 salmon originating in the same coastal areas. Age .1 steelhead of U.S. Pacific Northwest and Canadian origins are found in a band across the North Pacific nearly to 160°E, whereas age .1 salmon from the same coastal origins remain in more easterly waters. Ocean distributions of steelhead and salmon relative to sea surface temperature are comparable, but show some specific differences. The seasonal south to north movement of steelhead in the central North Pacific most resembles the seasonal movement of coho salmon.

The total annual abundance of all North American stocks of steelhead was estimated to be 1.6 million fish. The Columbia River basin is the center of abundance, followed by coastal Oregon, California, British Columbia, coastal Washington and Puget Sound, and Alaska. The proportion of hatchery fish was estimated at 50% overall. The Asian population of steelhead apparently consists of small runs to a few river systems, and is smaller than the combined North American population by orders of magnitude. No artificial rearing of Asian steelhead is known to occur.

Estimated recreational catches of steelhead (excluding fish caught and released) in North America for run-years 1980-81 to 1987-88 ranged from approximately 235,000 to 449,000 fish. Commercial and tribal catches for the same years ranged from 91,000 to 275,000 The estimated total annual inshore catch ranged from 331,000 to 703,000 fish. No data on inshore catch of Asian steelhead are available.

Reported catches of steelhead by the Japanese landbased driftnet fishery ranged from 29,000 in 1983 to 3,000 in 1989. Catches were concentrated between 42°N and 46°N, 165°E and 175°E. Although the data on recent incidental catches of steelhead by catcherboats of the Japanese mothership driftnet fishery are scant, the interception of steelhead has been of a much lower magnitude than the landed catch in the landbased salmon fishery primarily because of lower steelhead abundance in the time and area of the mothership fishery.

The extensive international high-seas driftnet fishery for flying squid (*O. bartrami)* is conducted in the central North Pacific generally south of the main concentration of salmonids. However, driftnet mesh sizes used are similar to those in Japan's directed high-seas salmon fisheries, distributions of salmonids and flying squid overlap to some extent, and the combined driftnet effort in the squid fishery is very large. Through 1989, catch and temperature data collected within the designated monthly squid driftnet fishery boundaries by research vessel personnel and observers aboard vessels of the commercial squid driftnet fleets indicate that apparently few steelhead have been present in the area. Because of the more northern center of distribution of steelhead trout, catches within the designated boundary of the squid fishery are expected to be minimal in normal years, despite the very large quantity of gear fished, but could occur in cold water years when steelhead would have a more southerly distribution that would extend south of the northern squid fishery boundary. Observer coverage of the squid fishery is continuing and is expected to provide sufficient data to quantify potential incidental take of steelhead trout.

Regarding effects of regulatory changes on high-seas catches of North American steelhead, closure of the North Pacific area east of 175°E to salmon fishing in 1978 served well to protect North American steelhead from capture because abundance of steelhead in this area is generally higher than west of 175°E. Within the squid driftnet fishery, Japan's 1989 shift of the northern boundary northward in July and August increases the probability of incidental interception of steelhead trout, but data are insufficient to quantify the effect of the regulatory change.

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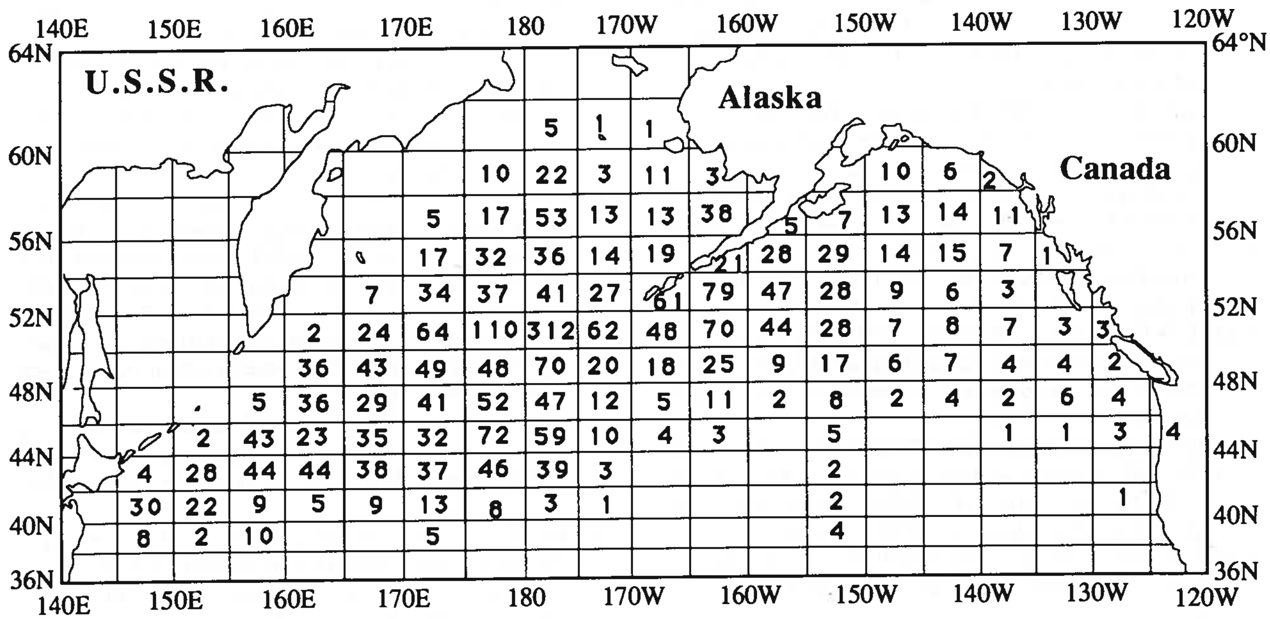
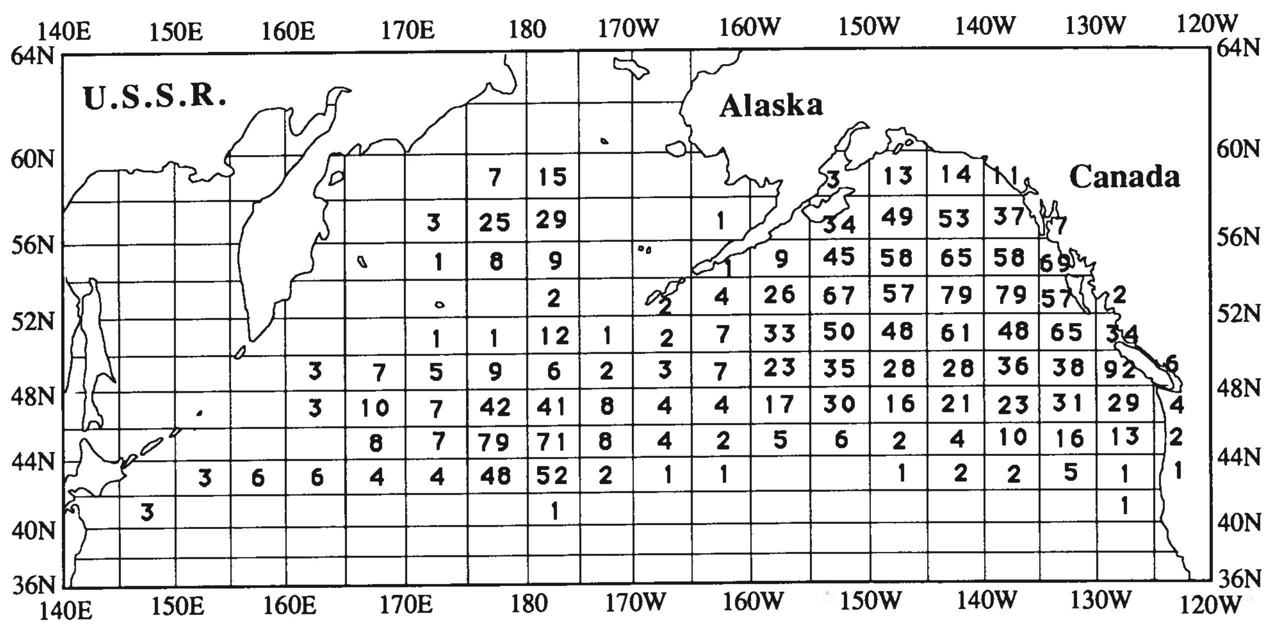
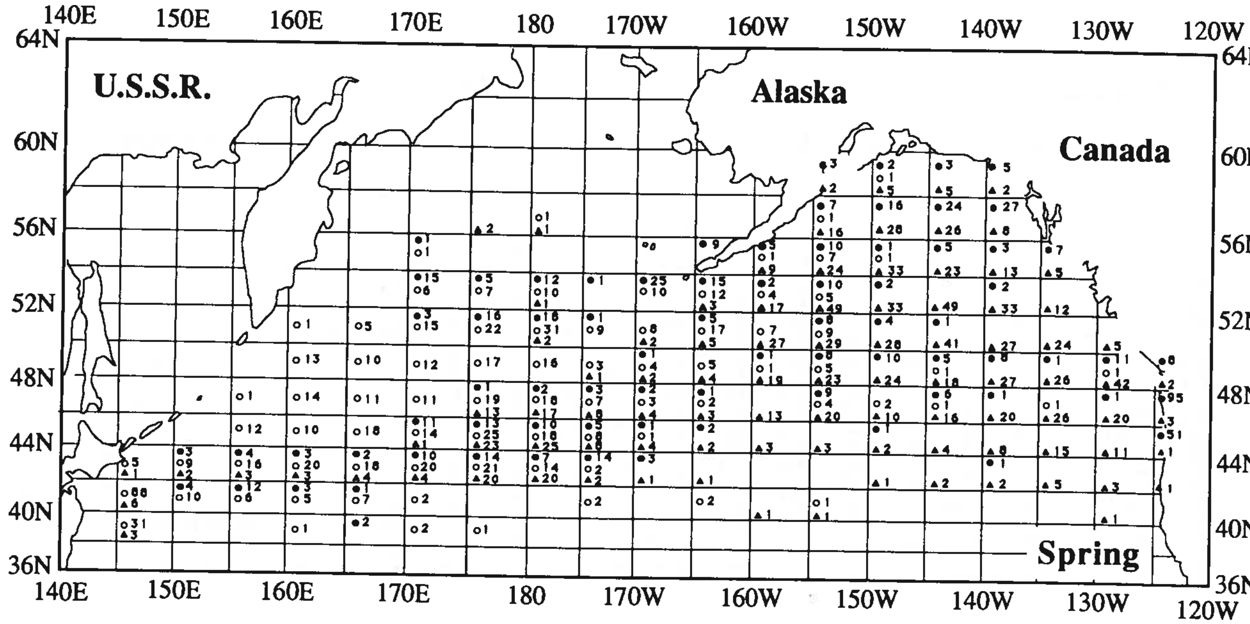


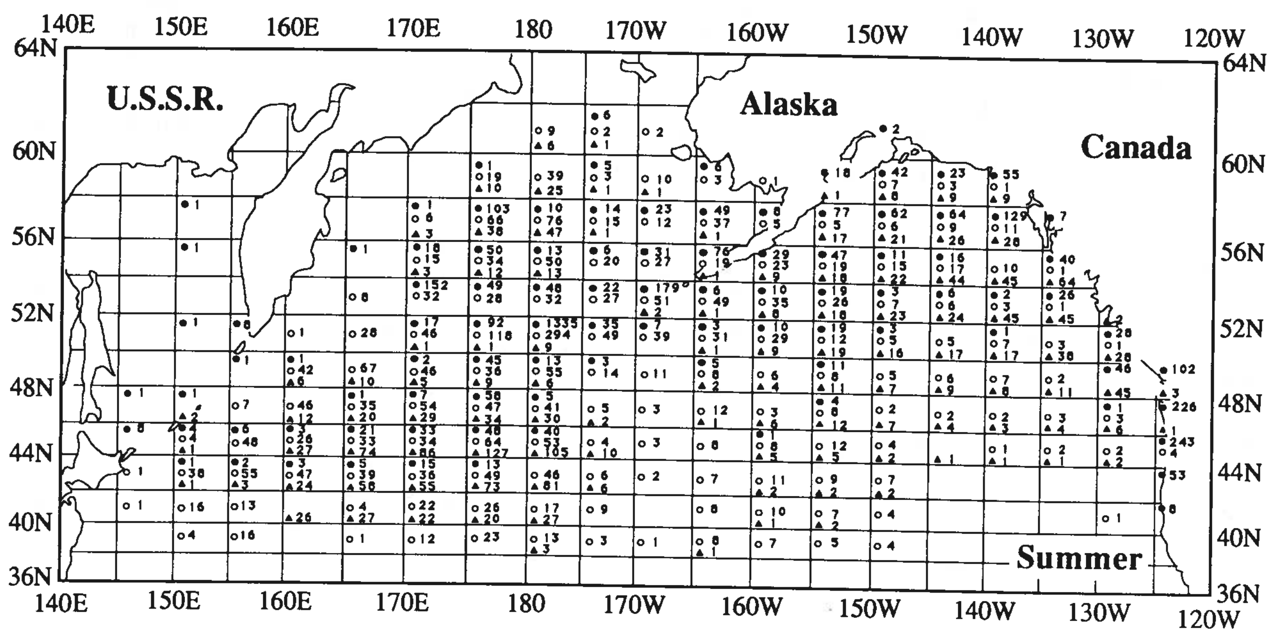
Appendix Figure 1. Distribution of gillnet effort (number of sets) by U.S. and Canadian (1955-1982) and Japanese (1981-1985) research vessels operating in the North Pacific Ocean and Bering Sea. These effort data were used in the calculations of steelhead ocean distribution by age.



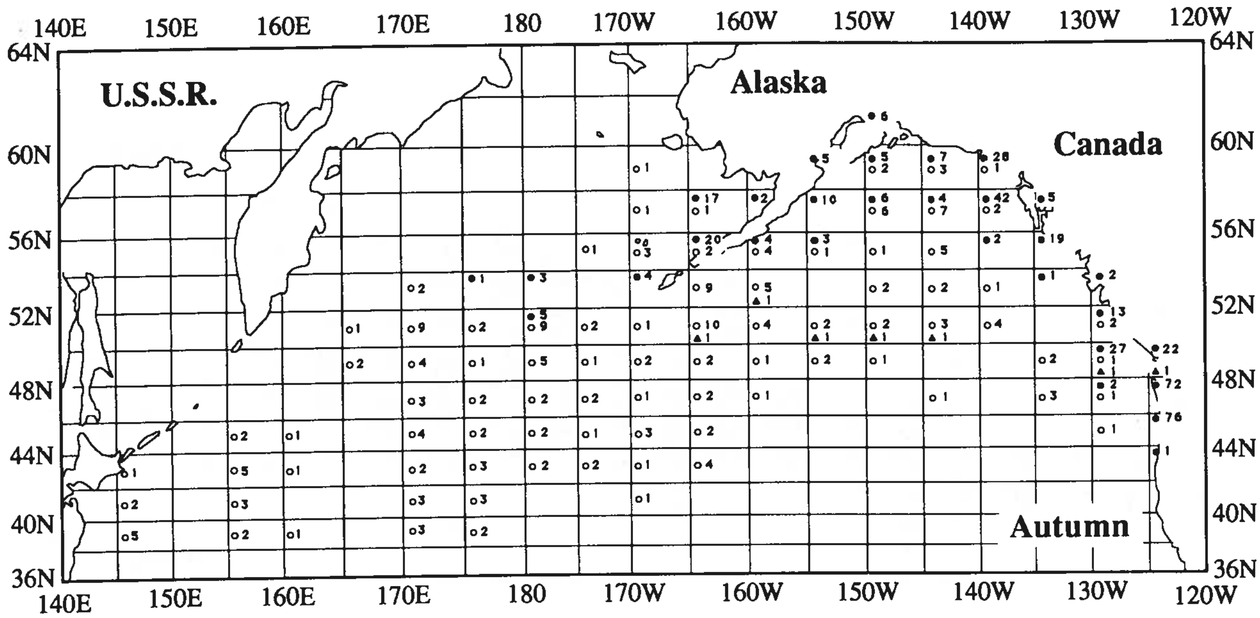
Appendix Figure 2. Distribution of longline effort (number of sets) by U.S. and Canadian (1955-1982) and Japanese (1981-1985) research vessels operating in the North Pacific Ocean and Bering Sea. These effort data were used in the calculations of steelhead ocean distribution by age.



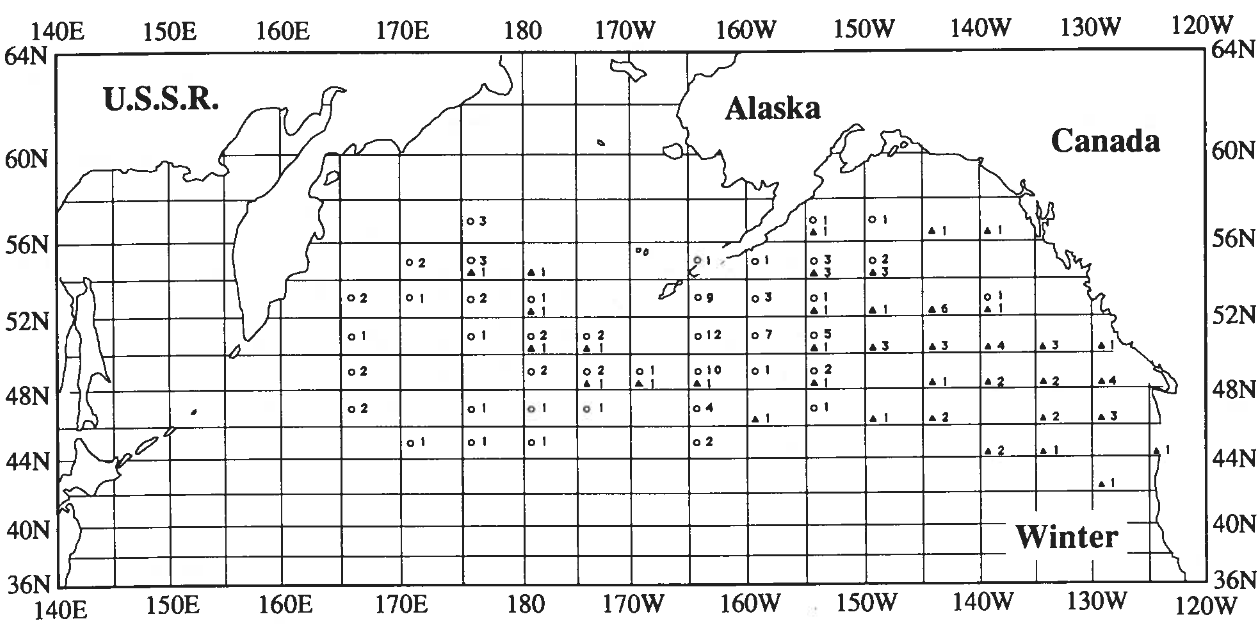
Appendix Figure 3. Spring distribution of fishing effort by U.S. and Canadian (1955-1990), Japanese (1981-1989), and U.S.S.R. (1983-1990) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in calculations of spring ocean distribution of steelhead.



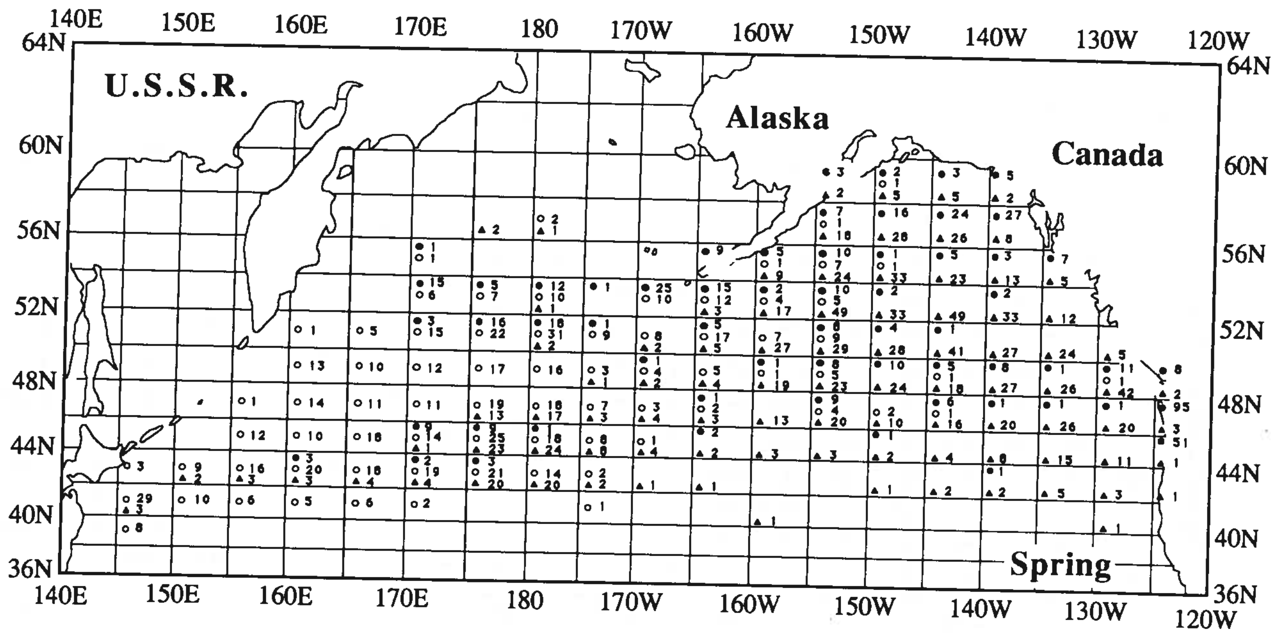
Appendix Figure 4. Summer distribution of fishing effort by U.S. and Canadian (1955-1990), Japanese (1981-1989), and U.S.S.R. (1983-1990) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in the calculations of summer ocean distribution of steelhead.



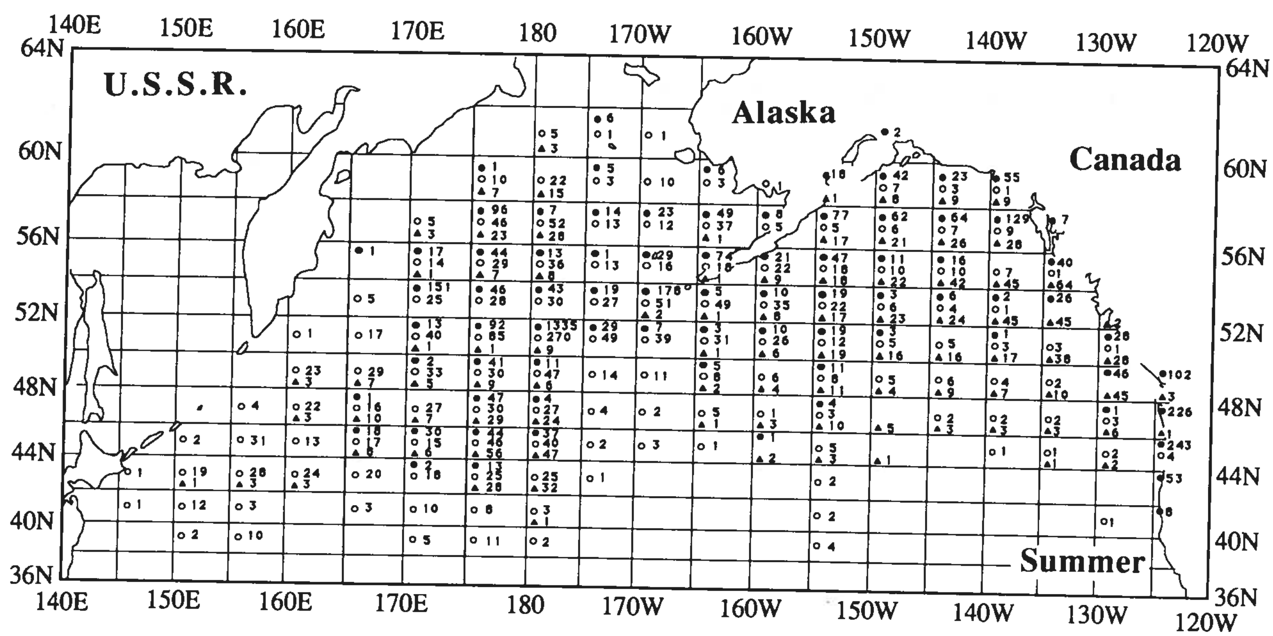
Appendix Figure 5. Autumn distribution of fishing effort by U.S. and Canadian (1955-1985) and Japanese (1981-1989) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in the calculations of autumn ocean distribution of steelhead.



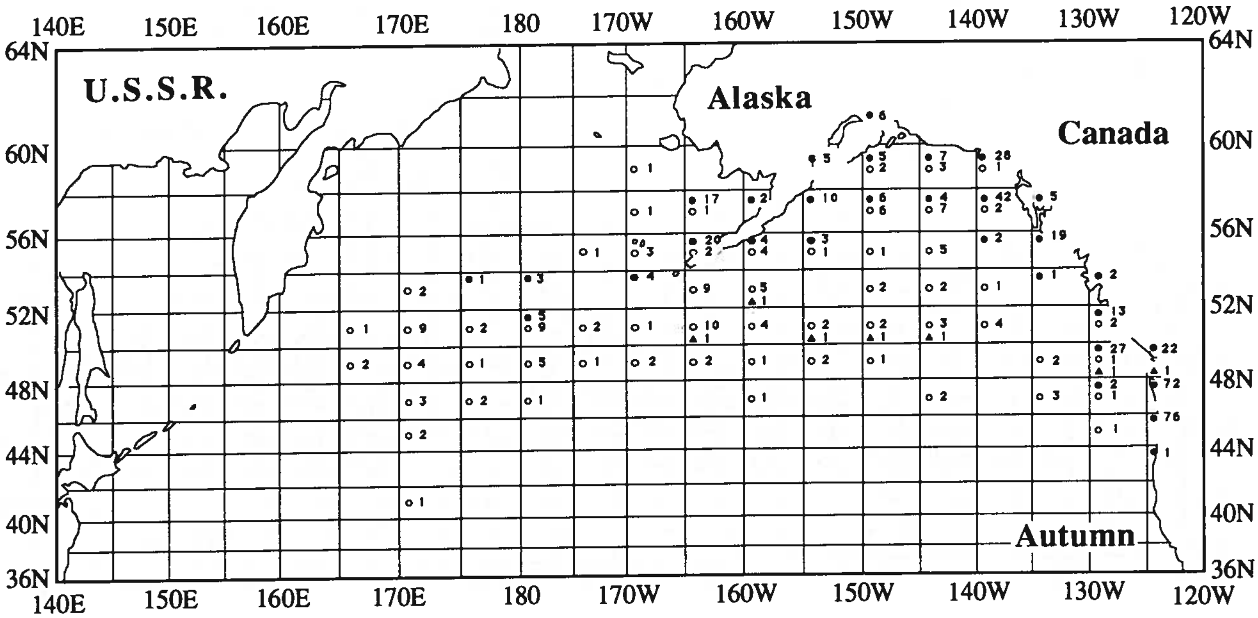
Appendix Figure 6. Winter distribution of fishing effort by U.S. and Canadian (1955-1982) and Japanese (1981-1985) research vessels. The numbers shown in each 2°X5° area are total sets of gillnets (○) and longlines (▲). No purse seines were used during winter. These effort data were used in the calculations of winter ocean distribution of steelhead, overall and by age and spawning history.



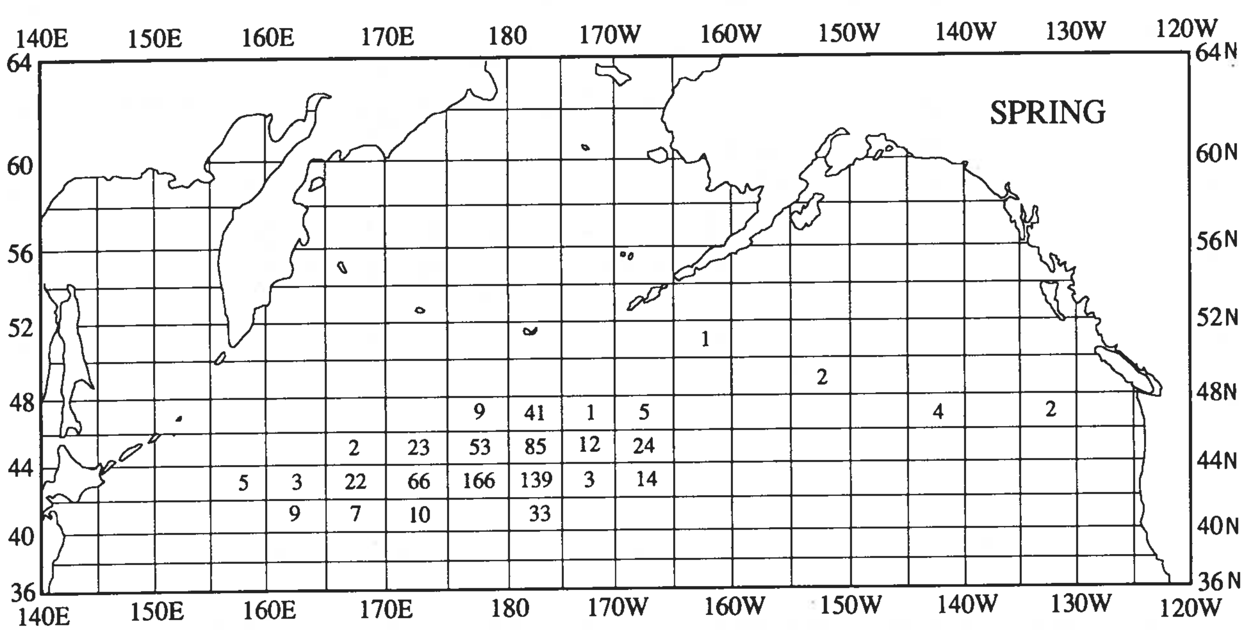
Appendix Figure 7. Spring distribution of fishing effort by U.S. and Canadian (1955-1985), Japanese (1981-1985), and U.S.S.R. (1983-1985) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in the calculations of spring ocean distribution of steelhead by age and spawning history.



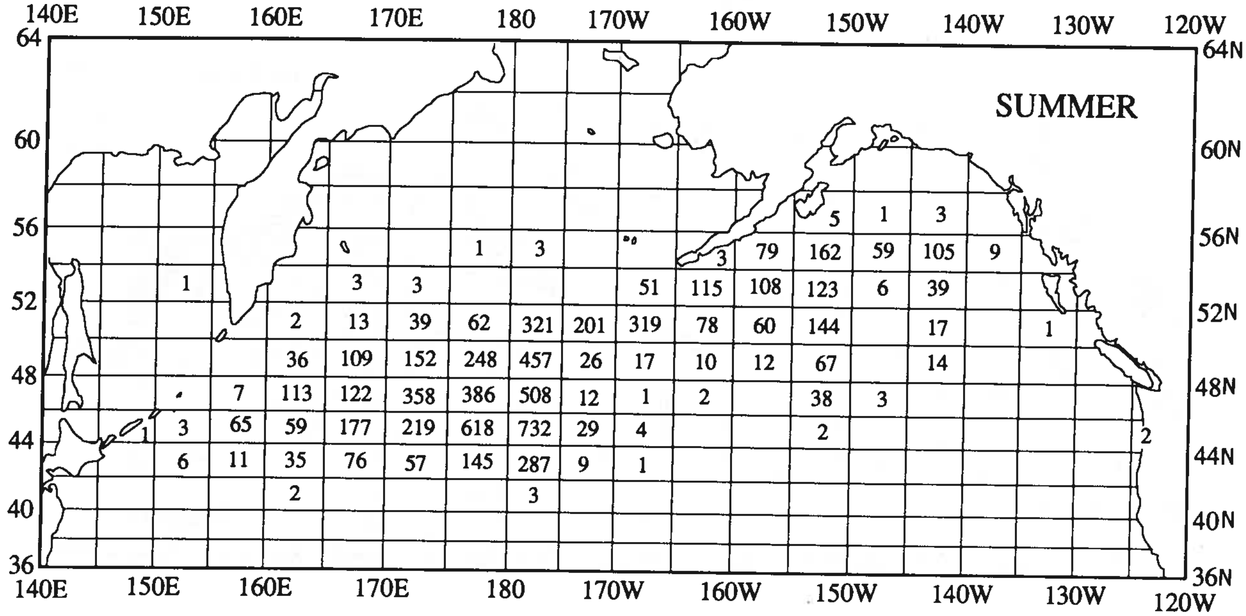
Appendix Figure 8. Summer distribution of fishing effort by U.S. and Canadian (1955-1985), Japanese (1981-1985), and U.S.S.R. (1983-1985) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in the calculations of summer ocean distribution of steelhead by age and spawning history.



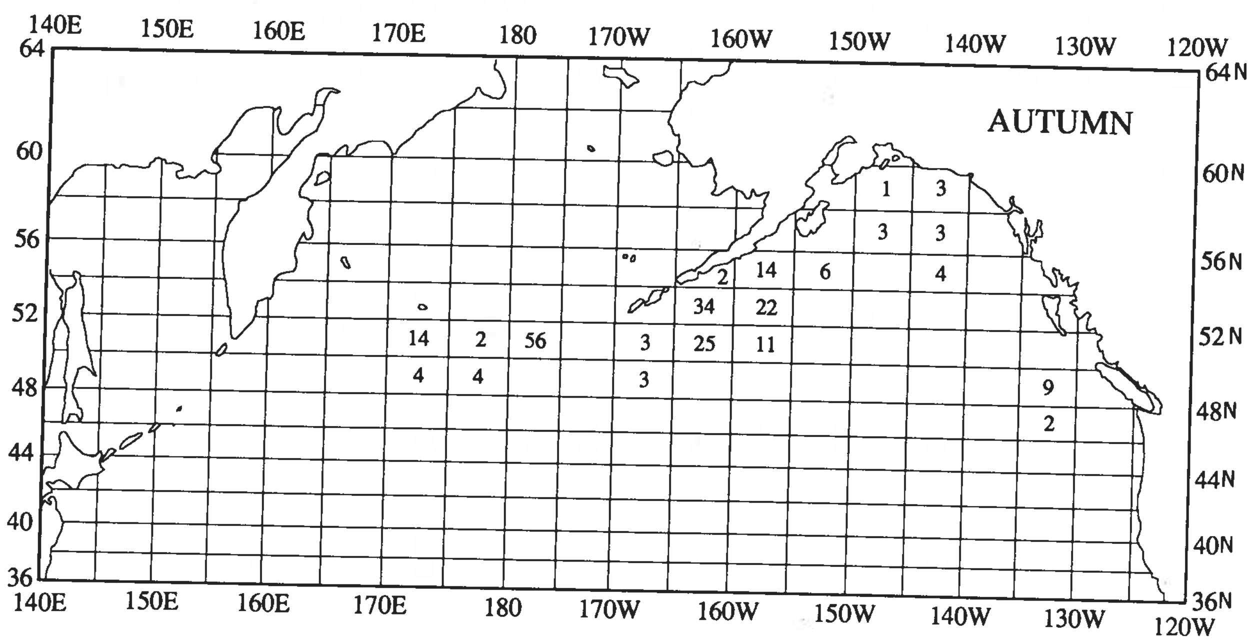
Appendix Figure 9. Autumn distribution of fishing effort by U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲). These effort data were used in the calculations of autumn ocean distrtibution of steelhead by age and spawning history.



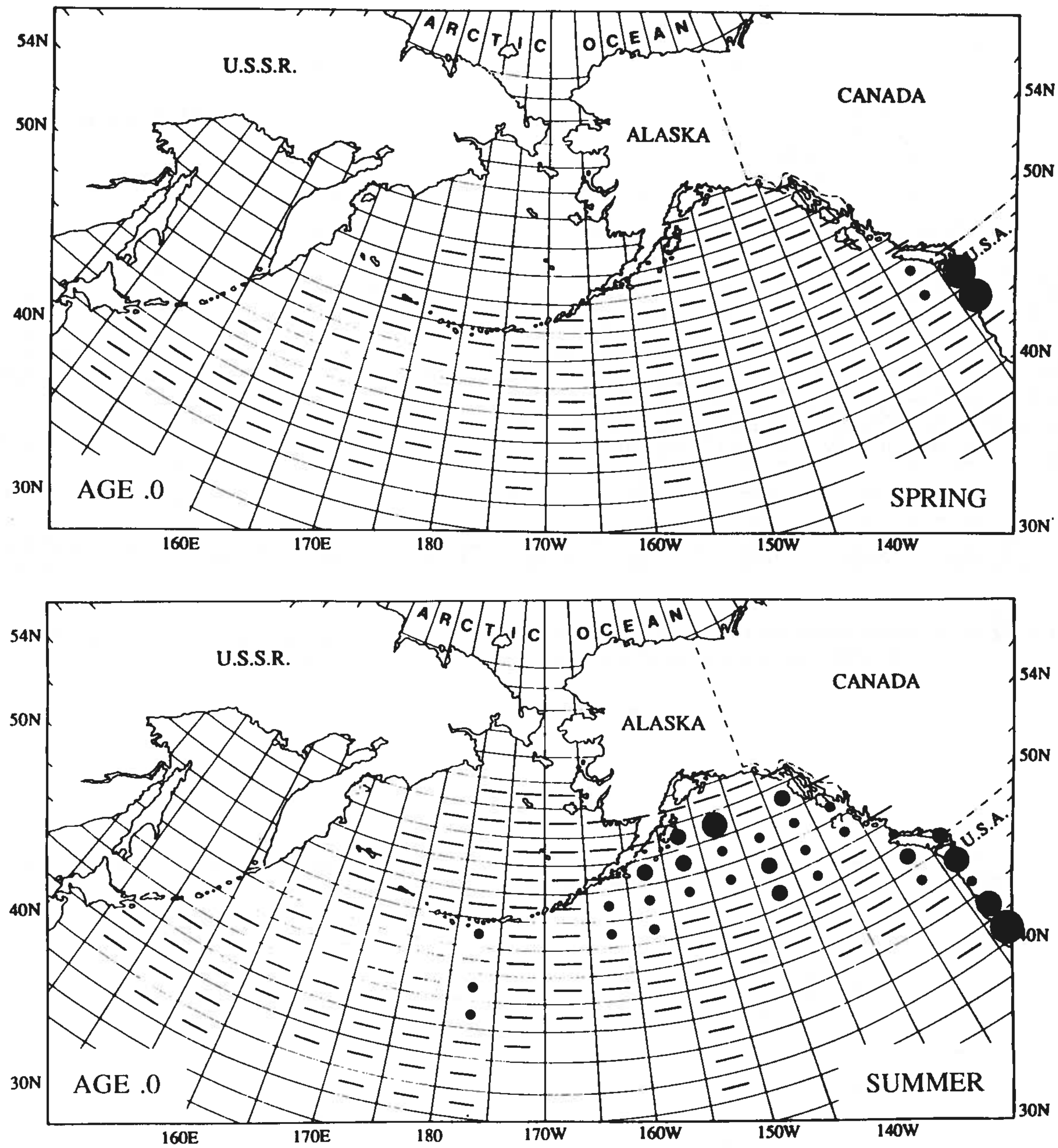
Appendix Figure 10. Sample sizes of steelhead available for sex ratio analysis from the combined Canadian and U.S. (1956-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessel sampling during spring (March-May).



Appendix Figure 11. Sample sizes of steelhead available for sex ratio analysis from the combined Canadian and U.S. (1956-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessel sampling during summer (June-August).



Appendix Figure 12. Sample sizes of steelhead available for sex ratio analysis from the combined Canadian and U.S. (1956-1985) and Japanese (1981-1985) research vessel sampling during autumn (September-November).

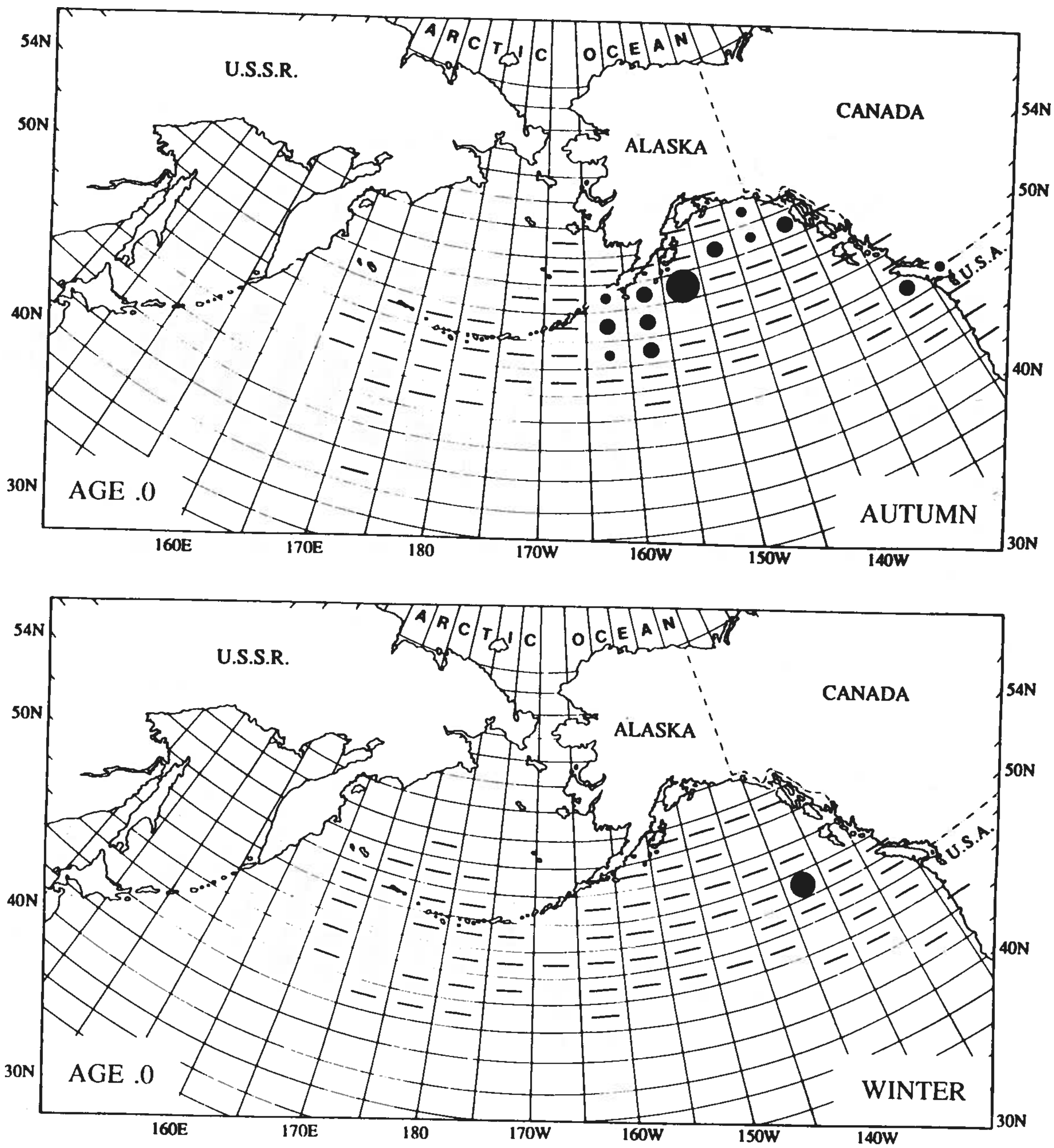


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 13. Ocean distribution of age .0 steelhead in spring (March-May) and summer (June-August) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

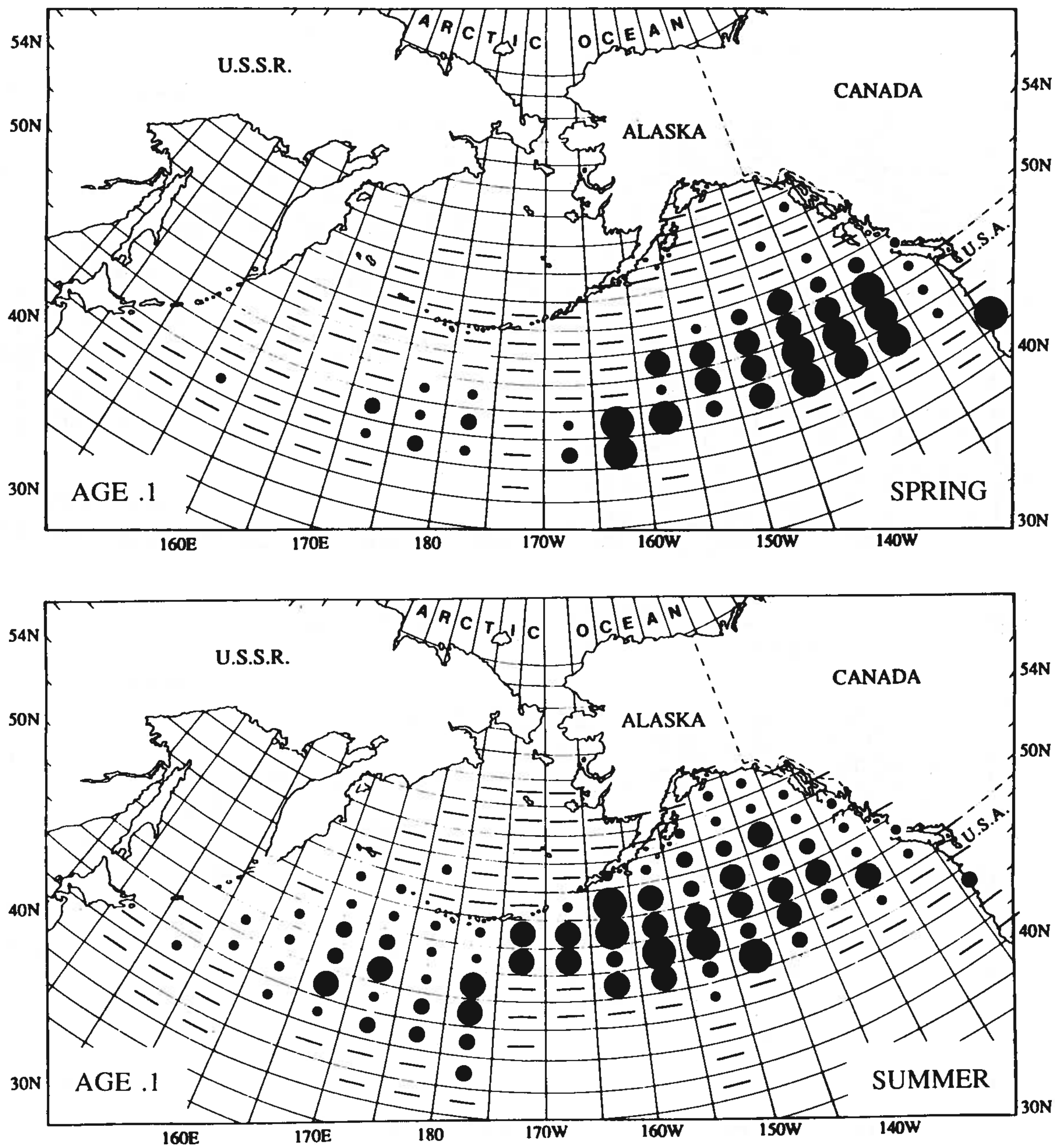


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 14. Ocean distribution of age .0 steelhead in autumn (September-November) and winter (December-February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

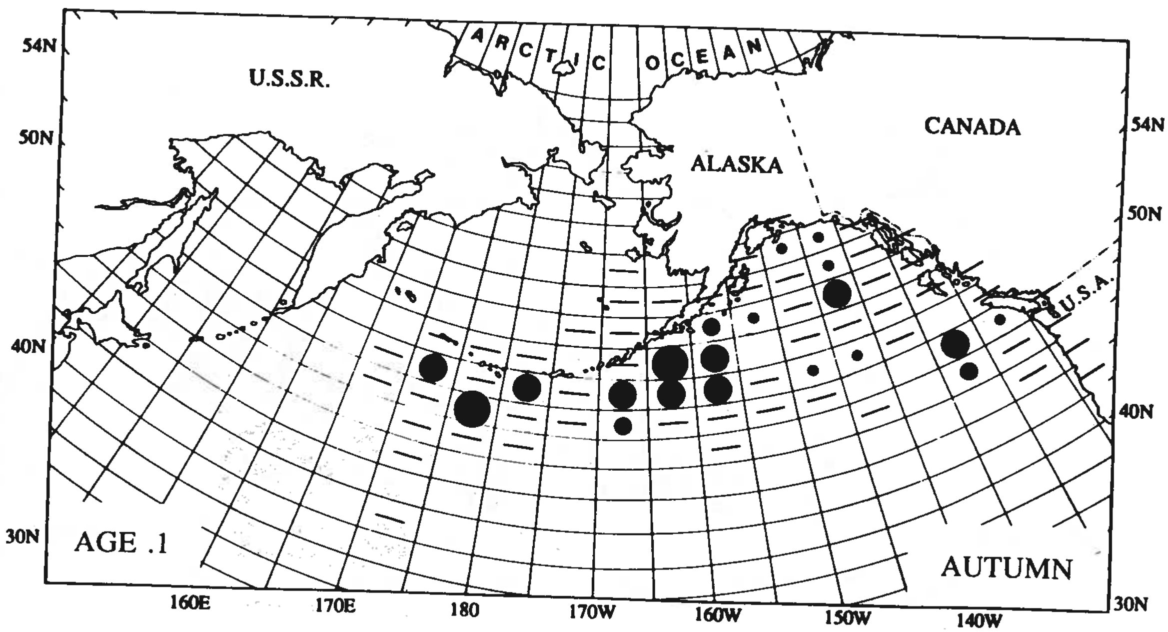


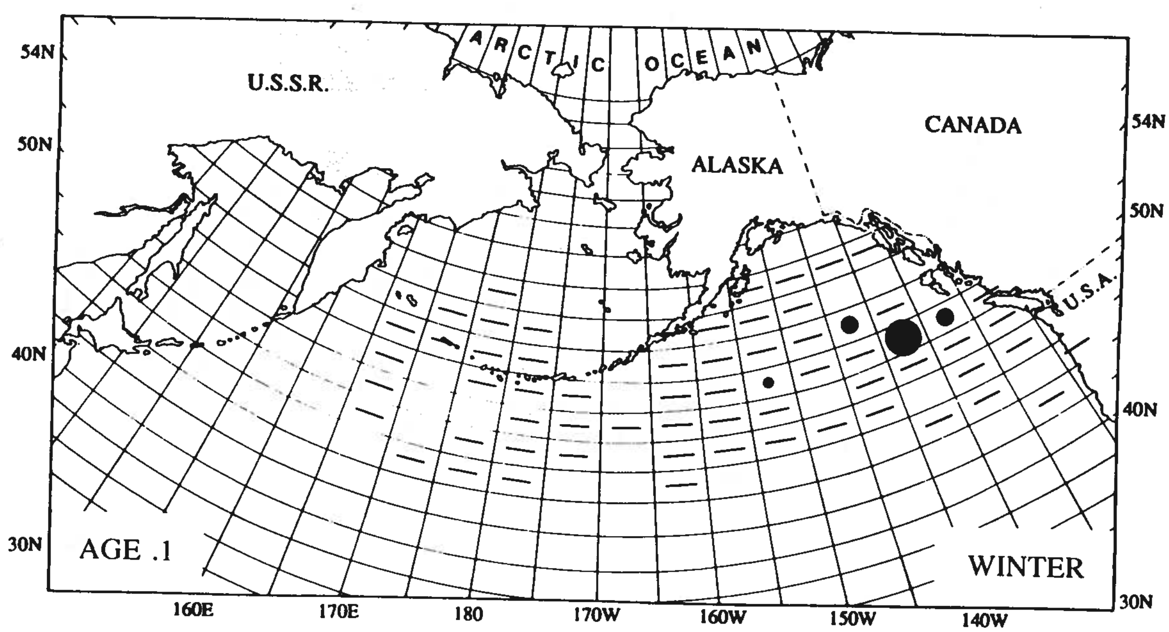
KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 15. Ocean distribution of age .1 steelhead in spring (March-May) and summer (June-August) based on weighted average catch-per-unit effort (CPUE) data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.



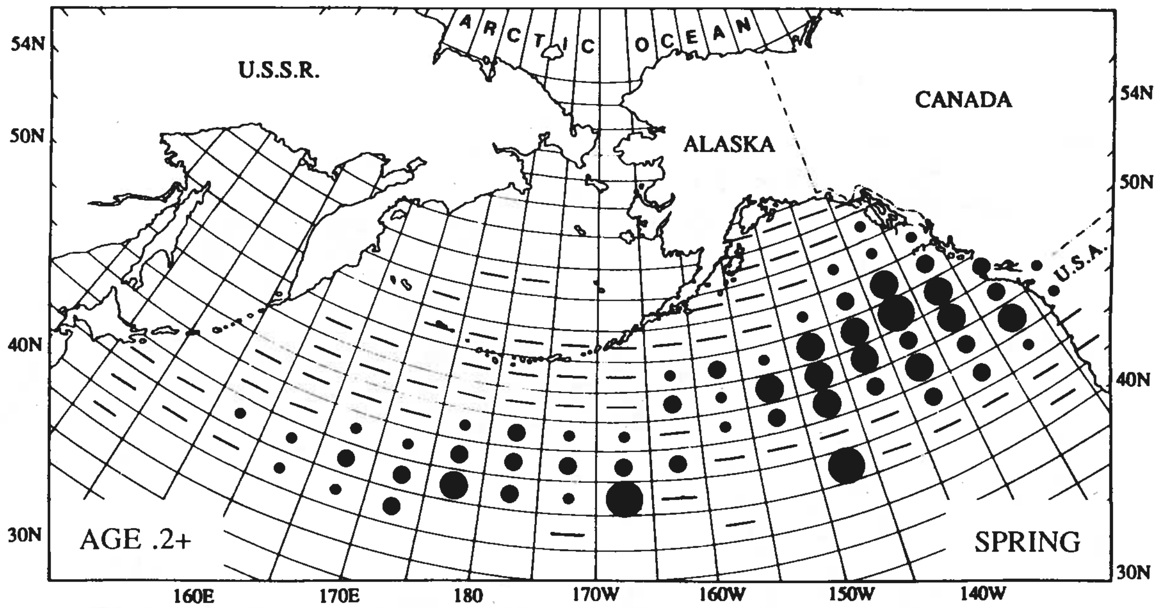


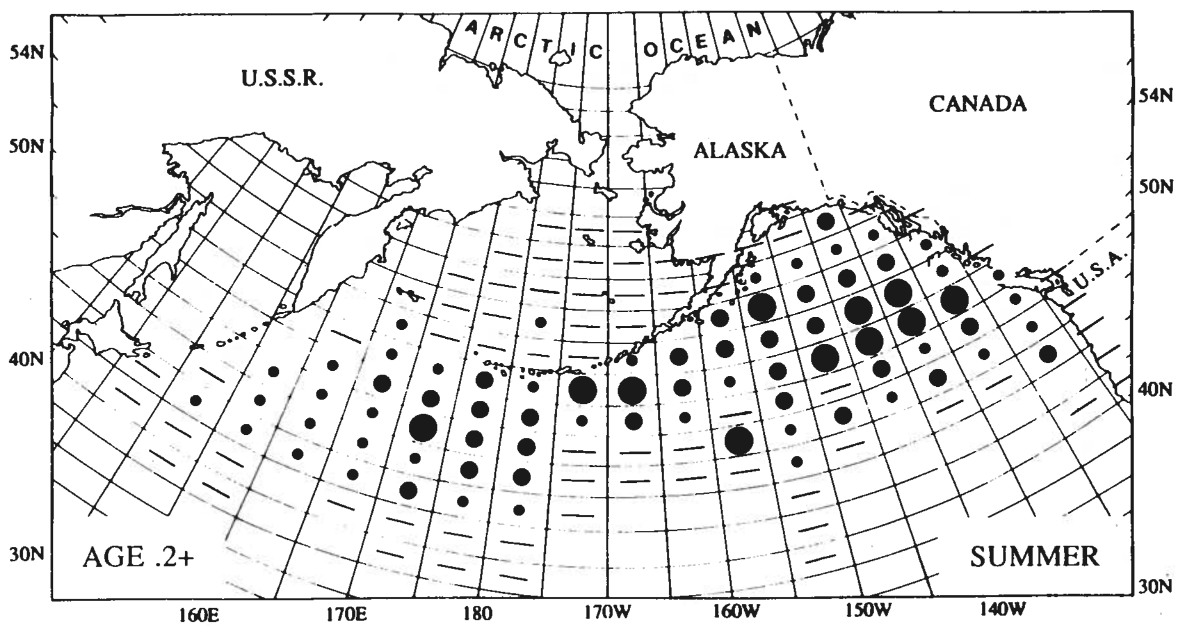
KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 16. Ocean distribution of age .1 steelhead in autumn (September-November) and winter (December-February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.



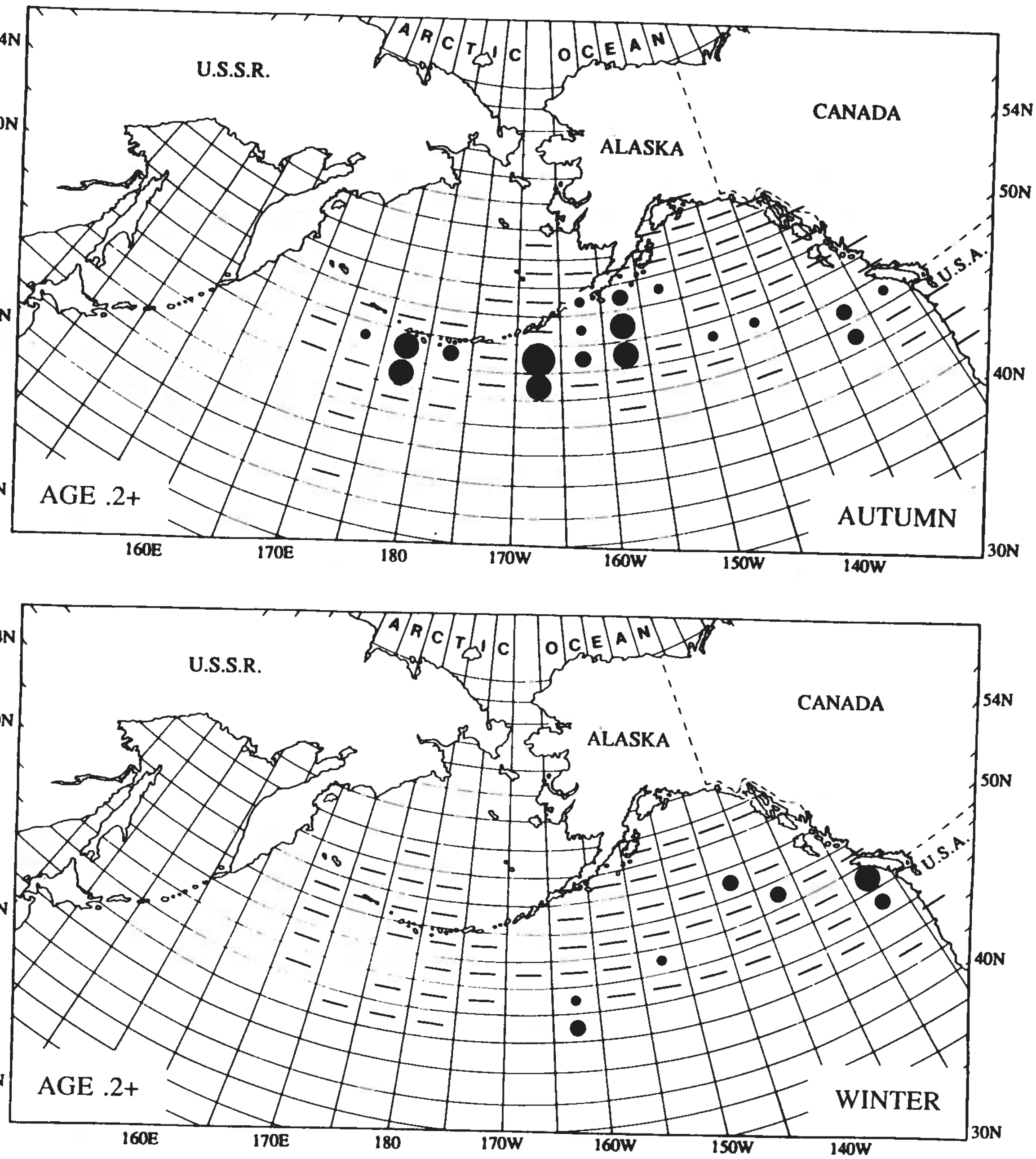


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 17. Ocean distribution of age .2 or older steelhead in spring (March-May) and summer (June-August) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

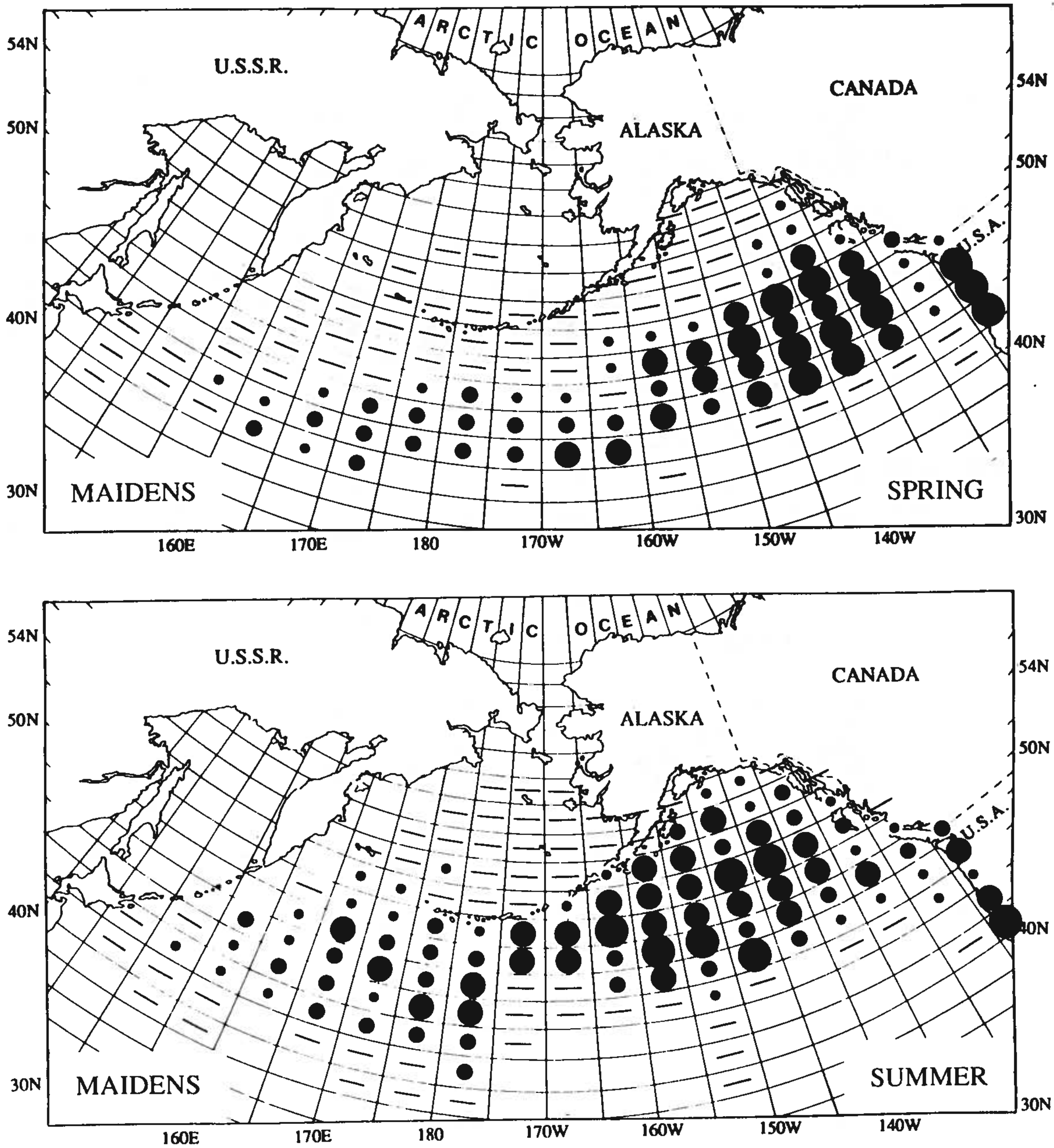


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

• = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 18. Ocean distribution of age .2 or older steelhead in autumn (September-November) and winter (December-February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

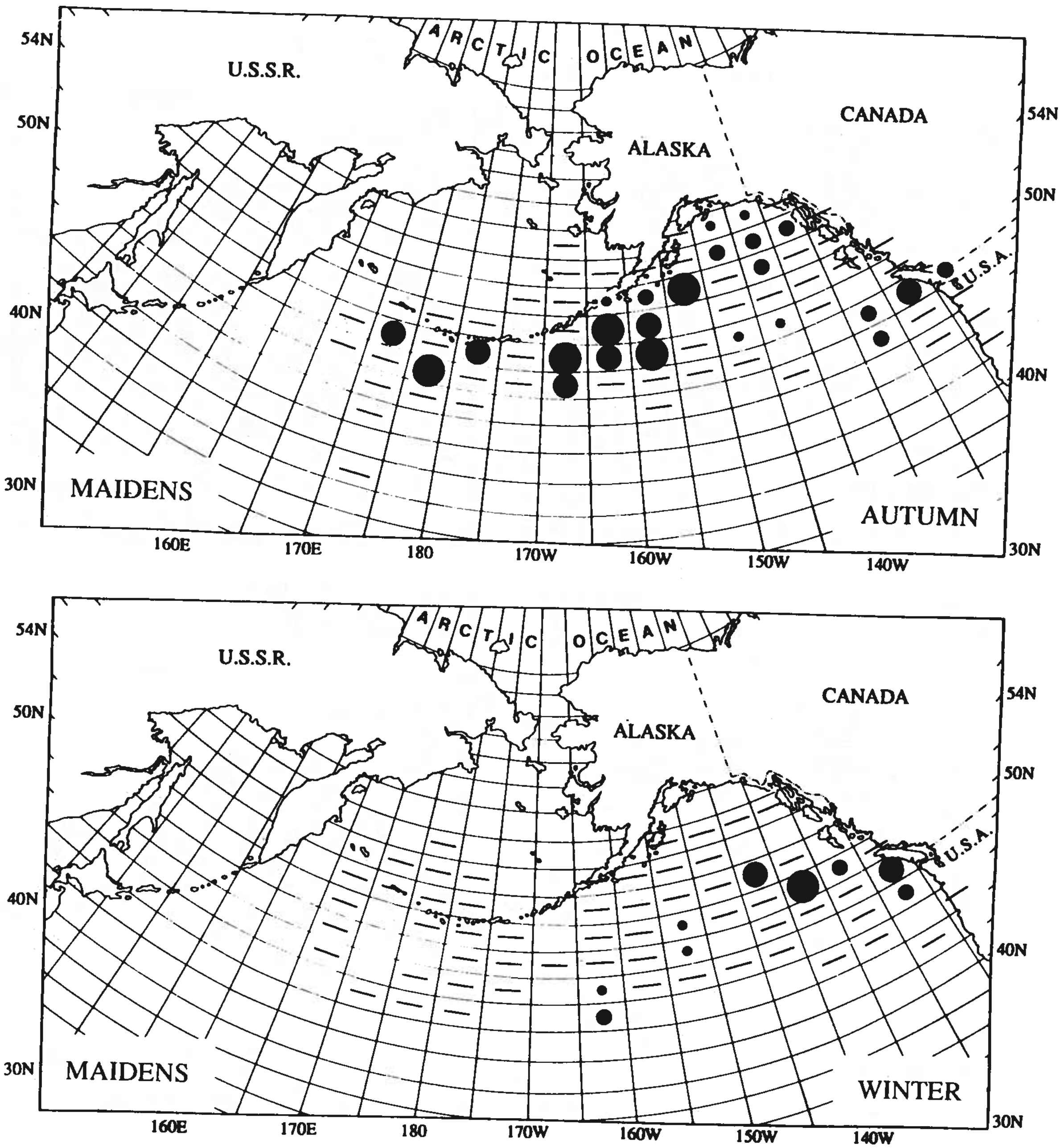


KEY TO CPUE INDEX VALUES:

—— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 19. Ocean distribution of immature (maiden) steelhead in spring (March-May) and summer (June-August) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

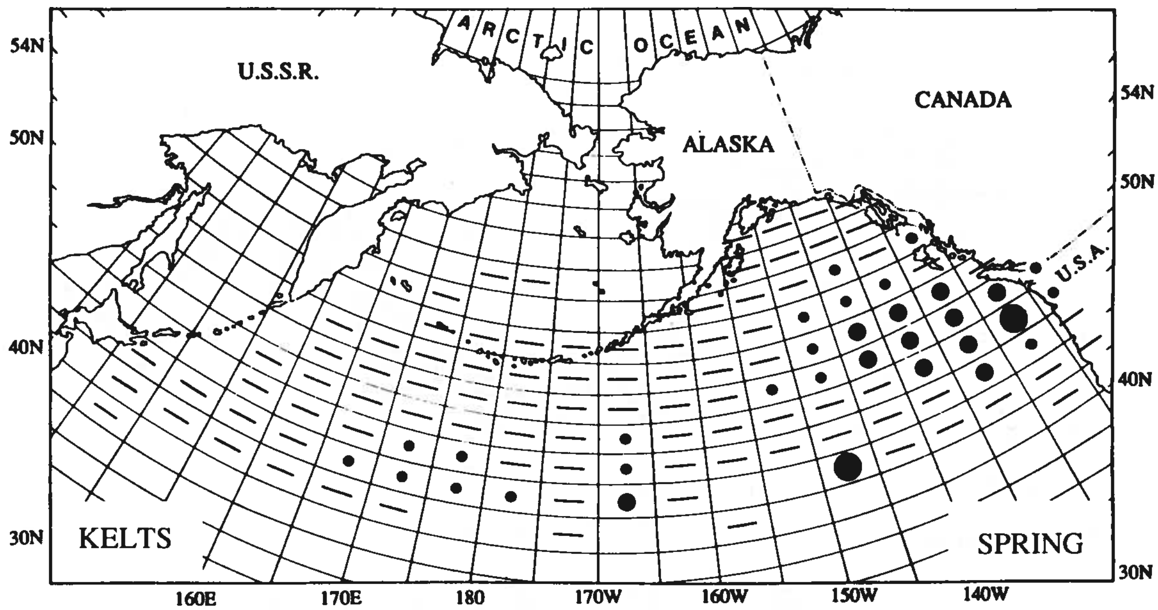


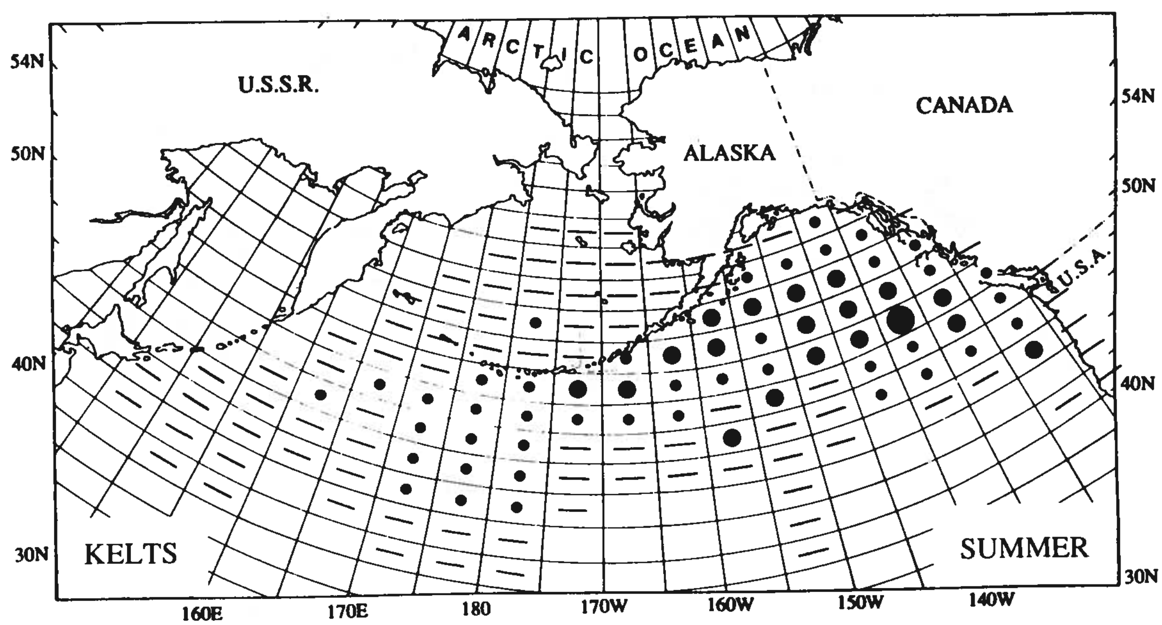
KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 20. Ocean distribution of immature (maiden) steelhead in autumn (September-November) and winter (December-February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.



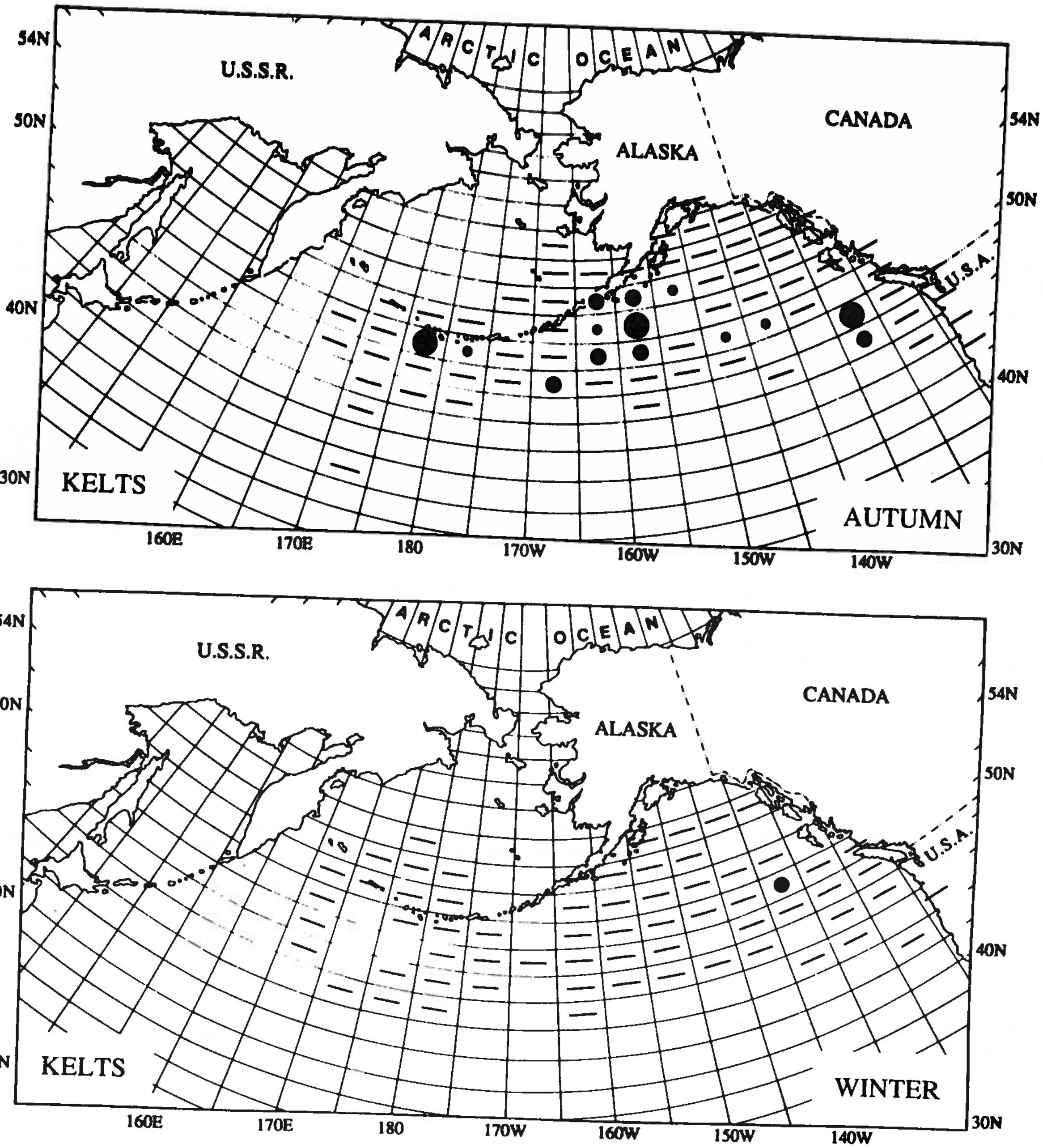


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 21. Ocean distribution of mature (kelt) steelhead in spring (March-May) and summer (June-August) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

● = 1 (lowest) ● = 2 ● = 3 ● = 4 (highest)

Appendix Figure 22. Ocean distribution of mature (kelt) steelhead in autumn (September-November) and winter (December-February) based on weighted average catch-per-unit-effort (CPUE) data from U.S. and Canadian (1955-1985) and Japanese (1981-1985) research vessels fishing with purse seines, gillnets, and longlines.

Appendix Table 1. Ranges of steelhead catch-per-unit-of-effort (CPUE) values for each of three gear types used to develop quartiles for seasonal ocean distribution and relative abundance analyses.

A. All age and spawning history groups, all years combined. Data used were catch and effort data from U.S. and Canadian (1955-1990), U.S.S.R. (1983-1990), and Japanese (1981-1989) research vessels operating in the North Pacific Ocean.

	CPUE QUARTILE			
GEAR	1	2	3	4
Purse Seines[1]	.0345- .0769	.0882- .1852	.2000- .3725	.4468- 17.0000
Gillnets[2]	.0001- .0075	.0078- .0301	.0320- .0725	.0750- .2740
Longlines[3]	.0011- .0108	.0110- .0262	.0271- .0541	.0546- .5738

B. By ocean ages all spawning history groups and years combined. Data used were catch (from biological data) and effort data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels operating in the North Pacific Ocean.

	CPUE QUARTILE			
GEAR	1	2	3	4
Purse Seines[1]	.0022- .0455	.0465- .1039	.1064- .2727	.2742- 14.0000
Gillnets[2]	.0001- .0051	.0052- .0126	.0127- .0278	.0297- .2050
Longlines[3]	.0009- .0081	.0084- .0203	.0213- .0387	.0390- .2667

C. By spawning history groups all age groups and years combined. Data used were catch (from biological data) and effort data from U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1981-1985) research vessels operating in the North Pacific Ocean.

	CPUE QUARTILE			
GEAR	1	2	3	4
Purse Seines[1]	.0022- .0426	.0455- .1111	.1132- .3000	.3333- 14.0000
Gillnets[2]	.0002- .0047	.0051- .0146	.0152- .0396	.0399- .2348
Longlines[3]	.0005- .0098	.0099- .0214	.0216- .0438	.0447- .2793

[1]CPUE = steelhead per set.
[2]CPUE = steelhead per 50-m tan.
[3]CPUE = steelhead per 49-hook hachi.

Appendix Table 2. Release and recovery information for steelhead tagged on the high seas during Japanese, U.S., U.S.S.R., and Canadian research vessel cruises, 1956-1989 (n=78).

Tag Number	RELEASE Date MDY	RELEASE N. Latitude	RELEASE Longitude	RECOVERY Date MDY	RECOVERY N. Latitude	RECOVERY Longitude	Elapsed Time (Days)	Distance to Recovery Pt (km)
M23341	071962	55°13′	134°35′W	073162	51°19′	127°48′W	12	869
27882	071461	56°56′	136°03′W	072761	54°06′	130°29′W	13	694
M17101	062362	52°05′	135°20′W	071062	46°16′	123°45′W	17	1,438
M49086	070667	55°30′	135°30′W	072967	54°38′	130°52′W	23	524
M19338	070962	51°58′	135°30′W	080562	52°15′	128°20′W	27	797
70149	070965	49°45′	132°05′W	080665	45°38′	121°31′W	28	1,259
M14811	050262	49°35′	151°00′W	081462	54°34′	130°28′W	32	2,345
M20382	071162	53°00′	136°10′W	081362	46°17′	123°39′W	33	1,576
MW3649	072361	54°21′	150°32′W	082961	54°05′	130°08′W	37	2,267
C21632	070688	44°59′	146°58′W	081288	49°10′	123°20′W	37	2,666
M31826	053163	51°00′	140°35′W	071063	46°15′	123°40′W	40	1,951
74310	051066	52°00′	137°00′W	062166	50°40′	126° –′W	42	1,231
M49068	070567	55°33′	134°40′W	082467	55°05′	127°50′W	50	76
M45387	060165	53°01′	137°20′W	082065	56°45′	131°45′W	65	746
81593	070566	58°00′	142°30′W	091666	55°15′	129°05′W	73	1,521
M39786	042863	45°56′	137°52′W	071063	41°50′	124°25′W	73	1,561
43774	061762	57°33′	141°40′W	090162	55°06′	127°47′W	76	1,567
M47766	052765	49°00′	132°30′W	081665	46°12′	123°25′W	81	1,056
M50148	050565	52°00′	139°00′W	072765	55°02′	130°00′W	83	1,055
M44836	051865	50°57′	137°33′W	081265	52°45′	128°40′W	86	1,007
M27057	041063	44°55′	136°08′W	071163	46°15′	123°35′W	92	1,402
S00667	060988	45°54′	156°18′W	090988	48°40′	125°53′W	92	3,393
M47350	050165	47°00′	150°00′W	081165	45°57′	124°00′W	102	2,892
74539	052466	50°58′	137°28′W	092466	54°25′	126°48′W	123	1,245
M09667	041862	47°00′	141°05′W	082062	48°40′	125°40′W	124	1,723
M37740	041165	49°00′	152°30′W	082065	46°10′	123°50′W	131	3,200
M09599	041262	44°55′	130°40′W	090662	42°51′	124°34′W	147	716
L08995	090670	51°00′	177°17′E	030571	46°57′	123°50′W	180	6,553
81885	070866	56°30′	145°00′W	011067	42°03′	124°16′W	186	2,788
Y8353	071985	46°28′	169°30′E	012286	47°20′	124°19′W	187	5,022
M11975	062162	49°42′	156°50′W	010163	47°20′	123°15′W	194	3,740
33516	052664	49°10′	147°00′W	121064	46° –′	124°–′W	198	—
T2732	070784	45°30′	178°26′W	013185	46°04′	123°44′W	208	6,079
N4285	062579	45°31′	179°28′E	011980	45°34′	122°22′W	208	6,464
M28926	052263	47°00′	159°00′W	122963	46°55′	122°35′W	221	4,047
MW6205	060162	48°00′	141°50′W	011663	46°11′	122°54′W	224	2,113
M28318	051663	49°00′	135°30′W	122763	43°20′	123°30′W	225	1,473
MW1625	062562	48°25′	154°00′W	020663	47°13′	122°20′W	226	3,522
M29261	052663	49°00′	141°04′W	011064	40°55′	124°06′W	229	2,083
M45455	060265	52°08′	137°33′W	012266	54°10′	127°25′W	234	1,148
A00183	080858	56°17′	150°08′W	033059	48°32′	122°25′W	234	3,189
1777	071957	50°17′	174°45′W	031358	47°00′	126°00′W	237	5,427
M39723	042763	48°06′	136°00′W	122563	39°29′	123°46′W	242	1,659
S1315	050682	43°31′	176°22′W	010783	47°21′	124°18′W	245	5,797
33502	052564	47°05′	145°45′W	012765	36°30′	123°00′W	246	2,775
M29747	011364	51°00′	135°00′W	092264	55°26′	126°41′W	252	1,047
M28240	051563	50°00′	139°00′W	012564	55°26′	126°41′W	254	1,494
BB0107	061788	42°30′	176°30′W	031289	47°55′	124°32′W	268	—
M28686	052063	47°00′	153°08′W	021364	46°05′	123°43′W	269	3,271
M28689	052063	47°00′	153°08′W	022564	47°20′	124°18′W	281	3,204
M36003	040465	51°35′	132°30′W	011566	46°10′	122°55′W	286	5,152
M28190	051563	50°00′	139°00′W	022964	40°37′	124°15′W	290	1,937
S1210	070482	46°30′	169°31′E	042683	47°20′	124°20′W	296	7,352
AA3928	061987	45°19′	176°36′W	041688	47°00′	122°38′W	301	5,999
M20706	072062	53°01′	142°52′W	052663	47°33′	124°20′W	310	2,144

Appendix Table 2, continued.

Tag Number	RELEASE Date MDY	RELEASE N. Latitude	RELEASE Longitude	RECOVERY Date MDY	RECOVERY N. Latitude	RECOVERY Longitude	Elapsed Time (Days)	Distance to Recovery Pt (km)
M27132	041263	46°08′	140°00′W	022364	43°05′	123°15′W	317	1,891
M67485	070767	54°27′	134°18′W	071768	54°59′	130°02′W	376	478
50117	071564	55°00′	147°25′W	073165	50°55′	127°50′W	377	2,221
M29766	011464	47°13′	133°50′W	020665	43°40′	123°40′W	388	1,196
51898	051565	46°00′	142°25′W	061366	42°29′	124°21′W	394	2,044
N0992	061079	43°32′	177°33′E	100580	45°35′	120°55′W	483	6,841
46288	090558	55°42′	151°49′W	020560	44°26′	124°05′W	519	3,308
P3930	053180	44°36′	177°29′W	111781	45°40′	121°30′W	536	6,222
MW1567	062262	47°15′	156°57′W	122663	39°05′	123°12′W	553	3,846
M20720	072062	53°01′	142°52′W	012564	39°00′	123°41′W	555	2,623
M50363	052965	47°00′	142°30′W	123166	45°27′	122°18′W	581	2,251
38927	071464	55°00′	150°05′W	021666	43°20′	123°15′W	583	3,232
M45422	060265	52°08′	137°33′W	010767	42°08′	124°11′W	585	1,849
M47671	052465	47°00′	137°30′W	011367	40°06′	123°48′W	600	1,701
T0624	062883	43°31′	179°29′W	022485	46°12′	123°45′W	607	6,199
51914	051765	46°02′	137°30′W	011567	46°01′	122°53′W	609	1,624
58048	050765	48°06′	143°05′W	010867	45°44′	122°24′W	612	2,313
M11950	062162	49°42′	156°50′W	022264	40°30′	124°00′W	612	3,774
S17312	062862	56°10′	148°00′W	071364	54°09′	130°05′W	746	2,003
M12021	041062	48°53′	133°15′W	03–63	54°25′	126°45′W	—	948
M27978	051163	47°39′	129°35′W	63	44°25′	124°00′W	—	270
33596	052664	49°10′	147°00′W	01–65	44°22′	124°00′W	—	2,608
C21638	070688	44°59′	146°58′W	10–88	45°38′	121°56′W	—	2,784

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Reports of research conducted in connection with the Commission's programs. Published irregularly.

No. 1 (E) (1955): The Pacific salmon of the Canadian Pacific coast (R.E. Forester), On the salmon in waters adjacent to Japan (T. Kubo et al.), A brief review of the salmon fishery in the Aleutian Islands area (C.E. Atkinson), The Pacific herring along the Pacific coast of Canada (F.H.C. Taylor), Oceanography along the Canadian Pacific coast (J.P. Tulley).

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