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**OCEAN DISTRIBUTION AND MIGRATION OF
STEELHEAD**
(Oncorhynchus mykiss, formerly Salmo gairdneri)

by

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(Oncorhynchus mykiss, formerly Salmo gairdneri)

ABSTRACT

Biological and oceanographic information is compiled to produce a comprehensive description of steelhead distribution and migration from the entry of smolts into the sea to the return of adults to freshwater, including continued oceanic migrations of fish after spawning. After reaching the ocean in the spring, juvenile steelhead from North America move quickly offshore and distribute themselves in pelagic waters of the Gulf of Alaska where they remain throughout their first year at sea. In the following year, steelhead characteristically move northward and westward from spring through summer then southward and eastward from autumn through winter. This pattern is repeated by steelhead for all remaining years at sea. Post-spawning steelhead also follow this same general migration pattern, but do not travel as far west as pre-spawning fish in spring or summer. Steelhead are found in epipelagic waters, principally within 10 m of the surface, though they sometimes travel to greater depths. The southern limit of steelhead migration is approximately 38°N latitude and is closely associated with the 15°C sea surface isotherm. The northern extent of their distribution occurs slightly north of the Aleutian islands (south of 56°N), but temperature does not appear to correlate with this boundary. Information from tagging studies shows little or no differences in ocean distribution among stocks, groups, or races. Information on Asian stocks is lacking, but their oceanic migration patterns probably mirror those of North American fish. Migration models were developed to bridge gaps between inshore and offshore life history information.

INTRODUCTION

The marine life history of steelhead trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*) is not well known. Knowledge of the seasonal distribution and abundance of steelhead is needed to complete our understanding of the steelhead life cycle, and is particularly important in estimating the impact of foreign high seas salmon and squid fisheries on North American populations. Earlier attempts at examining steelhead life history in offshore waters (Hartt and Dell 1986; Miller et al. 1983; Okazaki 1983, 1985; Sutherland 1973) provided useful but fragmented insights into many features of steelhead in the ocean. These studies suffered from incomplete information and described only gross distributional features of steelhead at sea. In this report, a compendium of catch, biological, and oceanographic information is used to build upon the works of previous authors to produce a comprehensive description of steelhead distribution and migration from the entry of smolts into the sea to the return of adults to freshwater, including continued oceanic migrations of fish after spawning.

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). 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, Mexico (MacCrimmon 1971, Needham and Gard 1959). The historical distribution of spawning stocks of North American steelhead presumably extended from the Bristol Bay area, Alaska, to Rio Santo Domingo, Baja California, just south of the California-Mexico border (Carl et al. 1959), but the present limit of their range has shrunk due to water diversions and habitat destruction and may extend no further than from Cold Bay on the Alaska Peninsula to central California (Burger et al. 1983, Gwartney 1983, Sutherland 1973, Taft 1933). 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 (Alekseev and Sviridenko 1985, Berg 1948, Savvaitova et al. 1973). 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 Okhotsk Sea continental coast (Kaganovski 1949, Savvaitova et al. 1973).

The taxonomic relationship between the Asian and North American forms of steelhead has been the subject of considerable review and discussion (Behnke 1966, Okazaki 1986, Savvaitova 1975, Savvaitova et al. 1973). Formerly, the two forms were considered as different species, namely *S. gairdneri* for the North American form and *S. mykiss* for the Asian form. Recently, 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 as 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*.

Major Steelhead 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 on ocean distribution. These subgroups include anadromous and resident forms, seasonal races, regional groups, and populations with unusual migration patterns. The geographical distributions of these groups are depicted in Fig. 2.

Resident and Anadromous Populations

Resident rainbow trout, fish that do not migrate to the sea during their lifespan, co-occur with anadromous steelhead throughout their range. Resident fish are mentioned here because current genetic, morphological, and morphometric evidence suggests that resident trout and anadromous steelhead are simply different life history forms within the same species (Currnes et al. 1988, Parkinson et al. 1984, Reisenbichler and Phelps 1985, Rybock et al. 1975). If the two forms occur together in streams where they are not separated by physical barriers, offspring of resident fish may migrate to the sea, and offspring of steelhead may remain in streams as resident fish. This aspect of steelhead life history complicates management of the species in North American streams because managers often desire to protect anadromous fish while allowing resident fish to be caught, and vice-versa (Currnes et al. 1988, Rybock et al. 1975). Moreover, an unknown (but possibly large) percentage of hatchery smolts released in streams do not migrate and instead become established as resident fish (Fish Passage Center 1988, Pevan and Hays 1989). At the northern edge of rainbow trout distribution in Bristol Bay streams, wild populations inhabit systems with other anadromous species, yet the trout remain in freshwater throughout their lives and often grow to large size (Gwartney 1983, Van Hulle 1985).

Seasonal Races

Seasonal races of steelhead occur throughout the range of this species (Bali 1959, Chilcote et al. 1980, Neave 1944, Savvaitova et al. 1973, Shapovalov and Taft 1954, Smith 1968, Van Hulle 1985, Withler 1966). 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 freshwater. Steelhead that return to freshwater between May and October are termed "summer" fish, and those that return between November and April are referred to as "winter" steelhead (Smith 1968, Withler 1966). This terminology is somewhat arbitrary, because steelhead populations are sometimes referred to as spring-run or fall-run according to season of entry (Savvaitova et al. 1973, Shapovalov and Taft 1954, 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. Summer steelhead are not sexually mature when they enter freshwater, and there is usually a delay of several months between the time when most fish enter the river and the time spawning begins (Light 1986, 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 are usually sexually mature when they enter freshwater, and there is much less time between freshwater entry and spawning. The upstream migration of winter steelhead often completely overlaps the spawning period. 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 coincide. In some streams the native populations are exclusively winter steelhead, while in others only summer steelhead are found. Some streams support both forms (Everest 1973, Leider et al. 1985, Van Hulle 1985, Withler 1966). Historically, summer steelhead were most prevalent in larger drainages such as the Sacramento, San Joaquin, and Klamath systems in California (Kesner and Barnhart 1972, Murphy and Shapovalov 1950), 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 Fraser and Skeena systems in British Columbia (Parkinson 1984, Withler 1966), and a few of the larger rivers in southeast Alaska south of Yakutat (Van Hulle 1985). A few scattered summer populations inhabit shorter coastal streams from northern California to southeast Alaska (Bali 1959, Crawford 1979, Pautzke and Meigs 1940, Shapovalov and Taft 1954, Van Hulle 1985, Withler 1966). Steelhead at the northern limits of their range (from Yakutat Alaska westward across to the Alaska Peninsula and into Asia) are virtually all "summer-run" fish that return to spawning streams in the fall (September-October) before the streams have frozen over, and then overwinter in these streams before spawning the following spring (Burger et al. 1983, Savvaitova et al. 1973, Van Hulle 1985).

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

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 coinciding with the crest of the Cascade Mountains (Fig. 2). These two groups are referred to as inland and coastal, and are defined on the basis of the frequencies of LDH-4 and SOD alleles (Allendorf 1975, Parkinson 1984). Coastal populations occur in streams west of the Cascade mountains and extend at least from Kodiak Island to northern California. Inland populations are exclusively summer-run and are only found in the Fraser and Columbia River drainages east of the Cascade Mountains.

Subgroups With Unusual Migration Patterns

Two notable life history subgroups of steelhead, namely the half-pounder populations of North America and coastal populations in Asia, are distinguished by unique behaviors that involve an anomolous aspect of the marine migration phase of their life histories.

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 freshwater only a few months after they first enter the ocean as smolts (Everest 1973, Kesner and Barnhart 1972). During their brief ocean residence, these fish grow to an average weight of one-half pound (.23 kg), hence the common name "half-pounders." These fish are usually sexually immature and do not spawn on their initial 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 freshwater after their second summer at sea as maturing adults on their first spawning migration. The adaptive advantage of this early return to freshwater as immature juveniles is not known.

Scale patterns of these fish are distinctive due to resorption of the edge of the scale while the fish are in freshwater. This resorption causes a check resembling a spawning check to form on the scale of these fish part-way into the first year's ocean growth region. Half-pounders are included in this report because of the possibility that once they have returned to sea after their first upstream migration, they may migrate offshore before returning as mature adults.

Asian Coastal Steelhead. 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 (*O. 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. By the very nature of their limited coastal migrations, this group of steelhead is unlikely to be found far at sea.

Pre- and Post-Spawning Steelhead

Steelhead populations can be further subdivided on the basis of spawning history. 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 a year or more and return to spawn the following season (alternate spawners). Scales from the former group have consecutive spawning checks separated by a single summer growth zone between them, while those from the latter group have an ocean annulus (and two summers of ocean growth) between spawning checks.

All of the above groups of steelhead exhibit distinctive life history traits that suggest possible differences in ocean distribution and migration. Summer- and winter-run fish have very different schedules for time of return to the coast. Coastal Asian steelhead and North American half-pounder steelhead are likely to have very limited ocean migrations, at least in the first year for the latter. Maidens and kelts may well have different migratory patterns.

MATERIALS AND METHODS

Information on ocean distribution and movements for all steelhead groups largely derives from catch 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 information was obtained from published or unpublished data records of fishing operations of salmon research vessels of the three member nations of the International North Pacific Fisheries Commission (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 1983-1985) and in nearshore waters (Fisher et al. 1983, 1984; Fisher and Percy 1985a,b; Miller et al. 1983). 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 abundance data and biological information. Effort data used in this analysis included 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 thorough description of the gear and fishing methods can be found in Kondo et al. (1965) and Sutherland (1973).

High seas research has not been consistently pursued by all INPFC member nations since the inception of the Commission, and steelhead were not initially a focus of this research (Light et al. 1988). 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 on-board sampling sheets. The task of obtaining, editing, and entering this information onto computer files was completed for catch and effort data for all three nations prior to this analysis, but for Japanese biological data the process is ongoing. Thus when biological data are used, the data will include U.S. and Canadian data for the years 1955-1985, but Japanese data will generally be restricted to the period 1981-1985. I consider the effect of the unavailability of early Japanese biological data on catch-per-unit-of-effort (CPUE) values to be inconsequential for most areas. 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 fish 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 even 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 was based on available catch and effort data for the years 1955-1985 and included fish from all age groups and spawning histories. In the second and third analyses, ocean age and spawning history information obtained from scales 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 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.

Fish that were sampled for 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 had damaged or unreadable scales. I assumed that the proportion of fish with damaged or unreadable scales did not differ enough in occurrence across all age 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 age group or spawning history were determined by biologists from the Fisheries Research Institute (FRI). This included U.S. and Canadian samples from 1955-1985 and Japanese samples from 1981-1985 (Davis and Light 1985). For Japanese scale samples collected prior to 1981, ocean ages assigned by biologists from the Fisheries Agency of Japan (FAJ) were used.

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 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).

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:

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

$$= \frac{1(25) \text{ gillnets} + 3(5) \text{ longlines}}{25 + 5} = \frac{40}{30} = 1.33 \text{ (rounded to 1)}$$

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.

RESULTS

Distribution of Sampling Effort

The distribution of fishing effort for purse seines, gillnets, and longlines over all years (1955-1985) is shown in Figs. 3-5. From this summary it is apparent that sampling was not uniform with regard to area, season, 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 composite effort distribution for all gear types is presented by season in Figs. 6-9. 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 latitude between 160°W and 175°W longitude 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 1989), 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 can be found in Appendix A for each of the three analyses.

Seasonal Distribution and Migratory Behavior

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 spring, steelhead are found in their greatest concentrations between 42°N and 52°N latitude from the North American coastline westward to 155°W longitude in the Gulf of Alaska (Fig. 10). To the westward their distribution in this season extends to 150°E longitude in a north-south band between about 40°N and 48°N latitude. Few fish were caught anywhere in waters off the North American or Asian Pacific coasts from Yakutat, Alaska westward. By summer, the center of abundance of the main migrating group has moved distinctly north and west to the area between 140°W and 180° longitude, and 42°N to the Alaska and southern Kamchatka coastlines (Fig. 10). Fish were also found in a few sets in the Bering Sea as far north as 56°N, and in far-western waters surrounding the Kuril Islands as far south as the northeastern tip of the Japanese island of Hokkaido and north to the west coast of Kamchatka. These steelhead in far western waters may be from Asia. 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. 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 longitude (Fig. 11). A few steelhead were taken off the west coast of Kamchatka south of 56°N. In winter, the fish in the North Pacific had moved further south and east across the Gulf to the area between 44°N and 58°N latitude (Fig. 11). 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.

Ocean Age .0

Nearshore sampling with fine-mesh purse seines in spring through autumn along the North American coast from northern California to British Columbia reveals that soon after ocean entry, juvenile steelhead move quickly offshore (Figs. 12 and 13). Purse seine set-direction data also indicate that age .0 fish off the coasts of Oregon and Washington move northward as they move westward (Wakefield et al. 1981). Details of nearshore movements from May to September by this age group are presented for North American fish in Fig. 14. In May, 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 southern Oregon and northern California. The abundant juvenile steelhead in this area 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 steelhead are rare or absent in nearshore areas (Fisher et al. 1983, 1984).

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. Age .0 steelhead apparently achieve their western-most extension in summer, as evidenced by the fish caught in the central North Pacific (Fig. 12). In autumn, juveniles are concentrated in the western Gulf of Alaska north of 50°N latitude, between 165°W and 135°W longitude (Fig. 13). Only three age .0 steelhead were taken in winter during longline operations in area W4050 (Fig. 13).

No age .0 steelhead were caught in nearshore Asian waters in spring (Fig. 12), but by summer these fish began to show up in catches on the southwest coast of the Kamchatkan peninsula (shown with asterisks to indicate that fish of this age group were caught in these time-area combinations, but the data were incomplete). In fall and winter age .0 fish again disappear from catches in western waters (Fig. 13), although most of the fishing in these areas after summer was with gillnets, the gear least likely to catch these small fish (<450 mm; Okazaki 1984, Sutherland 1973).

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 (500-650 mm) and are more vulnerable to gillnet and longline sampling gear (Sutherland 1973). Age .1 fish are concentrated offshore in the Gulf of Alaska, especially between 150°W-130°W longitude, and 44°N-50°N latitude in a pattern that tapers westward to about 155°E longitude in a band of decreasing abundance (Fig. 15). Fish are scarce or absent in nearshore areas from Yakutat, Alaska westward along the Alaska Peninsula and Aleutian Island chain. Sampling in coastal Asian waters south and east of the Kamchatka Peninsula during this season produced very few age .1 fish.

Interestingly, a dense concentration of age .1 juveniles appears in the spring off the coast of southern Oregon and northern California (INPFC area W2542, see Fig. 15). These fish are separated from the main mass of age .1 fish and are likely half-pounders

returning to the sea after their initial (non-spawning) migration into freshwater (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, most age .1 fish have moved north and west to areas north of 46°N or 42°N in the eastern and western North Pacific, respectively (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 to beyond the Kuril Islands into the Sea of Okhotsk. They are scarce west of 165°E. Fish are most abundant in waters roughly between 175°E and 140°W. Also, fish were found in summer in Bering Sea catches north of the Aleutian and Commander Island chains.

Much as they did their first year at sea, age .1 steelhead achieve their maximum westward extension in summer and then travel south and east from their feeding grounds to take up residence in the southern Gulf of Alaska during fall and winter (Fig. 16). In autumn, age .1 steelhead catches were irregular but still showed concentrations in areas south of the Aleutian Islands. Small groups of age .1 fish were found south of the Aleutian Islands in the central North Pacific, and in the south-central Gulf of Alaska and offshore from Vancouver Island, B.C.

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 (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 age .1 fish, a few age .2+ fish are found in the Bering Sea in summer.

Virtually the same pattern of northwestward movement from spring through summer is seen for age .2+ fish as was found for age .1 fish (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. 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 distribution for age .2+ fish also closely resembles that of age .1 (Fig. 18).

Maidens (Immature, Pre-Spawning Fish)

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 (Fig. 19), then southeasterly in fall and winter (Fig. 20). As with age .1 fish, maidens of all ages remain fairly distant from the shores of either continent throughout their oceanic migration except for summer months when they are abundant in nearshore waters immediately south of the 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 (Fig. 20).

Kelts (Mature, Post-Spawning Fish)

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 (Fig. 21). The center of abundance of kelts occurs in the area between 44°N and 54°N latitude and from the coast westward to 145°W longitude. A scattering of kelts occurs in other localities within the Gulf of Alaska or westward to 165°E longitude between 42° and 48°N latitude. 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 165°W. Also apparent is the lower overall abundance of kelts as compared to maiden fish, owing to the generally small fraction of most populations that survive spawning and return to the sea. The familiar pattern of southward and eastward movement into autumn and winter exhibited by other groups of steelhead is also exhibited by kelts (Fig. 22).

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. In the history of the combined offshore tagging programs conducted by the INPFC and the inshore programs conducted by North American fisheries research and management agencies, a total of some 200 tags that might yield insight into the offshore distribution of individual stocks or races has been recovered (French et al. 1975, Light et al. 1988).

The tag recoveries show no clear differences in ocean distribution among groups (Light et al. 1988). Fish from populations of summer and winter, inland and coastal, hatchery and wild, and from widely separated streams along the coast appear to mingle in common feeding grounds. All undergo substantial migrations, although some fish may move farther afield than others simply due to differences in distance between the location of their home stream and centers of abundance on the high seas (e.g., fish from southern Oregon travel farther than those from south-central Alaska). No tagged California fish have been recovered west of the Gulf of Alaska, indicating that they do not migrate as far to the west as do fish from more northerly regions. Also, as pointed out earlier, half-pounder populations do not move far offshore in their first summer in the sea, nor do post-spawning fish move as far offshore as maiden fish, at least in the season immediately following their re-entry into the sea.

Studies of internal parasites as indicators of continental area of origin have recently been published (Dalton 1989; Margolis 1984, 1985), and the collective results corroborate tag-recovery information by showing fish of U.S. Pacific Northwest origins (northern California to coastal Washington) to be widely dispersed and well mixed, at least in the west-central North Pacific where the samples were collected.

Okazaki (1984) 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. 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) weakened his conclusions, which are even further eroded by knowledge of the likely overwhelming numerical superiority of North American relative to Asian steelhead (Harris 1988, Light 1987a). 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.

Light (1987b) used otolith microstructure to identify racial origins of ocean-caught steelhead. 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.

In the absence of other direct evidence, tag-recovery information continues 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 (Light et al. 1988).

Distribution Relative to Sea Surface Temperature

While the east-west distribution of North American steelhead is very broad, the north-south distribution is predictably confined. An examination of sea surface water temperature at the point of capture for over 11,000 steelhead reveals a close relationship between occurrence of steelhead and a particularly narrow temperature range (Okazaki 1983, Sutherland 1973). All of these fish were found in waters between 3°C and 16°C, and nearly 96% were found in waters 12°C or colder (Fig. 23). These temperature boundaries are important in determining the exposure of steelhead to offshore fisheries, but are also ecologically important and may help explain the distribution of the species, especially for the southern limits of their range.

When viewed beside temperature data, the seasonal distribution of steelhead closely corresponds to shifts in the subarctic temperature boundary (Dodimead et al. 1963). As water temperatures rise in subtropical waters south of 38°N latitude from spring to summer, and the subarctic boundary, expressed by the 15°C sea surface isotherm, presses northward and westward, steelhead also move north and west. The location of the 5°C isotherm also moves northward as the seasons progress, often far into the northern Bering Sea (Robinson 1976), but steelhead distribution lags far behind this northern temperature boundary and typically extends only slightly north of the Aleutian Islands to around 56°N. This suggests that the northern distributional limits of steelhead are governed by factors other than sea surface temperature.

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 net set at 15-23 m, revealing that steelhead do occur in deeper waters. Steelhead are also found near the surface in coastal waters (Oguss and Evans 1978). Summer steelhead outfitted with depth-sensitive sonic transmitters spent 72% of their time within 1 m of the surface as they moved through coastal waters en route to the Dean River, B.C. (G. Ruggerone and T.P. Quinn, FRI unpublished data).

Model of Migration

A composite picture of steelhead movements during their marine residence can be created from the life history information presented earlier¹. In spring through early summer of their first year, steelhead smolts enter the sea and move directly offshore (Hartt and Dell 1986, Wakefield et al. 1981, this report) (Fig. 24). 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. Asian fish have also cleared coastal waters and are presumably en route eastward, except for fish that purportedly remain in coastal waters throughout their marine residence (Savvaitova et al. 1973). Because Asian coastal forms of steelhead likely inhabit coastal waters near to their home streams, they will be excluded from the following discussions. A small contingent 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. As fall approaches, North American fish turn south and east toward the North American coastline. The center of abundance and details of steelhead movements in winter are currently unknown. Half-pounders return to freshwater at this time. Provided Asian fish overwinter in the same areas as North American steelhead, i.e., the eastern North Pacific, they probably join their North American counterparts by fall or winter of their first year in the sea.

Westward movement begins and continues during winter months, and by spring of their second year at sea, young steelhead are widely distributed over a large area of the North Pacific west to about 150°E longitude (Fig. 25). Most of these fish are found between 175°E-130°W and 44°N-50°N latitude. Except for half-pounders re-entering coastal waters, age .1 fish are probably relatively scarce near the shores of both continents in spring. In late July of their second ocean year, the main group of age .1 steelhead has moved a considerable distance west and north. Fish are concentrated south of the Aleutian Islands in this period.

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

¹ Because no direct evidence confirms the presence of Asian steelhead in offshore catches, any inferences made regarding their migration patterns are purely speculative and should be treated as wholly provisional.

shoreward movements of winter-run fish bound for North American streams may contribute to the overall appearance of eastward movement of fish in the fall and winter (Figs. 11, 16, 18). This movement would place winter-run fish inshore along the coast on schedule (Fig. 26). These maturing fish will continue eastward to enter spawning streams in November-April.

By the spring of their third year at sea (with two winter ocean annuli on their scales), steelhead are broadly distributed across the North Pacific (Fig. 27). A notable feature of this season is the appearance of post-spawning fish that are beginning to move offshore from both continents. The northwest to southeast seasonal movements of immature fish in their third and later years at sea resemble those of age .1 fish. Kelts from North America lag behind maidens in their westward distribution but still travel a considerable distance offshore before returning to spawn again (Fig. 28). Alternate-year spawners may join the main group of fish, whereas consecutive spawners probably never return to the distant waters they may have travelled as maidens. Figure 29 depicts movements from late autumn into winter, including the shoreward movement of maturing winter-run fish. Some question remains as to whether winter-run stocks occur among Asian populations (Savvaitova et al. 1973). 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.

DISCUSSION

Steelhead travel great distances in offshore waters of the North Pacific Ocean during their marine life history phase. The general northwest-southeast pattern of their seasonal movements, first noted by Sutherland (1973), then later by Okazaki (1985), appears to be consistently followed by fish from all age groups and spawning histories in each year the fish are at sea. Interestingly, most migrating steelhead are found within two oceanographic regions described by Dodimead et al. (1963). In the winter and spring, steelhead are most abundant in the Central Subarctic domain that includes the Alaskan gyre. In summer and autumn, as steelhead move north and west, they also enter the Alaskan Stream domain. The western end of the Alaskan Stream (around 170°E) is also the area where steelhead abundance diminishes. The oceanographic conditions associated with both the Central Subarctic and Alaskan Stream domains are fairly low salinities (except within the Alaskan Gyre) and warm surface waters (Dodimead et al. 1963). A slow (3 km/d) counter-clockwise current sweeps east along the southern fringe of the Central Subarctic domain from approximately 170°E to 135°W longitude, then north to about 58°N latitude, where it curves westward and speeds up (13-16 km/d) to form the Alaskan Stream south of Kodiak Island (Dodimead et al. 1963).

Also of interest is the absence of steelhead in the Bering Sea and Bristol Bay. As described earlier in this report, sea surface water temperatures north of the Aleutian Islands, at least in summer and autumn, do not seem to be unsuitable for steelhead. Neither should food supply be a deterrent to steelhead, at least judging by the presence of other salmonid species in this area (Manzer et al. 1965). Because relatively high salinities prevail in waters of the Western Subarctic domain, an area that includes part of the Bering Sea (Dodimead et al. 1963), salinity may be an important determinant of the northern limit of steelhead distribution on the high seas.

One steelhead life history feature that continues to elude detection is the location and timing of departure of maturing summer- and winter-run fish en route to spawning streams. The time of return to freshwater is distinctly different for these two races, and presumably requires a somewhat different ocean migration pattern. Depending upon the race of a

particular fish, maturing steelhead would be expected to leave ocean feeding grounds and return to the coast of either continent anywhere from June to September for summer-run fish and December to April for winter-run fish. However, the seasonal distribution analysis does not provide any indication of the timing of spawning migrations, and the events must be hypothesized using migration models.

In the absence of any empirical evidence, the marine distribution and migration patterns of Asian steelhead were presumed to mirror those of North American fish. This requires that at some point in their offshore migration, Asian steelhead join the North American contingent of migrating fish. Because information on Asian fish is so scarce, their distribution and migration patterns could only be hypothesized. It is possible that these fish do not migrate far from the Asian coast and intermingle with North American fish, but instead they may remain in far western waters, perhaps in the area of the Western Subarctic Gyre (Dodimead et al. 1963). Implementation of a tag recovery program in Kamchatka coupled with increased tagging in western waters might greatly increase our knowledge of Asian fish distribution on the high seas.

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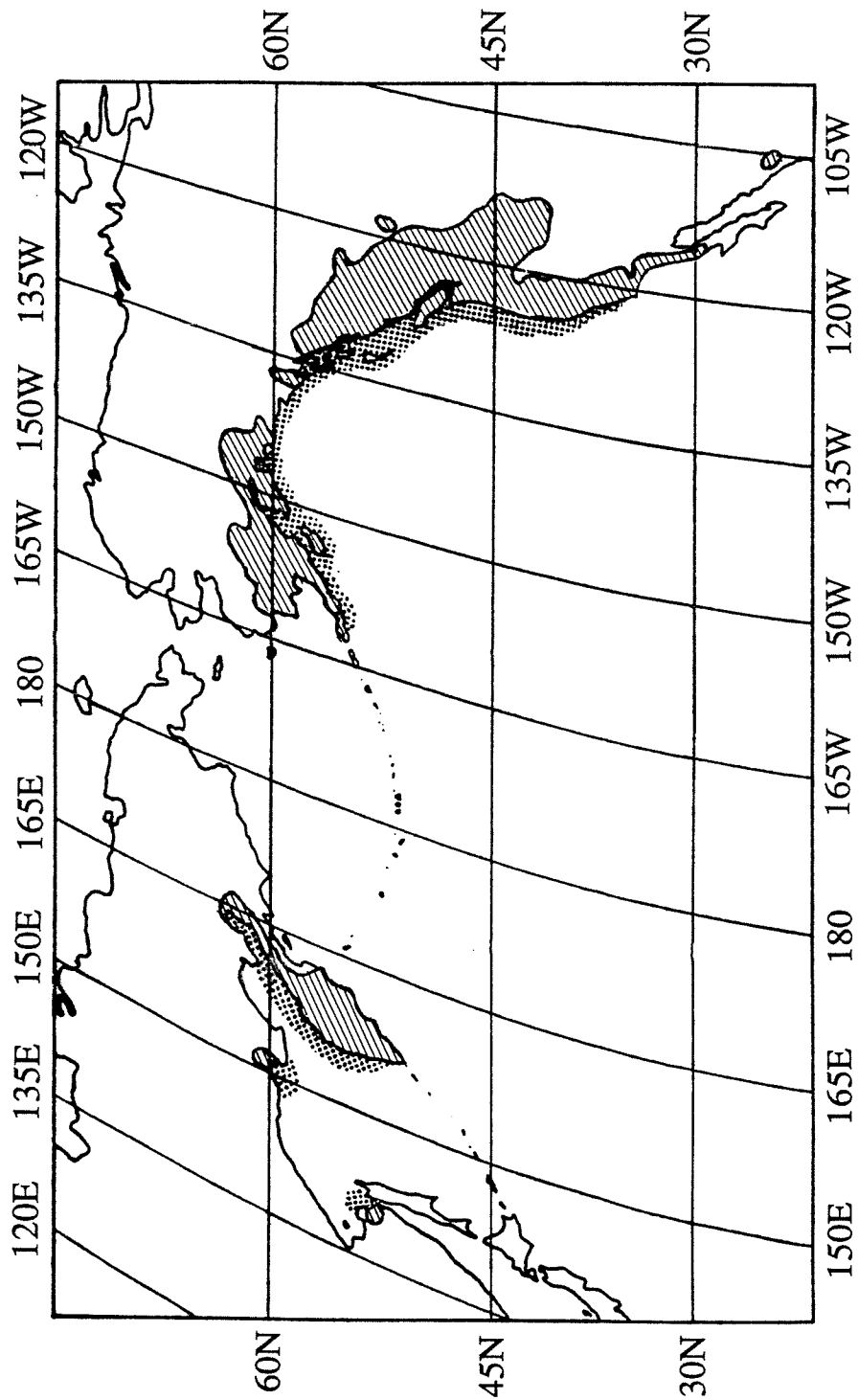


Figure 1. Endemic range of rainbow trout *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) (shaded). Stippled areas indicate coastal areas where watersheds containing anadromous forms empty into the sea (modified from Okazaki 1983).

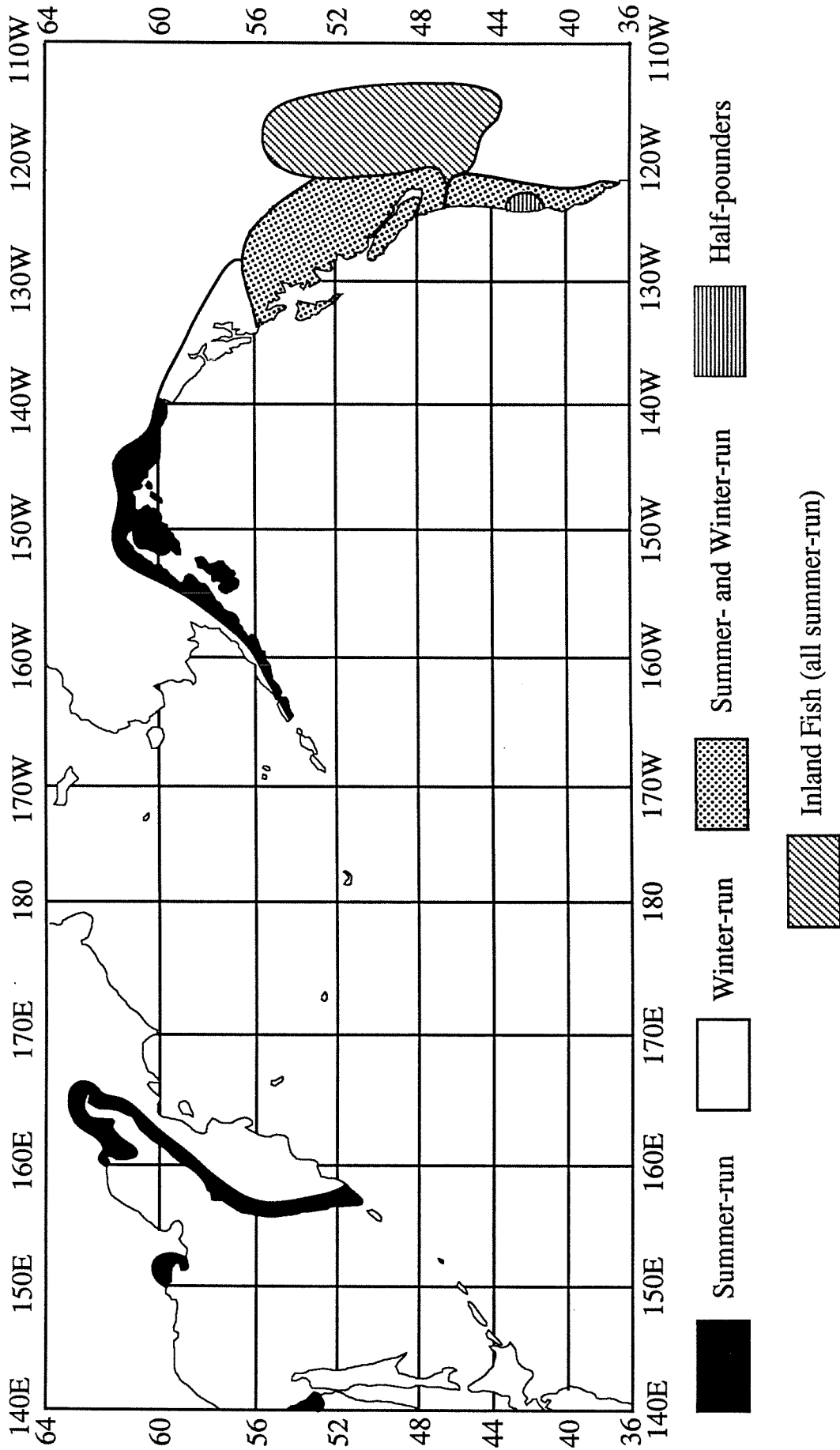


Figure 2. Geographic distribution of major steelhead life history subgroups (see text for subgroup definitions and characteristics).

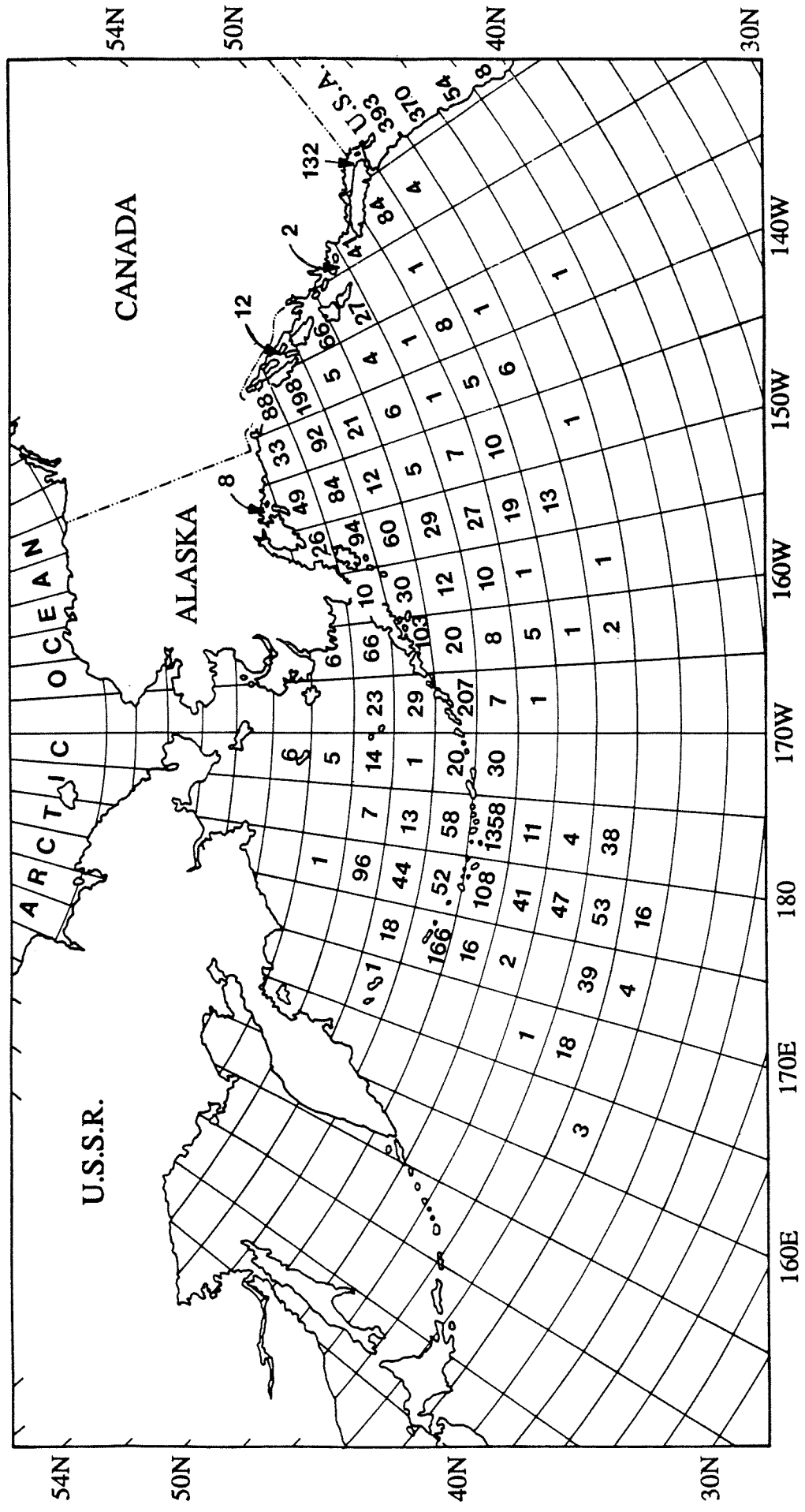


Figure 3. Distribution of purse seine effort (number of sets) by U.S. and Canadian (1955-1985), and U.S.S.R. (1983-1985) research vessels operating in the North Pacific Ocean and Bering Sea.

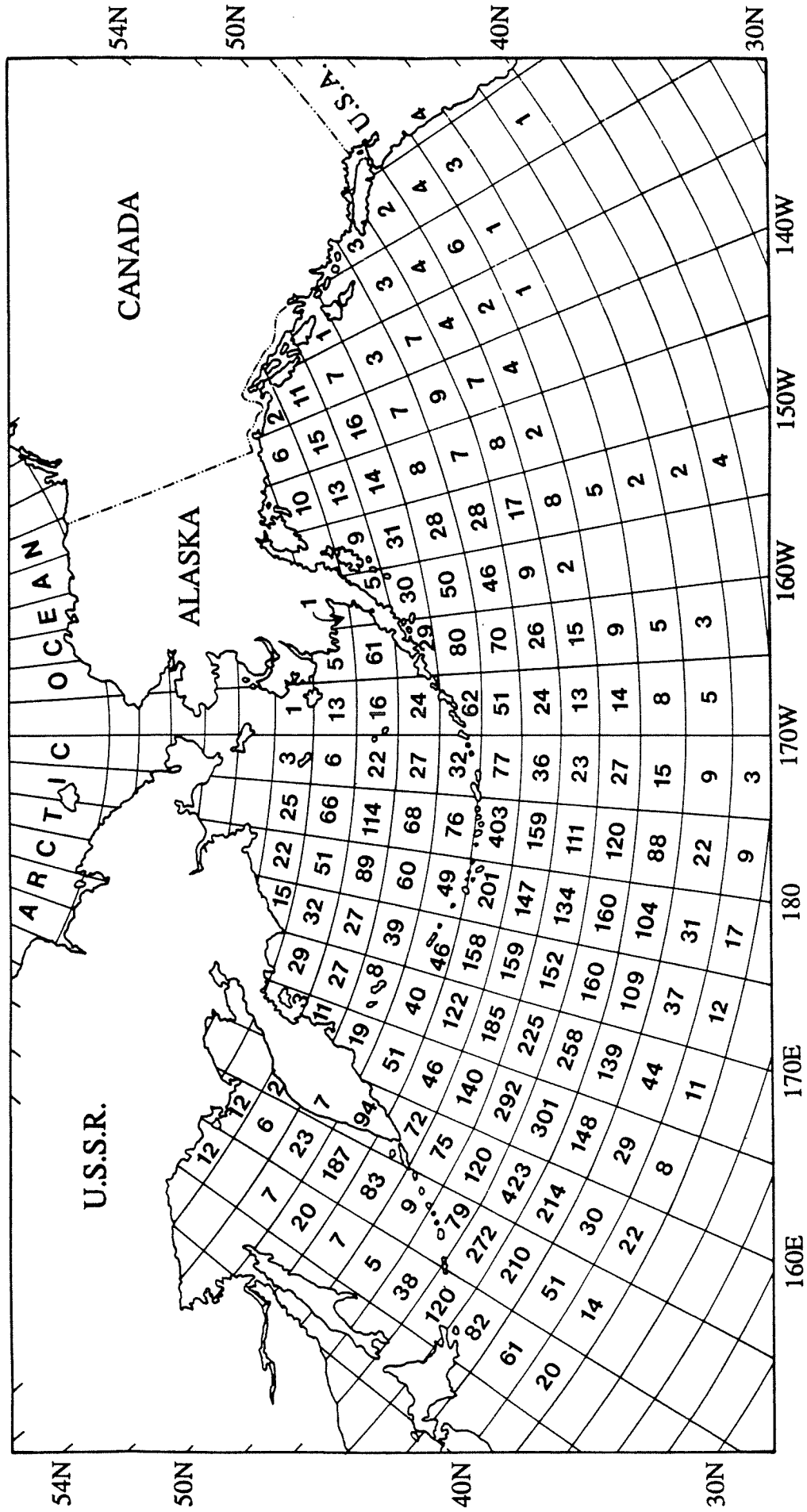


Figure 4. Distribution of gillnet effort (number of sets) by U.S. and Canadian (1955-1982) and Japanese (1972-1985) research vessels operating in the North Pacific Ocean and Bering Sea.

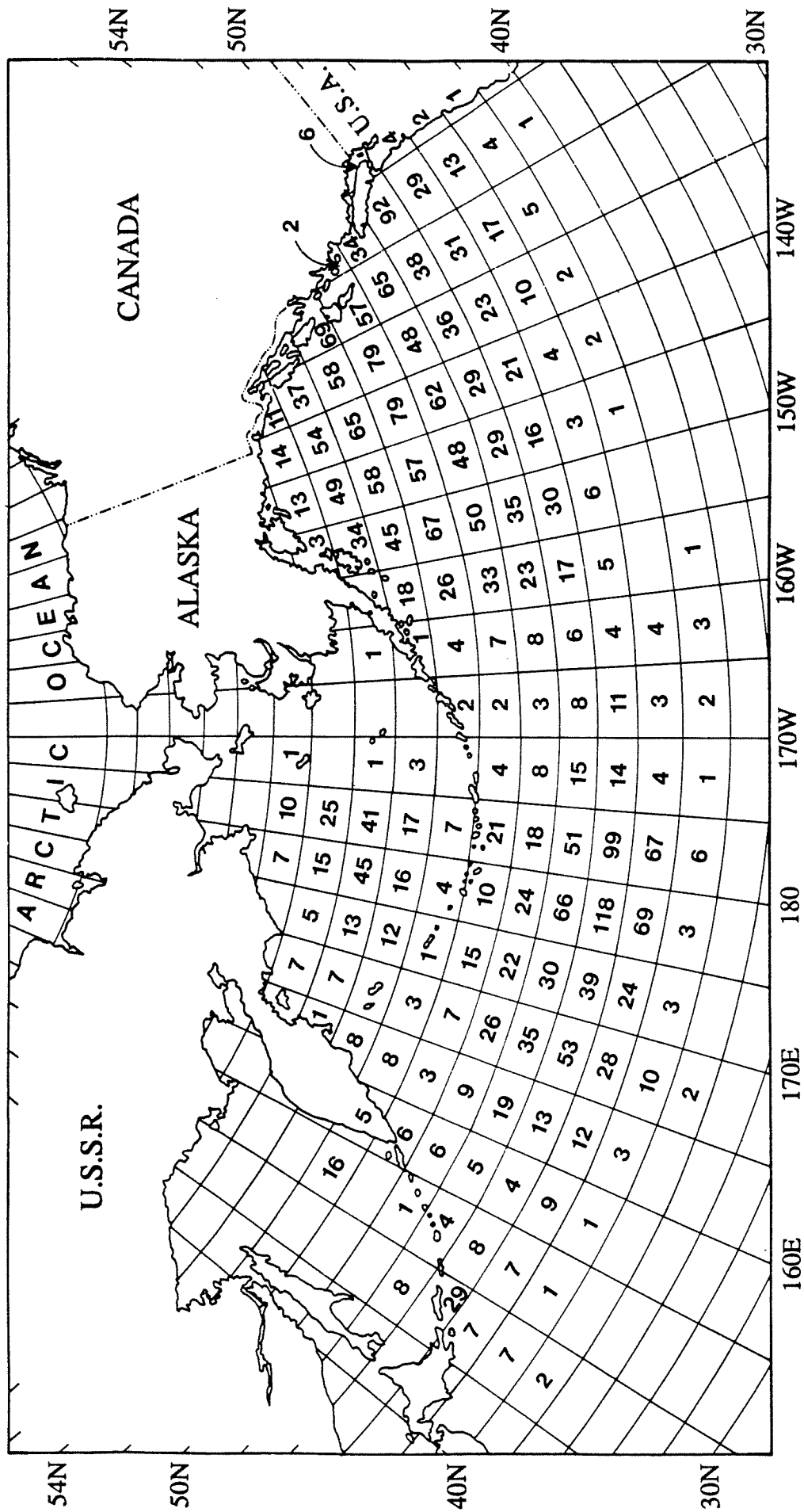


Figure 5. Distribution of longline effort (number of sets) by U.S. and Canadian (1955-1982) and Japanese (1972-1985) research vessels operating in the North Pacific Ocean and Bering Sea.

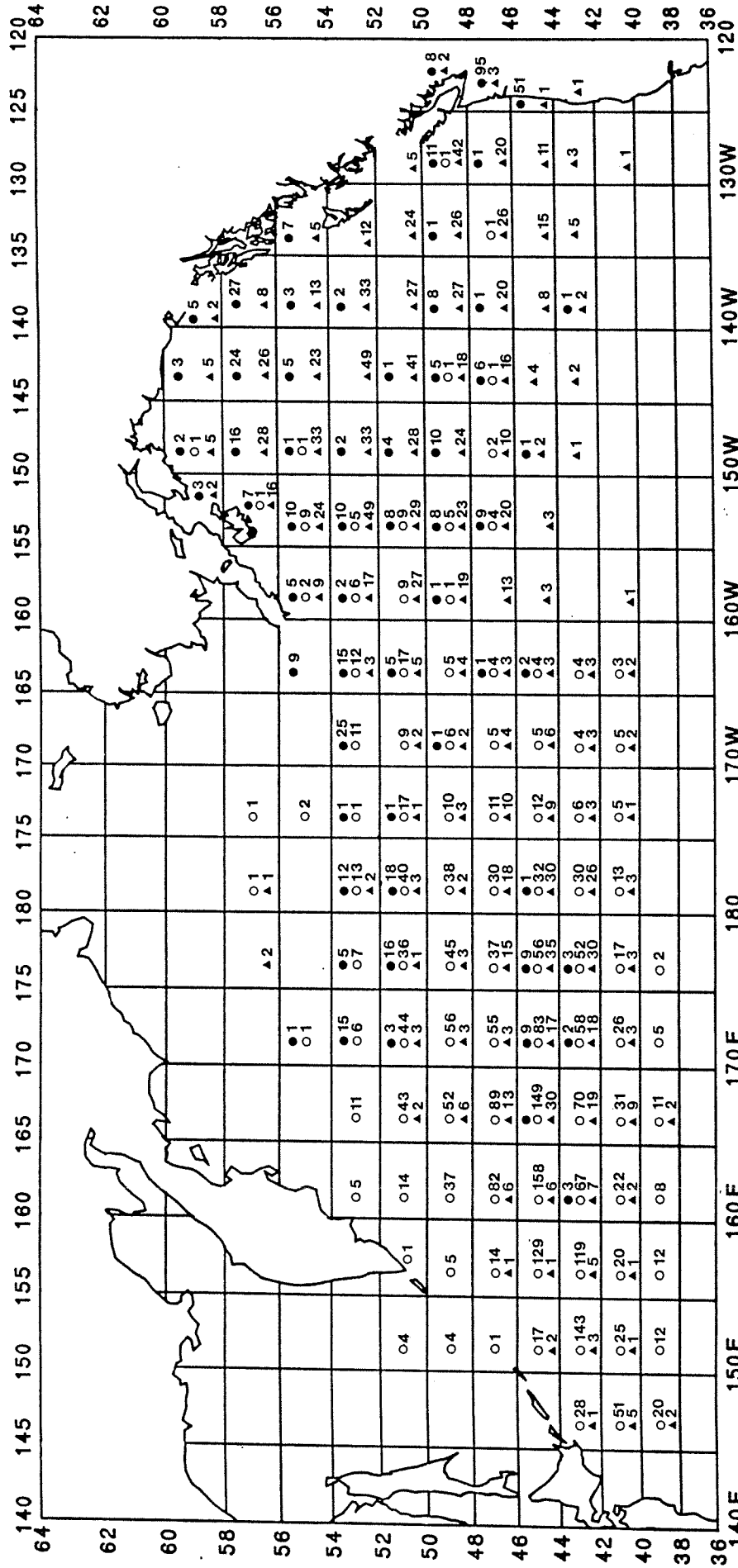


Figure 6. Spring distribution of fishing effort by U.S. and Canadian (1955-1985), Japanese (1972-1985), and U.S.S.R. (1983-1985) research vessels. The numbers shown in each 2°x5° area are total sets of purse seines (●), gillnets (○), and longlines (▲).

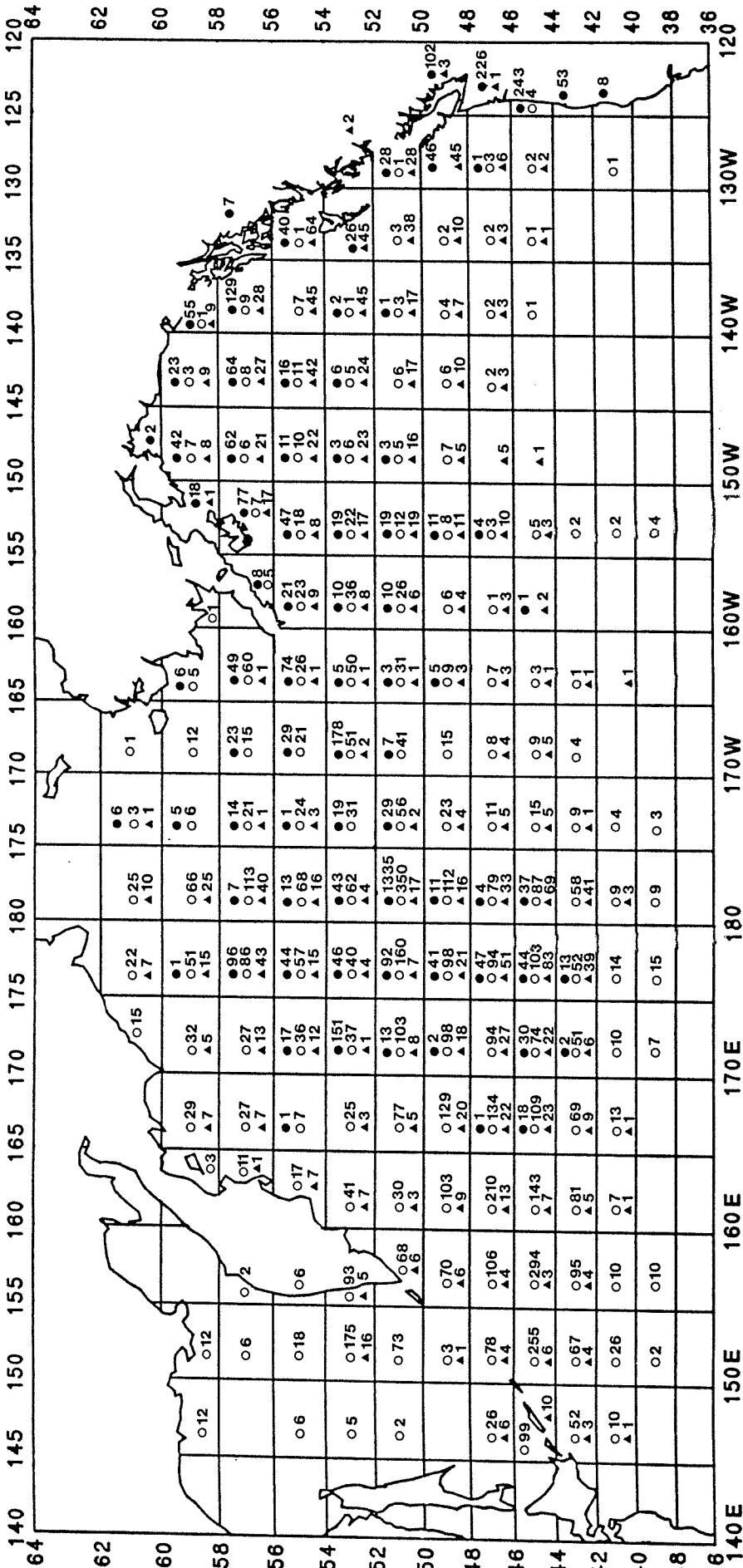


Figure 7. Summer distribution of fishing effort by U.S. and Canadian (1955-1985), Japanese (1972-1985), and U.S.S.R. (1983-1985) research vessels. The numbers shown in each 2°X5° area are total sets of purse seines (●), gillnets (○), and longlines (▲).

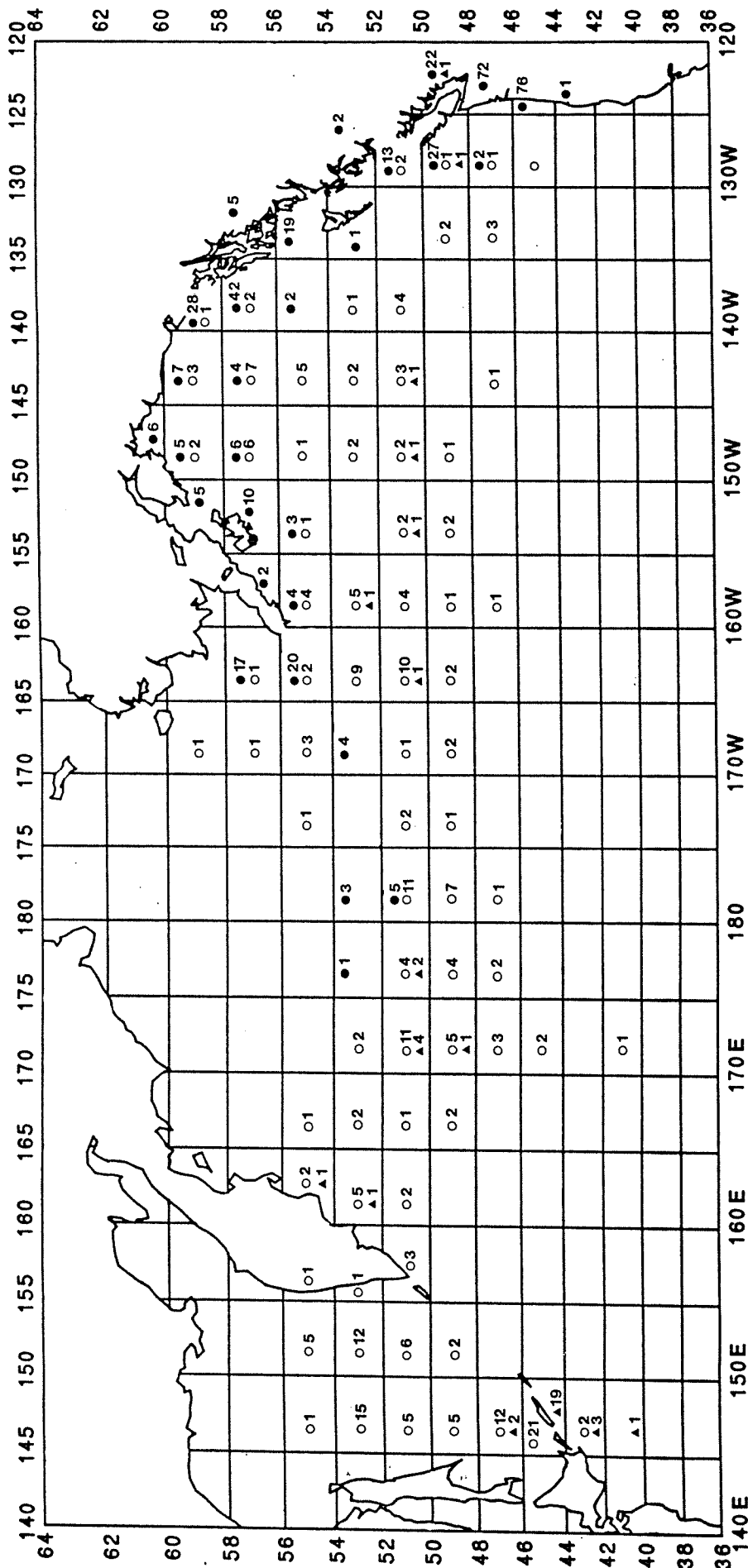


Figure 8. Autumn distribution of fishing effort by U.S. and Canadian (1955-1985) and Japanese (1972-1985) research vessels. The numbers shown in each 2°x5° area are total sets of purse seines (●), gillnets (○), and longlines (▲).

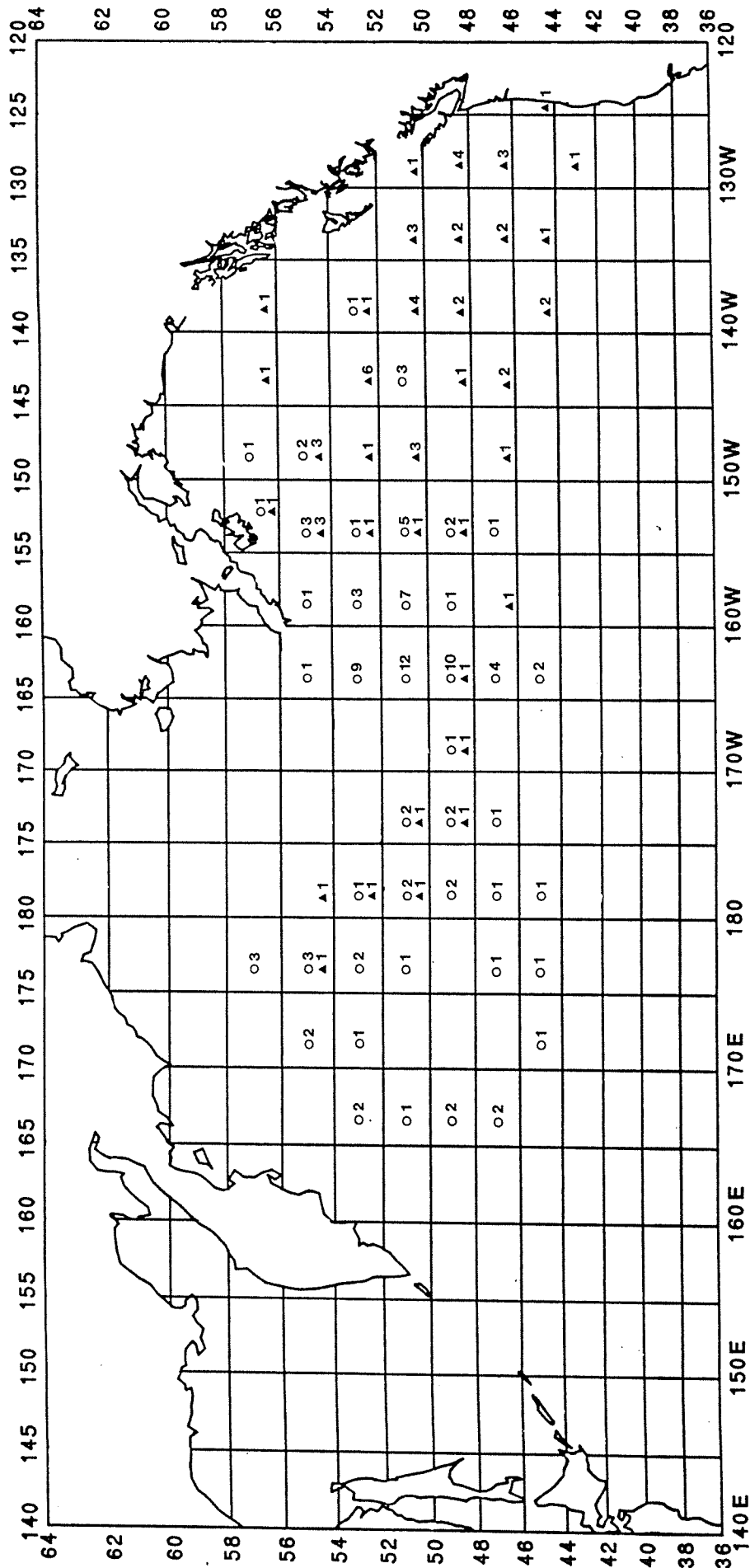
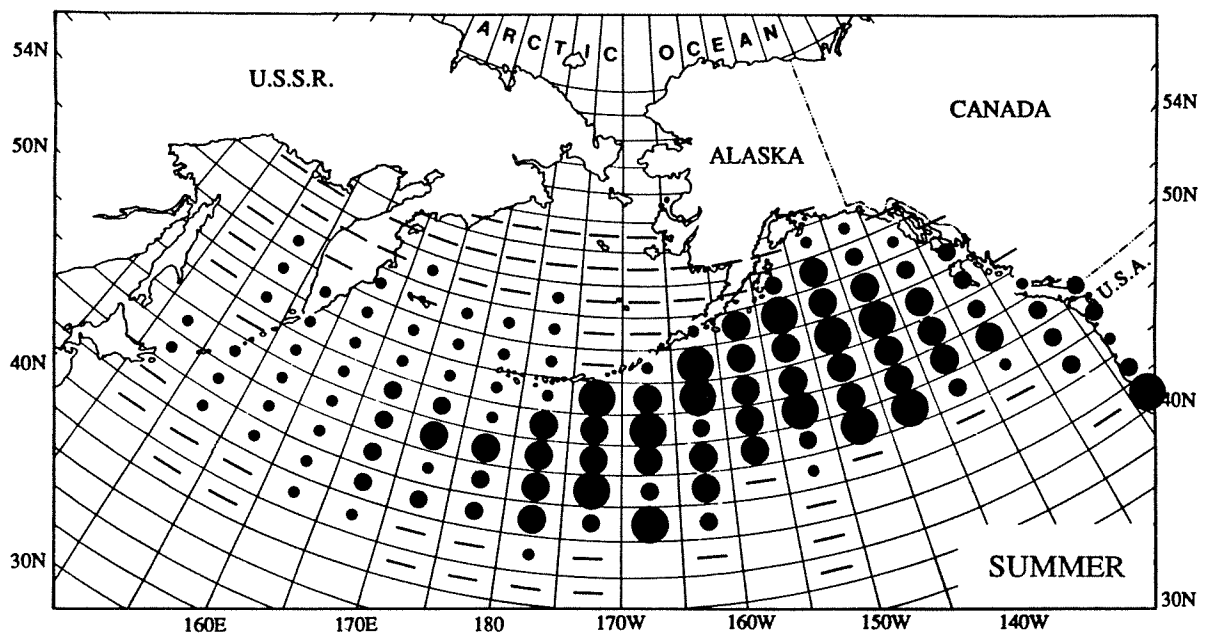
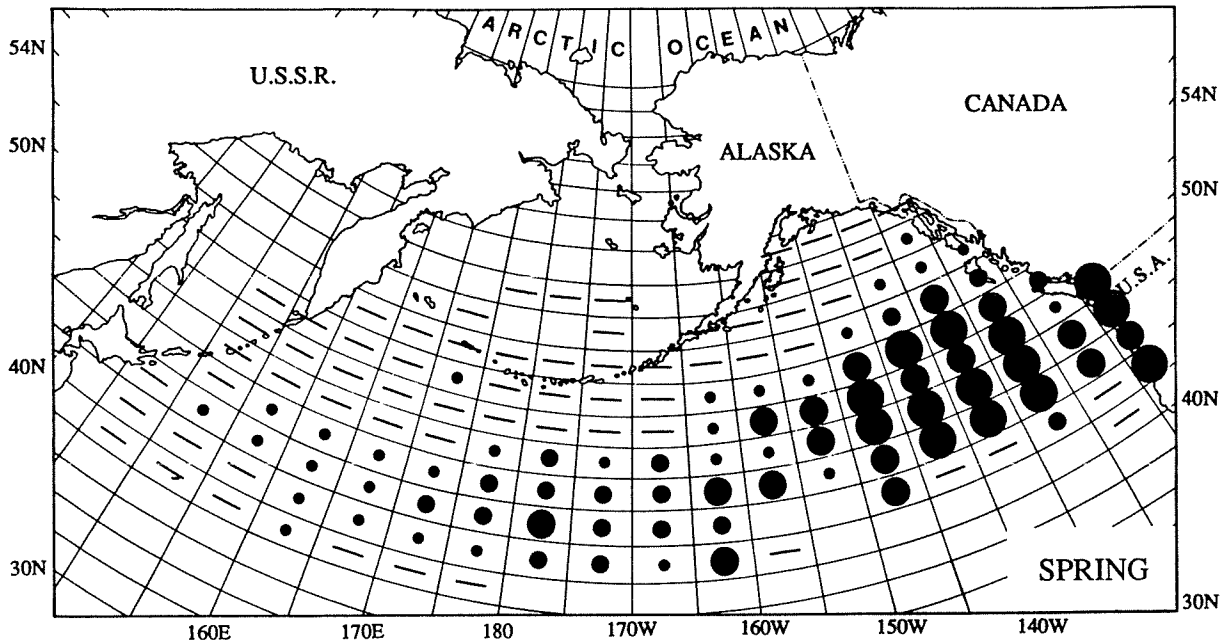


Figure 9. Winter distribution of fishing effort by U.S. and Canadian (1955-1982) and Japanese (1972-1985) research vessels. The numbers shown in each 2°X5° area are total sets of gillnets (O) and longlines (▲). No purse seines were fished during winter.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

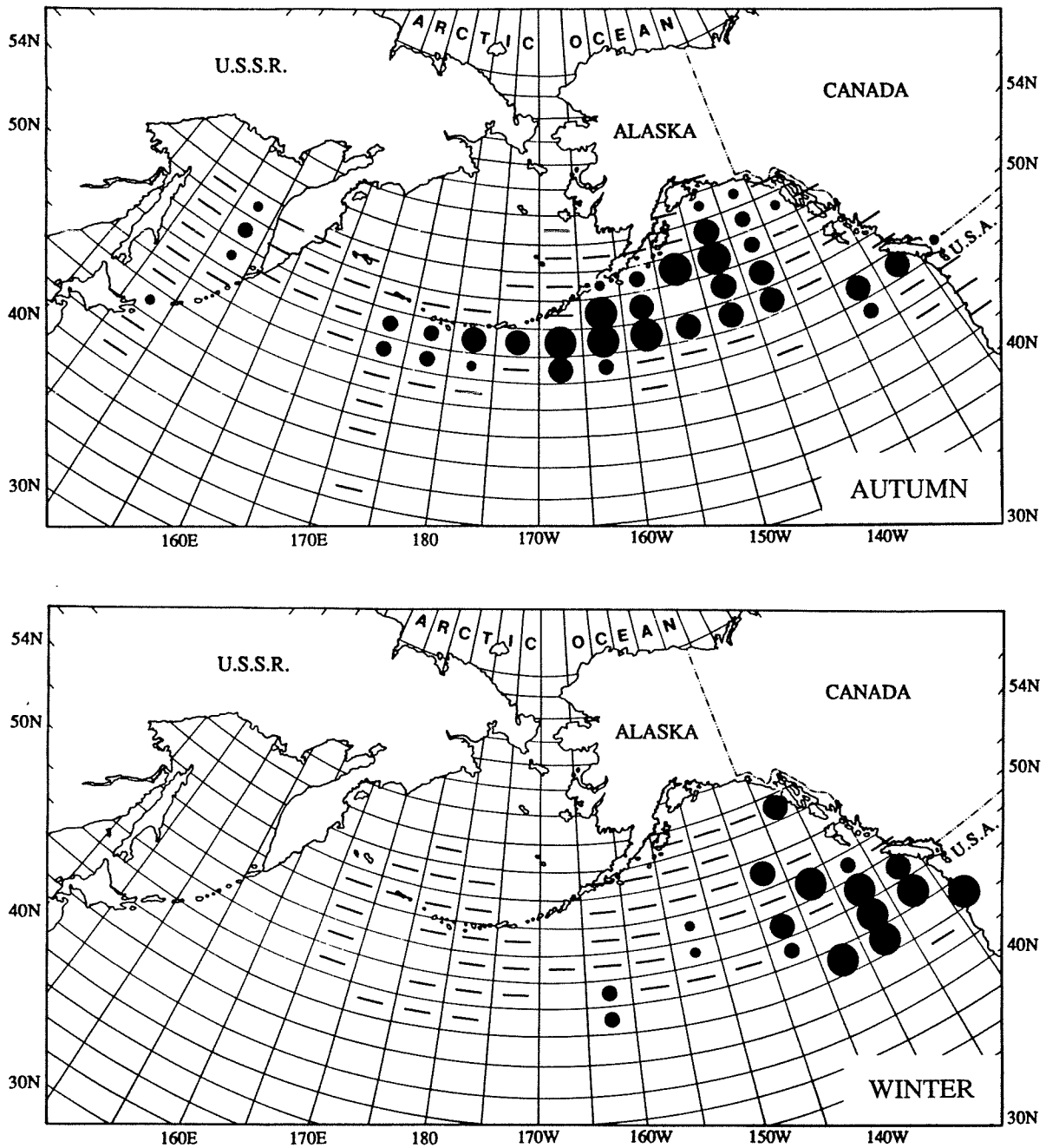
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

Figure 10. 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 (1955-1985), U.S.S.R. (1983-1985), and Japanese (1972-1985) research vessels fishing with purse seines, gillnets, and longlines.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

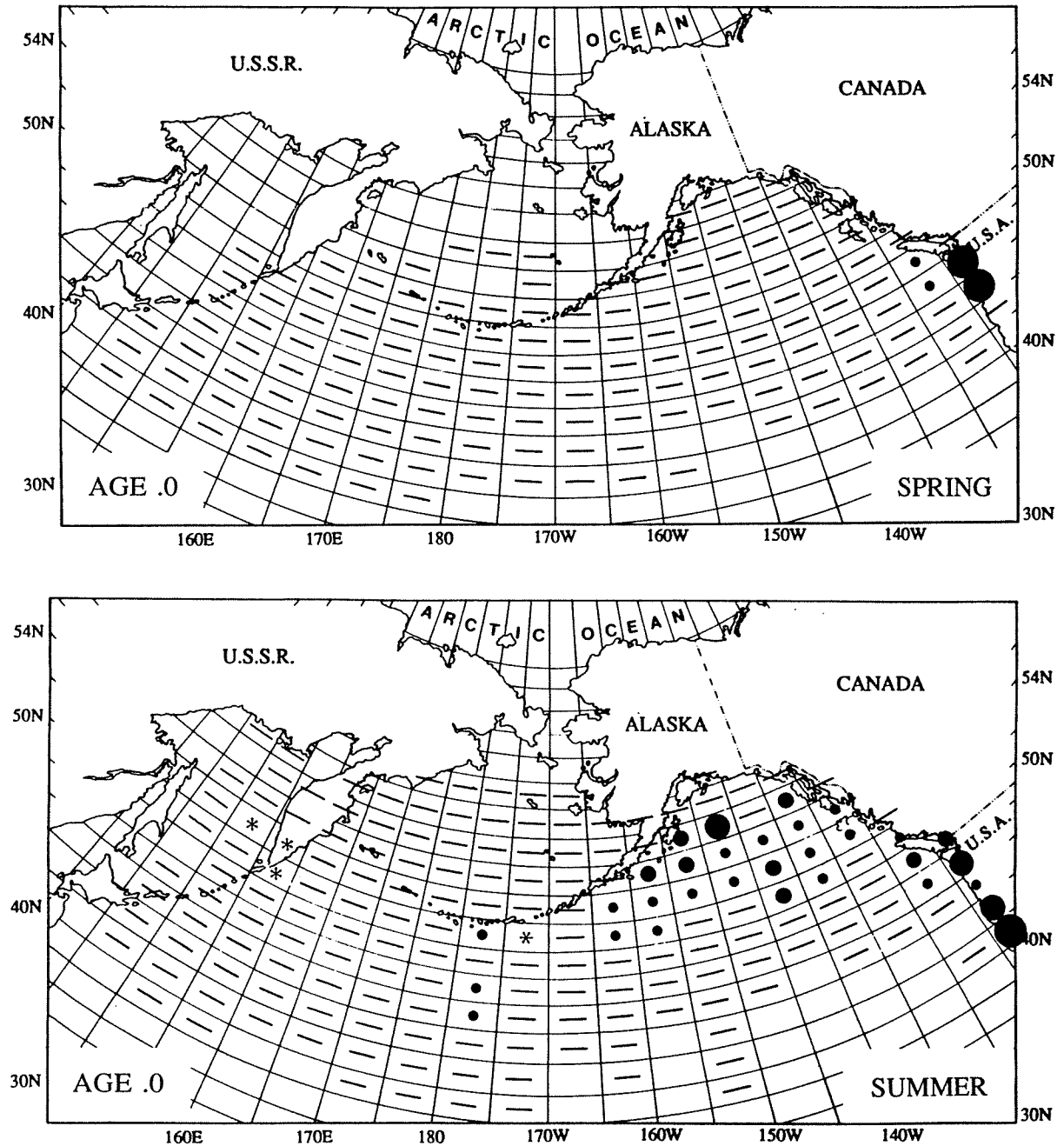
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

Figure 11. 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 (1972-1985) research vessels fishing with purse seines, gillnets, and longlines.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

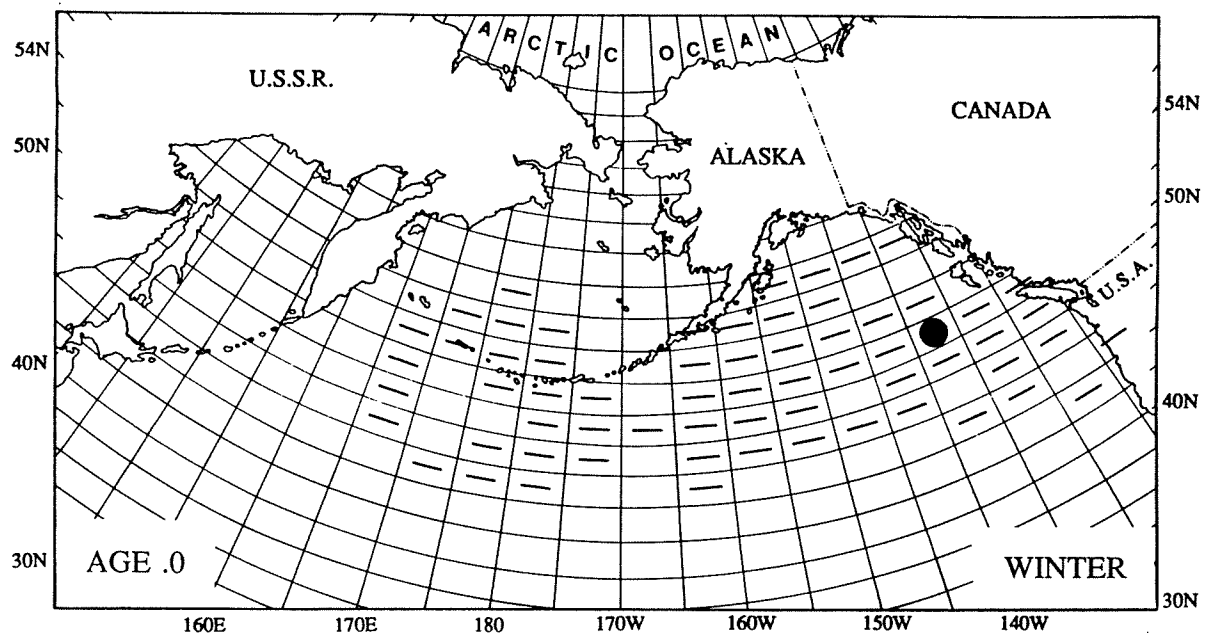
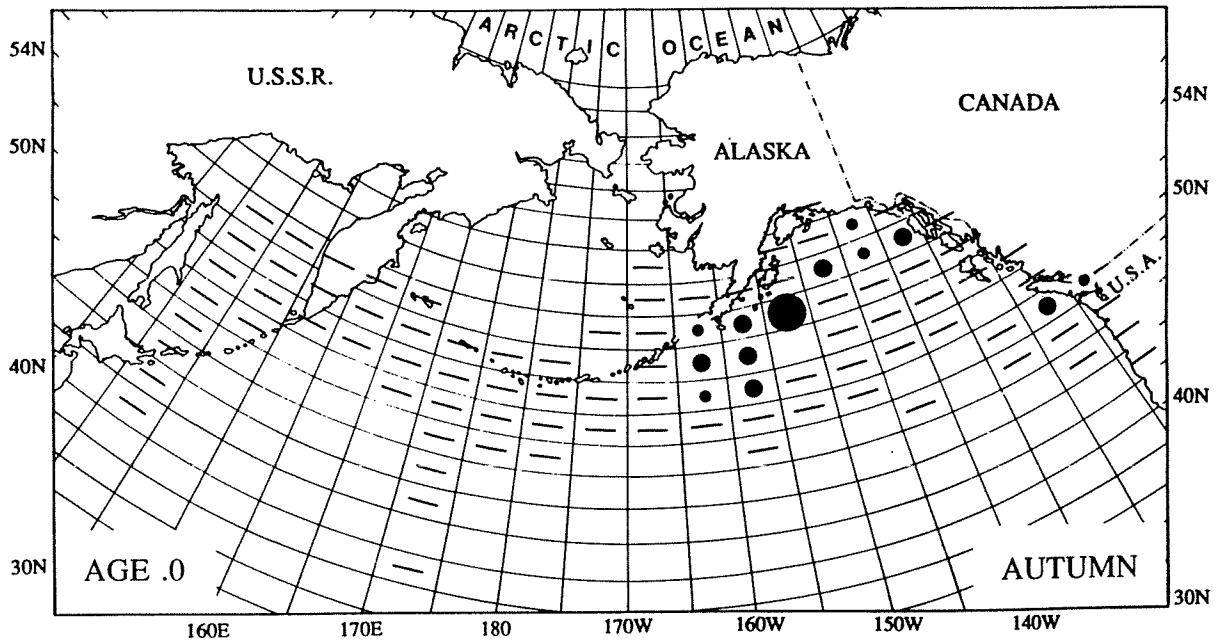
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

Figure 12. 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. Asterisks show areas where age .0 fish were caught by Japanese research vessels in each season, 1972-1980. Incomplete biological data for these years precluded their use in CPUE calculations.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

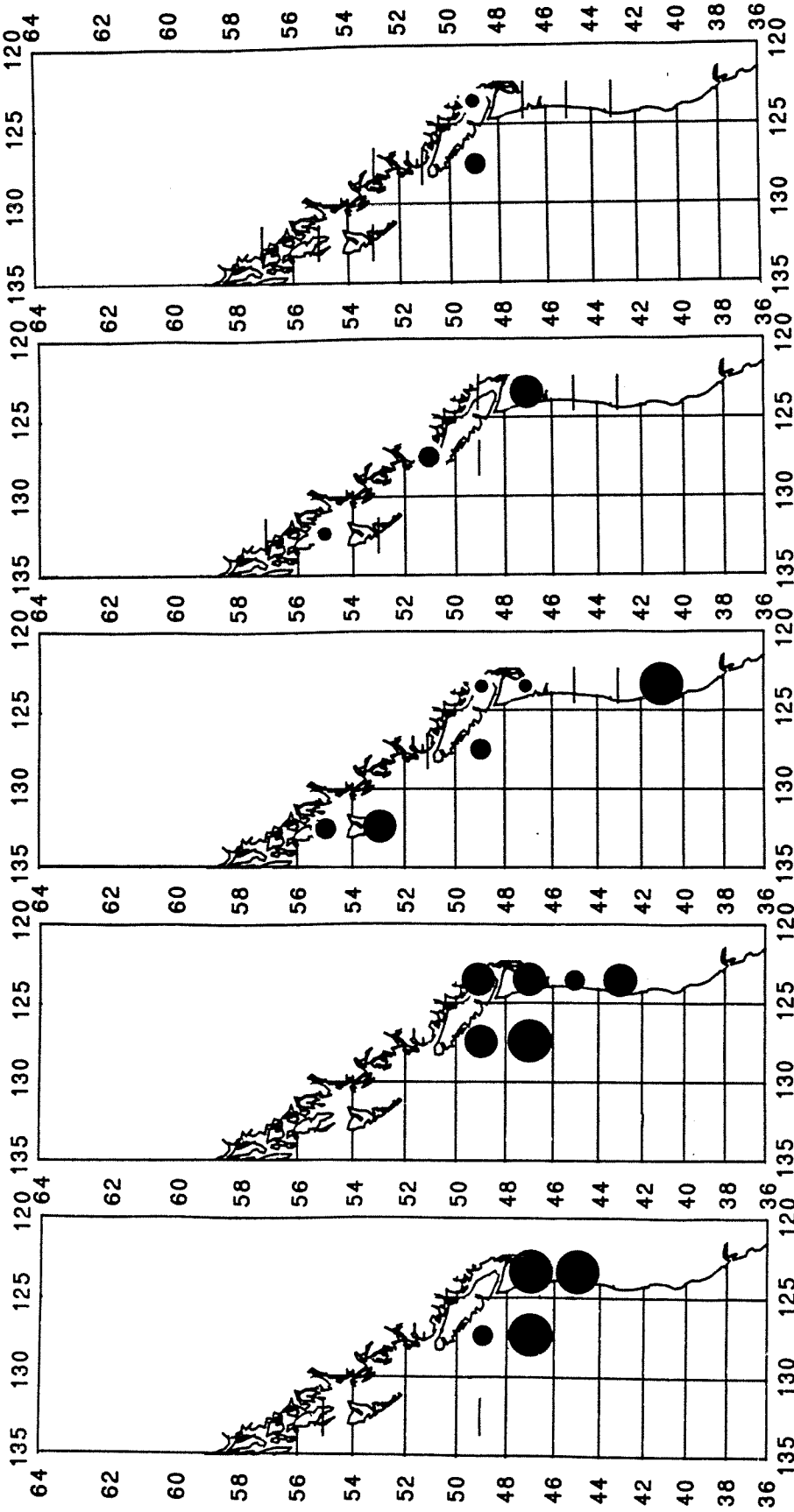
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

Figure 13. 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.

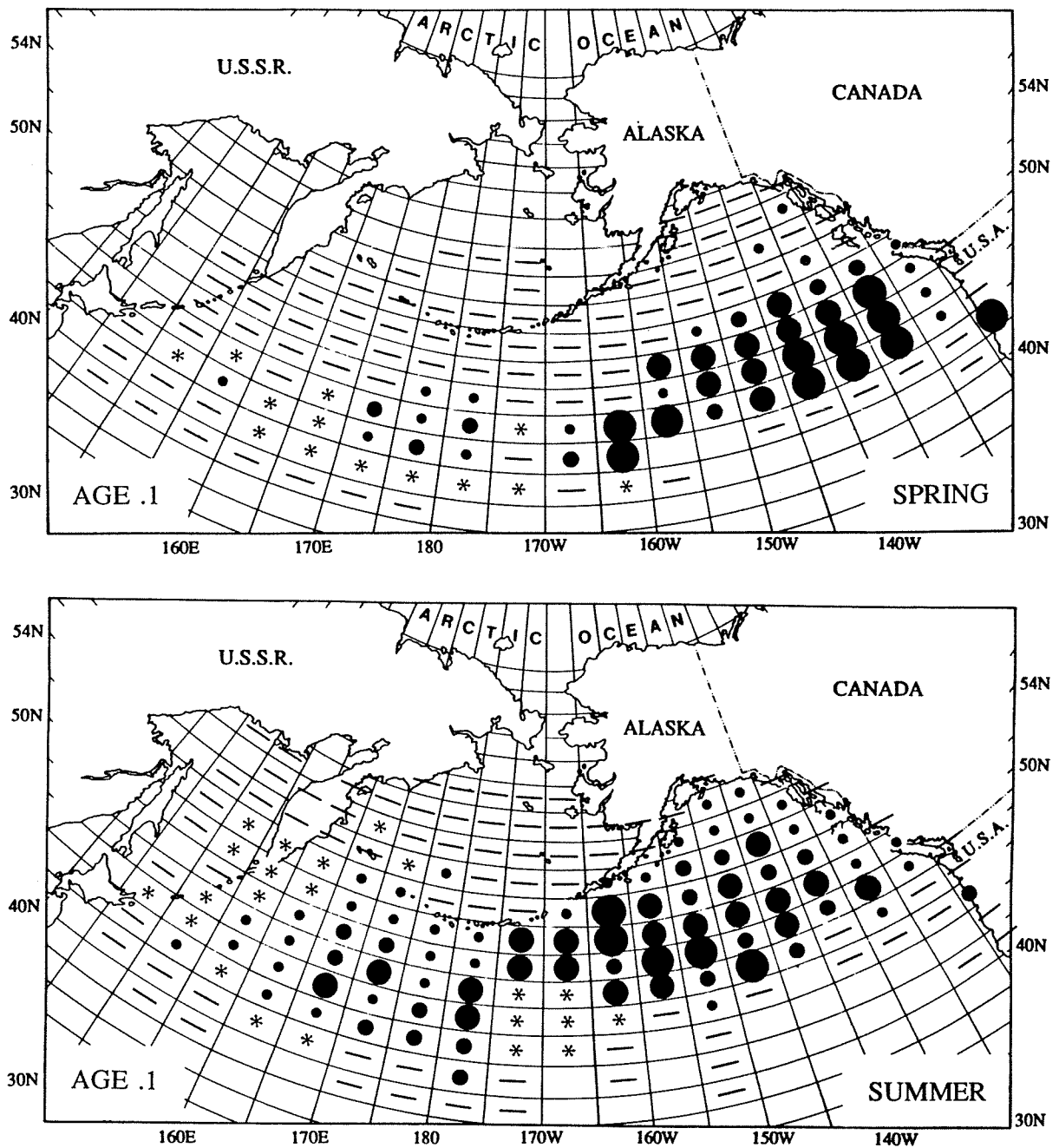


KEY TO CPUE VALUES (steelhead per set):

— = sampling, but no catch

- = .0204 - .0536
- = .0625 - .0909
- = .1176 - .3125
- = .3725 - 14.0000

Figure 14. Nearshore distribution of age-0 steelhead from May to September based on U.S. and Canadian (1955-1985) purse seine catch-per-unit-effort data.

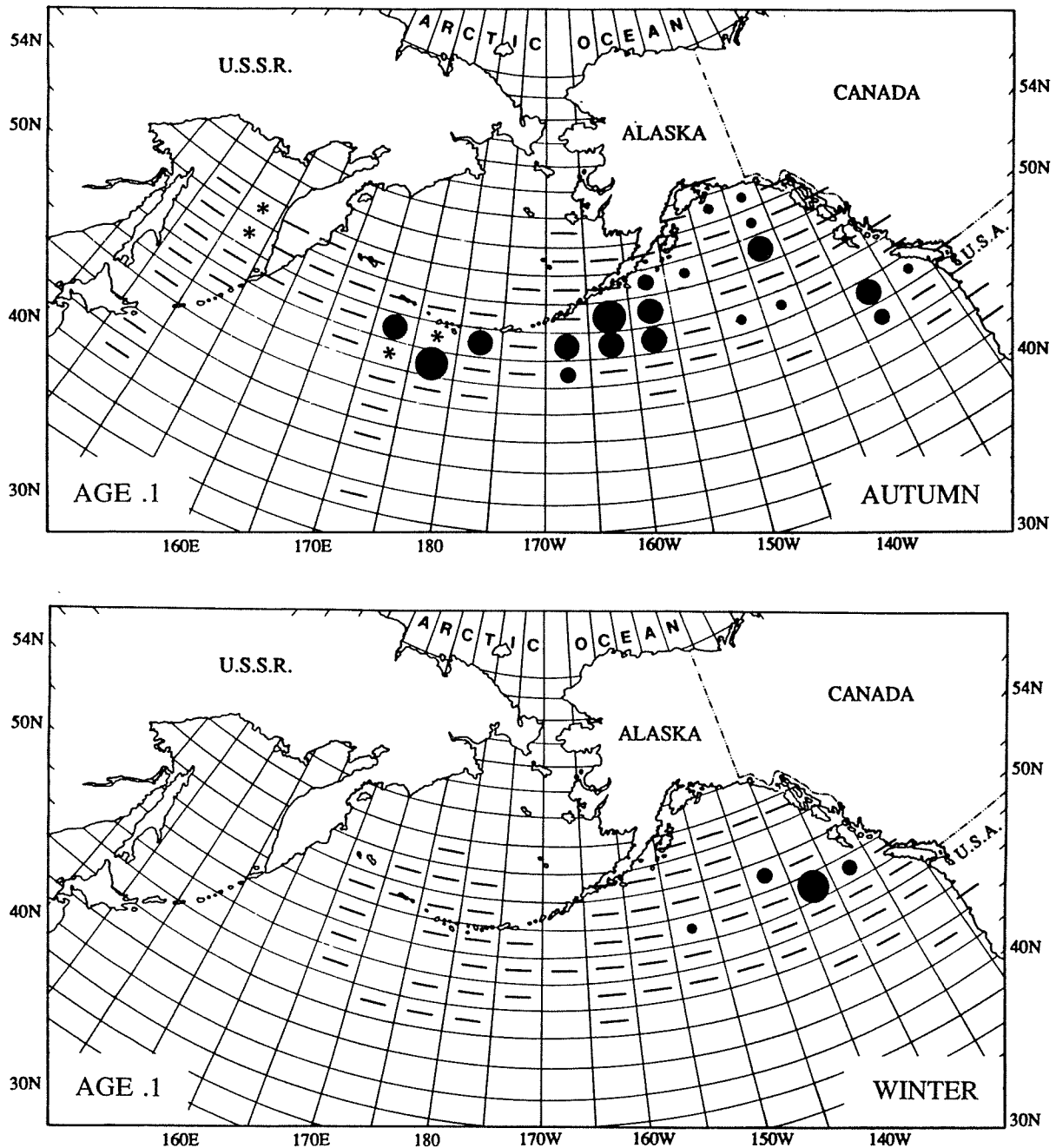


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

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

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. Asterisks show areas where age .1 fish were caught by Japanese research vessels in each season, 1972-1980. Incomplete biological data for these years precluded their use in CPUE calculations.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

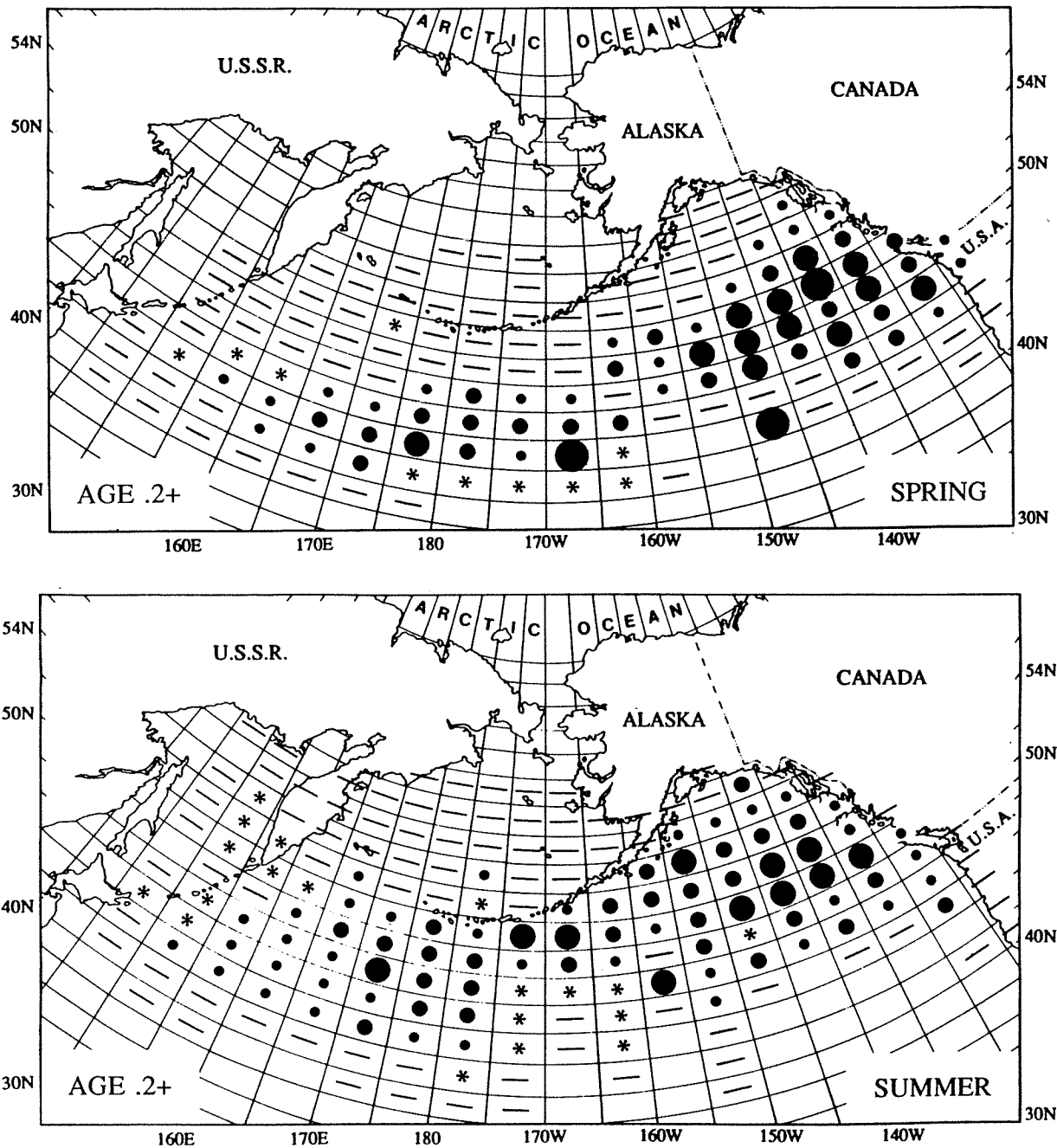
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

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. Asterisks show areas where age .1 fish were caught by Japanese research vessels in each season, 1972-1980. Incomplete biological data for these years precluded their use in CPUE calculations.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

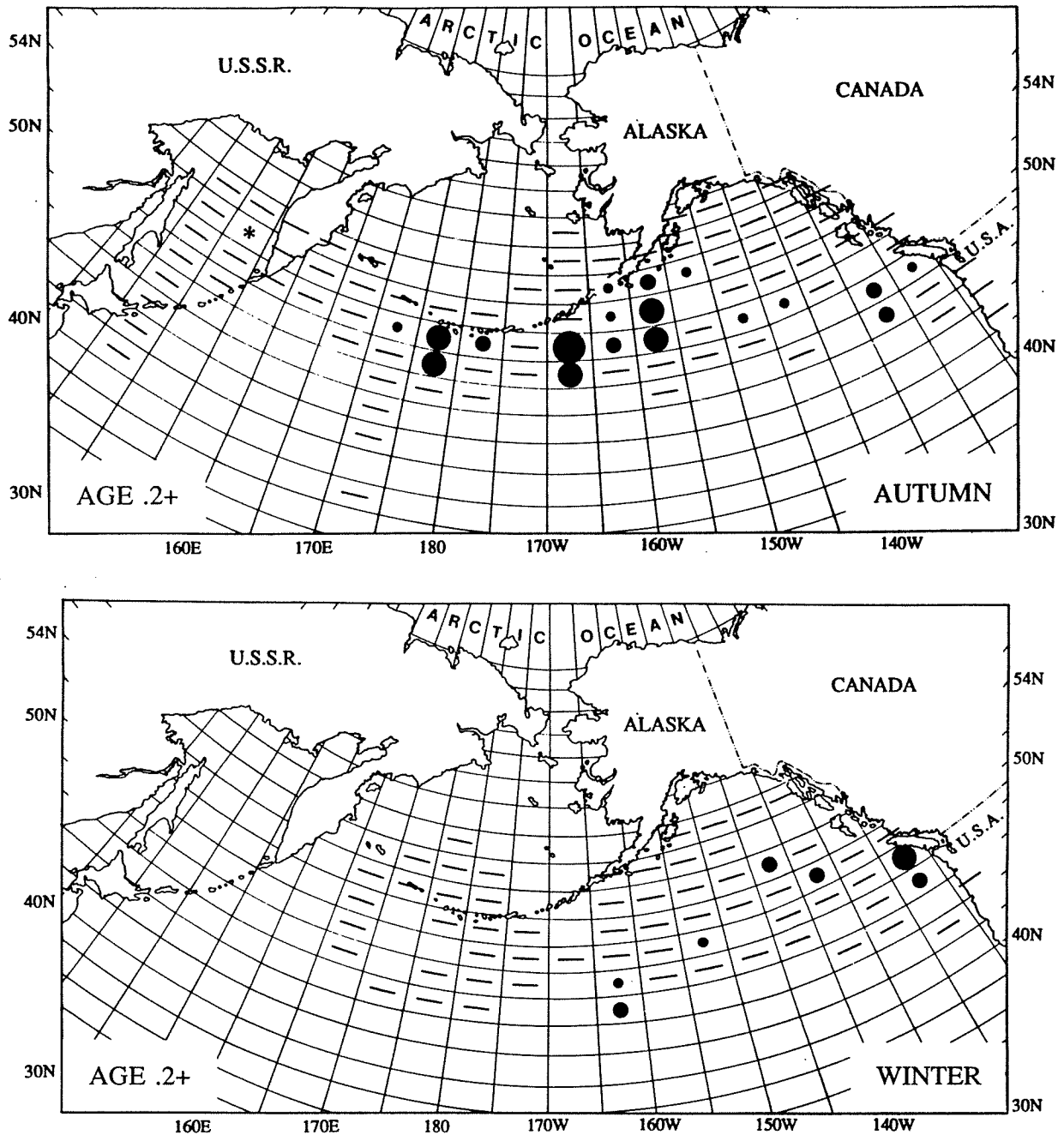
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

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. Asterisks show areas where age .2+ fish were caught by Japanese research vessels in each season, 1972-1980. Incomplete biological data for these years precluded their use in CPUE calculations.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

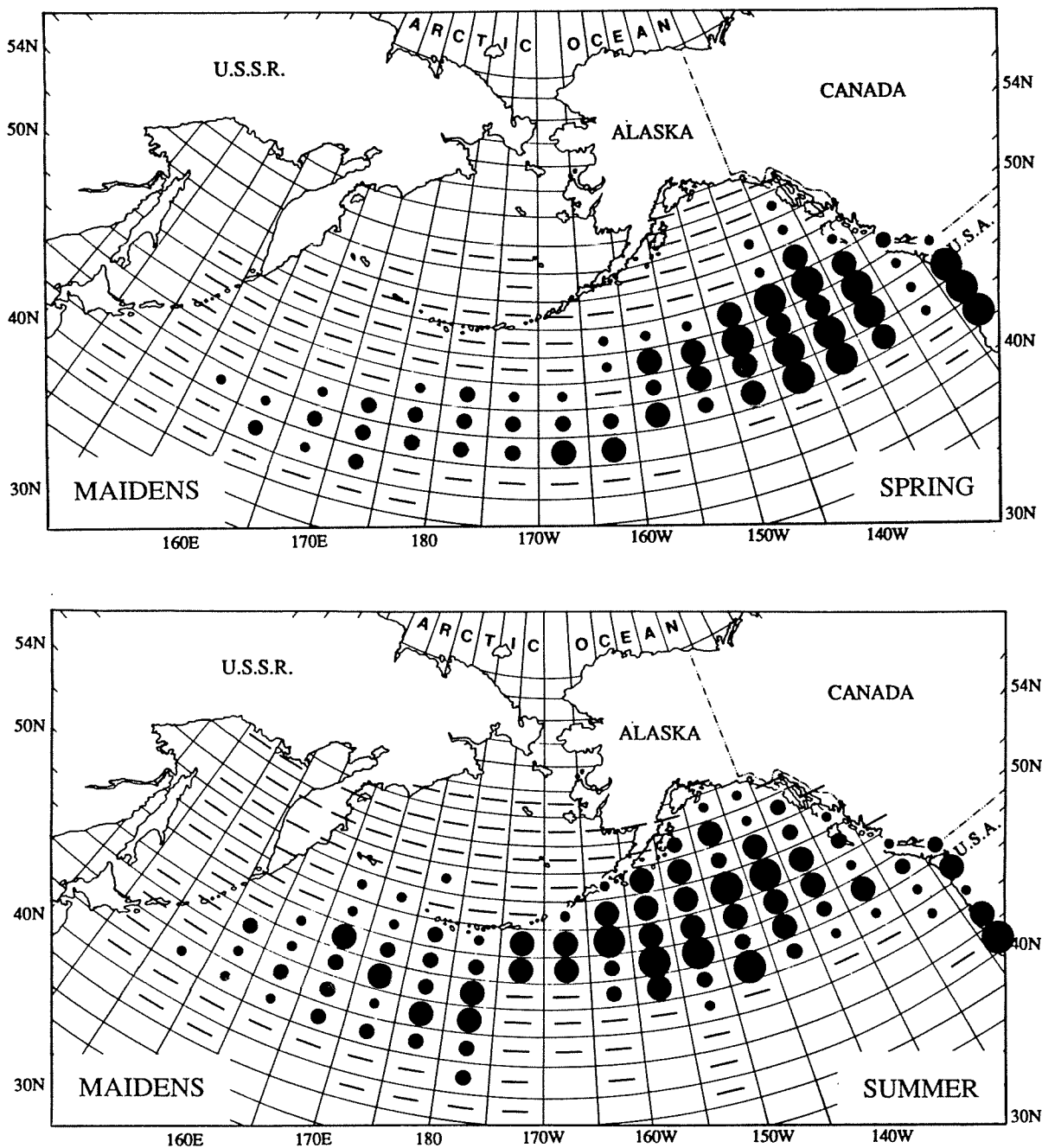
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

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. Asterisks show areas where age .2+ fish were caught by Japanese research vessels in each season, 1972-1980. Incomplete biological data for these years precluded their use in CPUE calculations.



KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

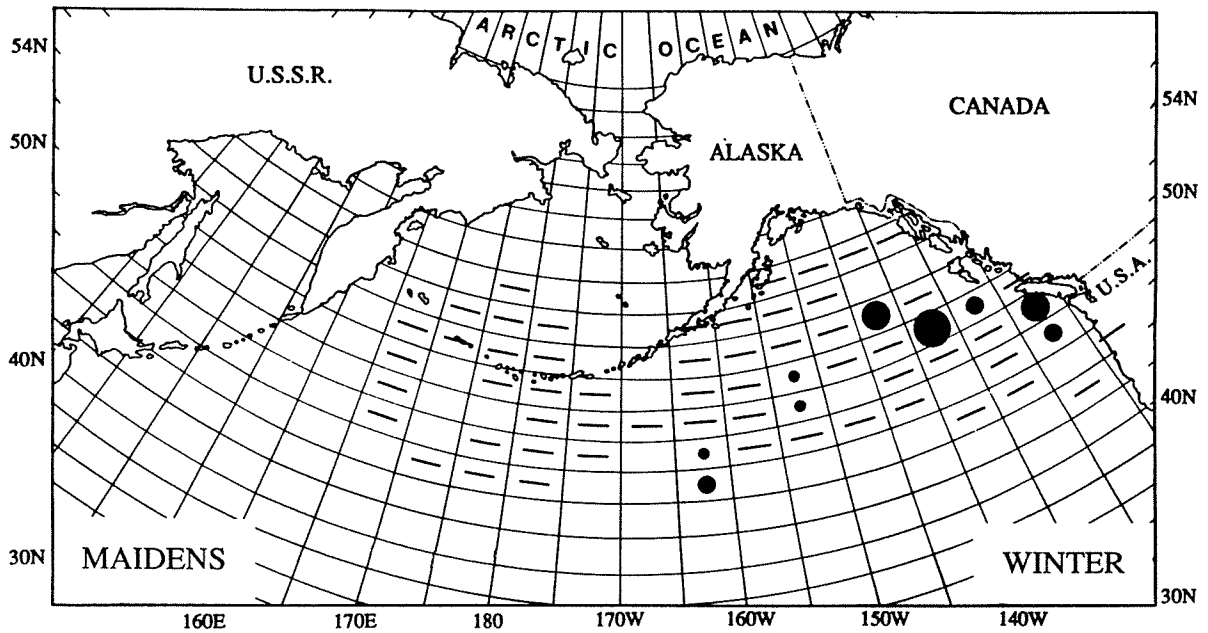
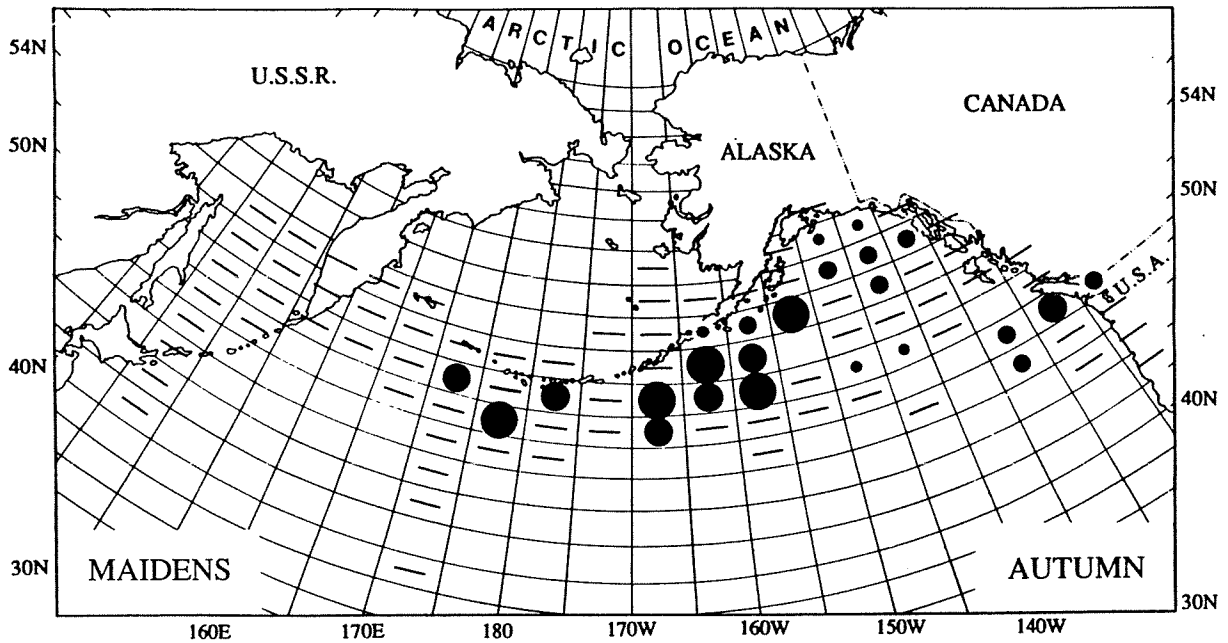
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

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.

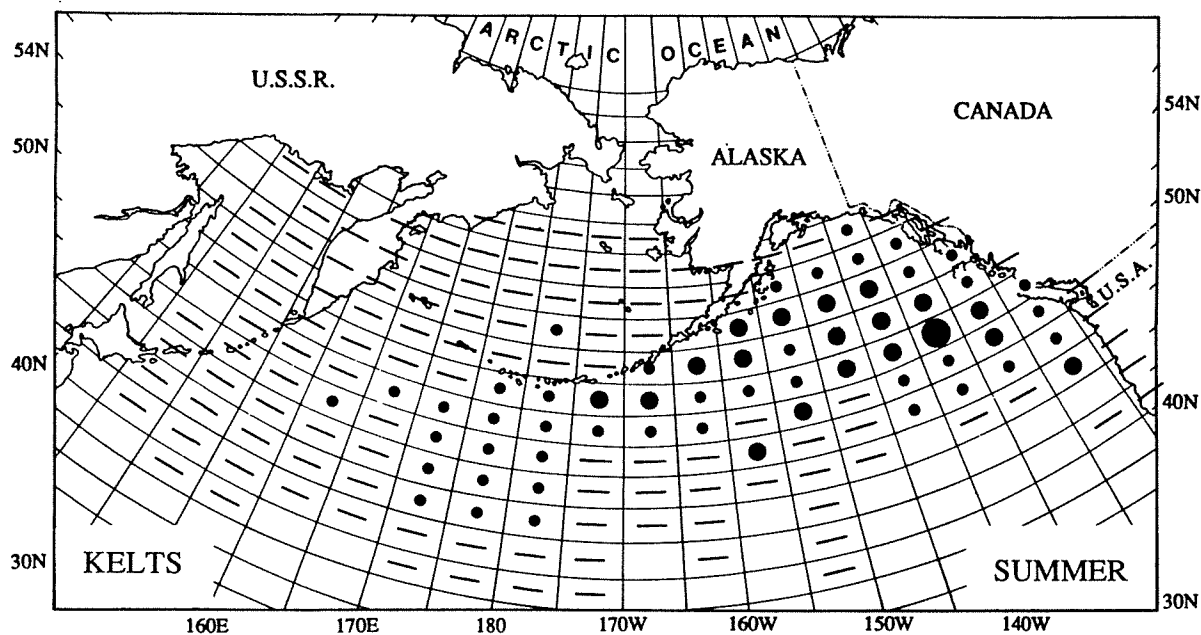
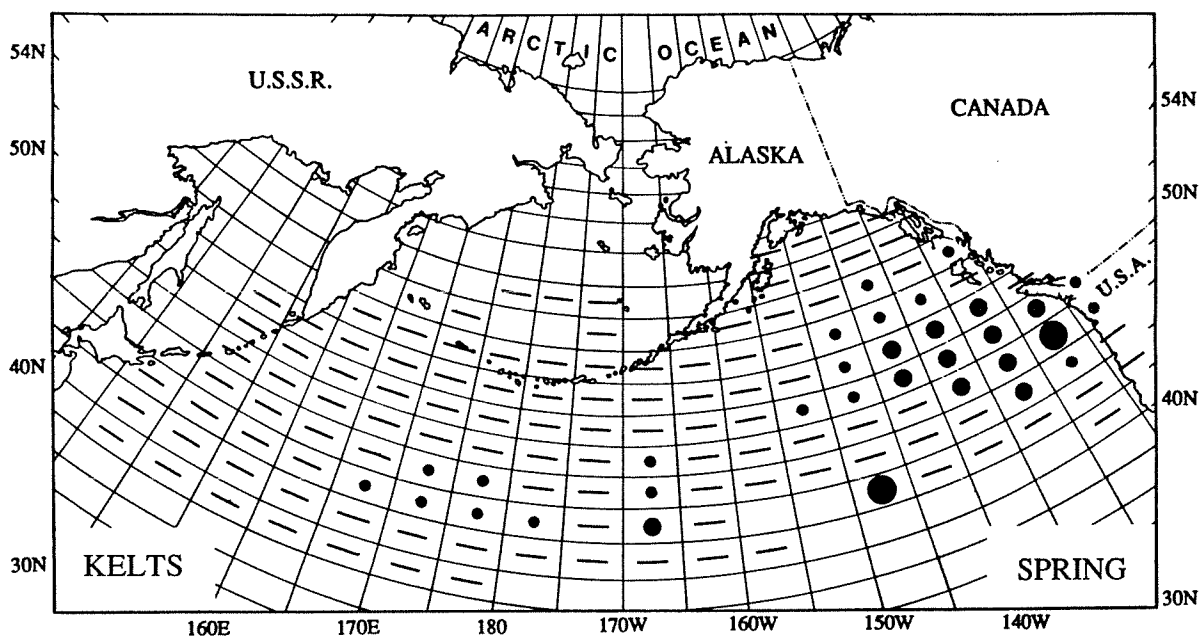


KEY TO CPUE INDEX VALUES:

— = sampling, but no catch

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

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

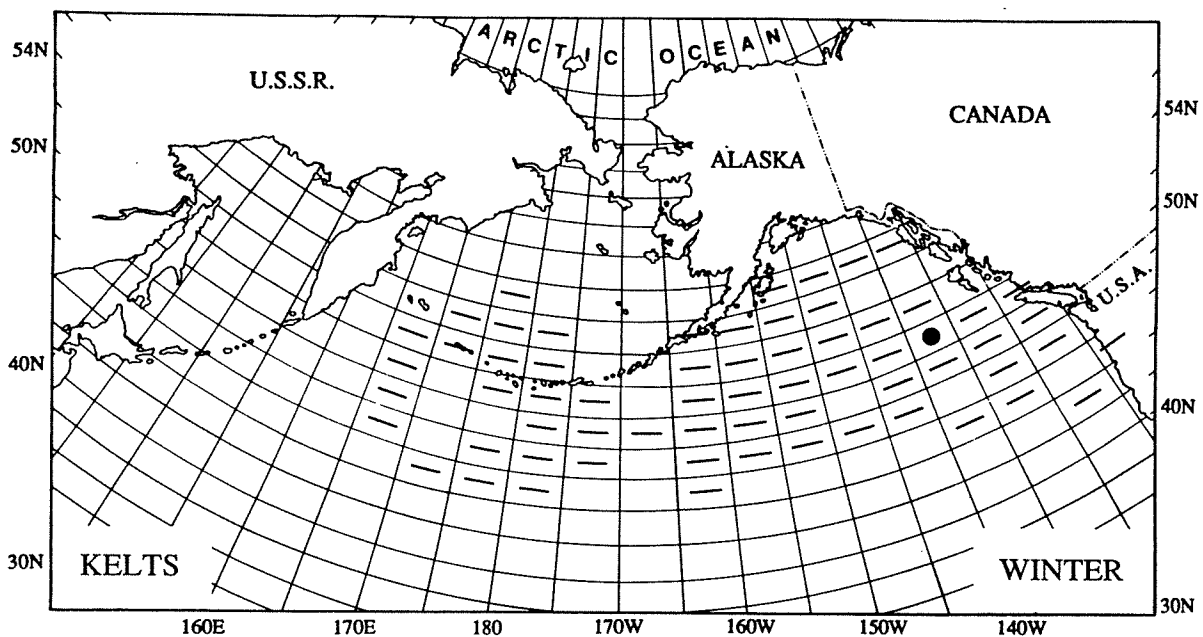
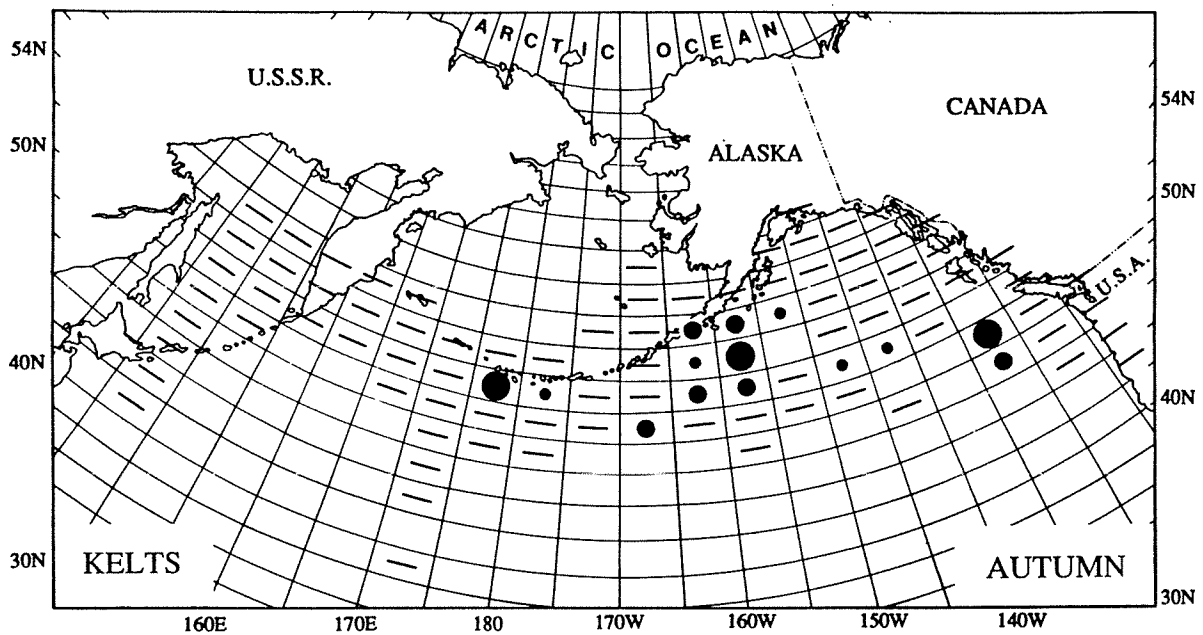
● = 1 (lowest)

● = 2

● = 3

● = 4 (highest)

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)

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.

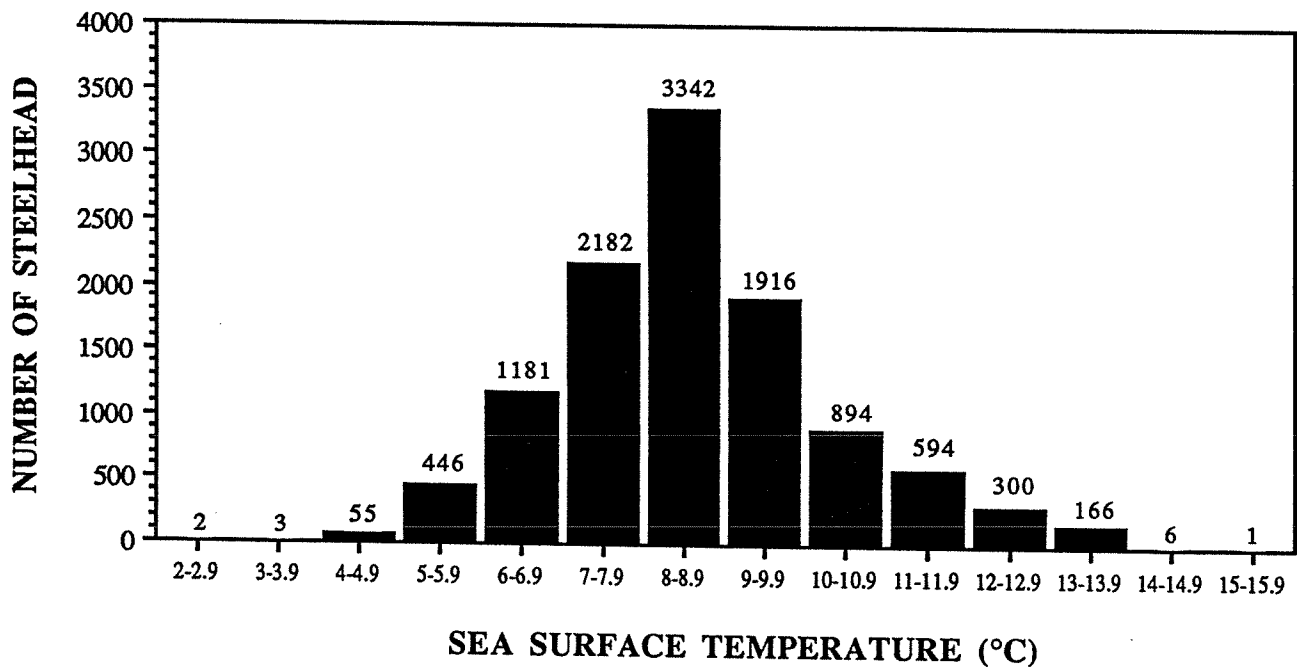


Figure 23. Distribution of steelhead catches by sea surface water temperature. (Data from Sutherland [1973] and Okazaki [1983]).

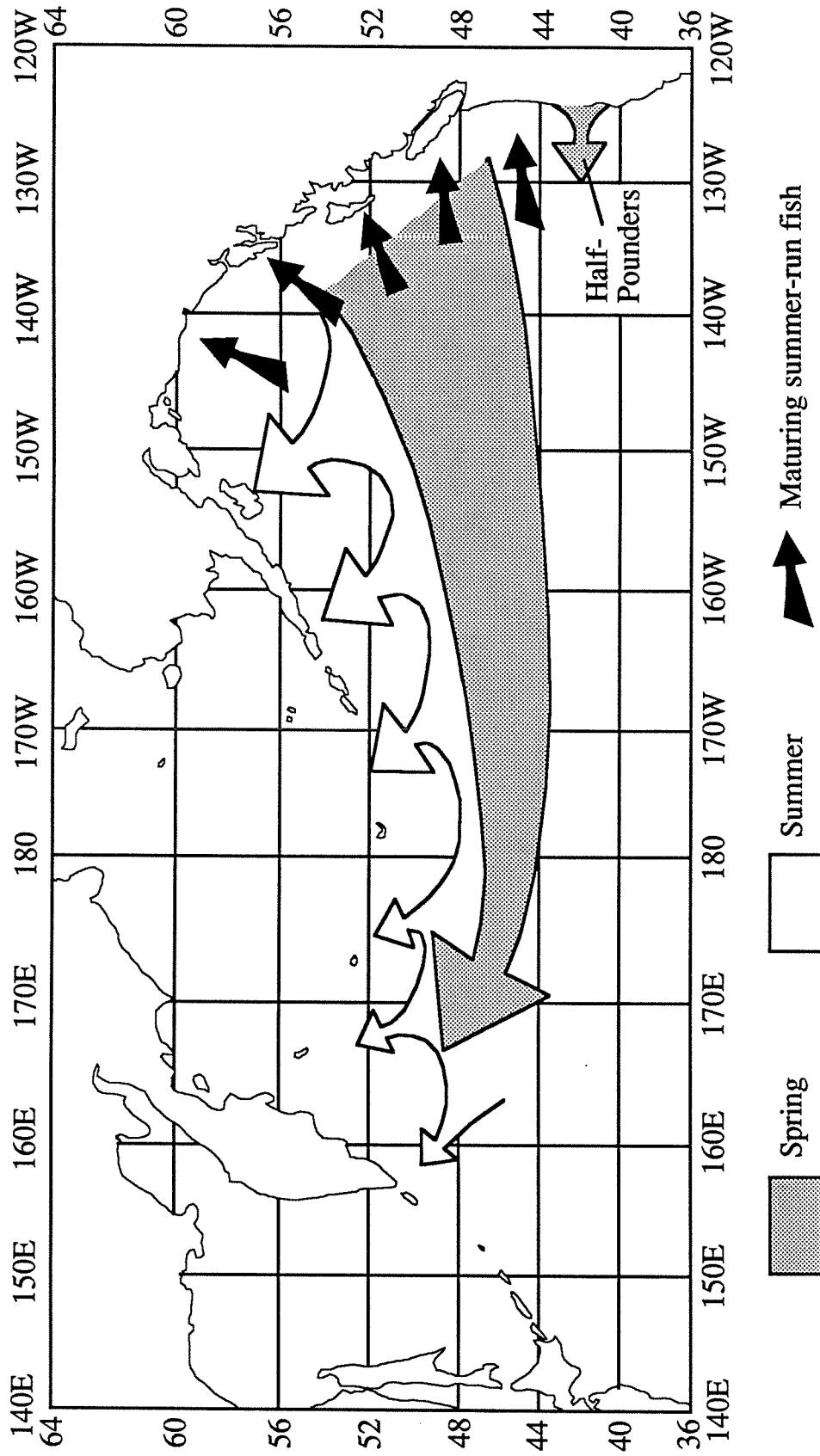


Figure 25. Model of steelhead oceanic migrations during spring (March-May) and summer (June-August) of their second year at sea (ocean age .1).

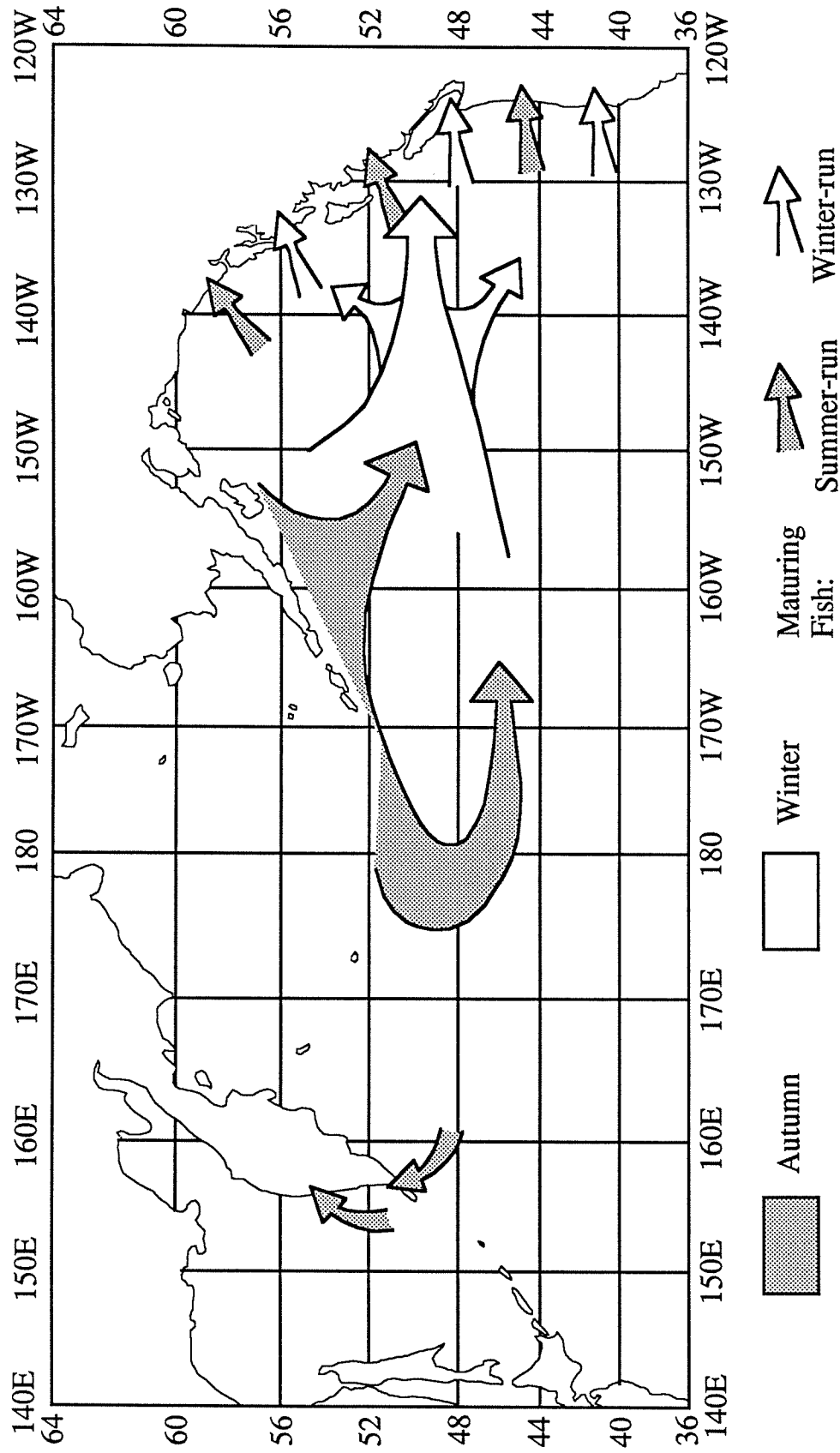


Figure 26. Model of steelhead oceanic migrations during autumn (September-November) and winter (December-February) of their second year at sea (ocean age .1).

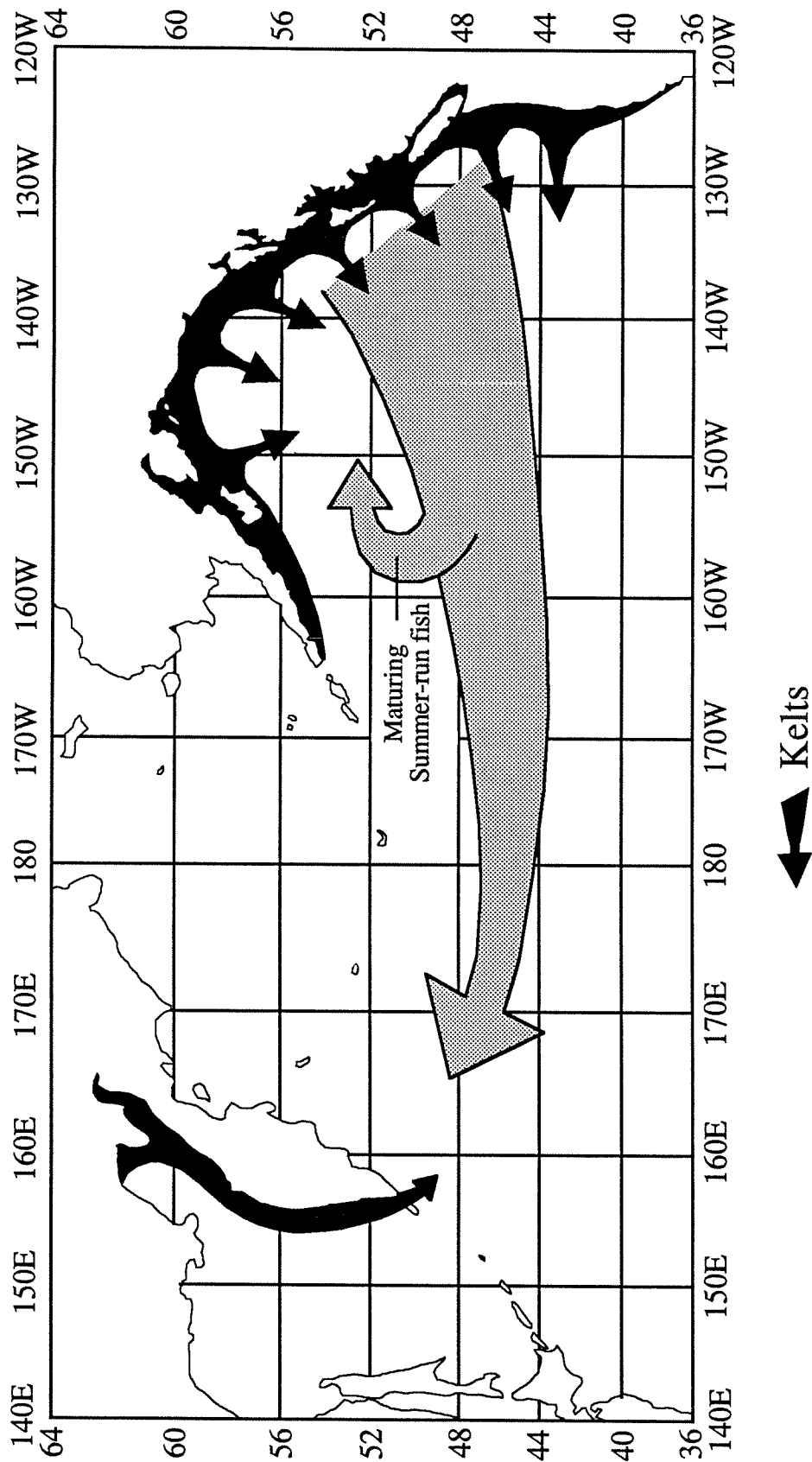


Figure 27. Model of steelhead oceanic migrations from March to early June of their third year at sea (ocean age .2). This same pattern would be followed by fish during all subsequent years at sea.

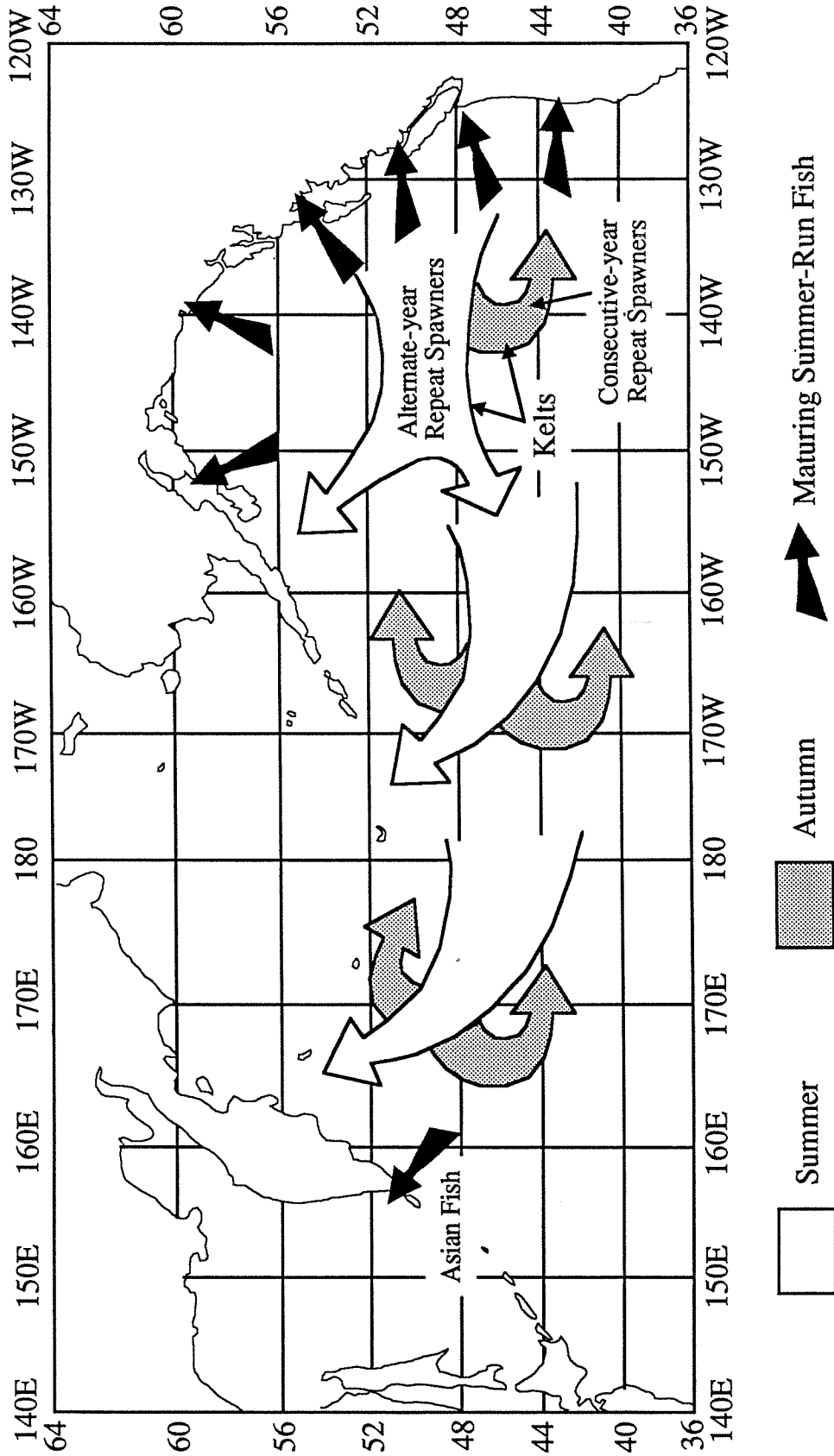


Figure 28. Model of steelhead oceanic migrations from mid-June through October of their third year at sea (ocean age .2). This same pattern would be followed by fish during all subsequent years at sea.

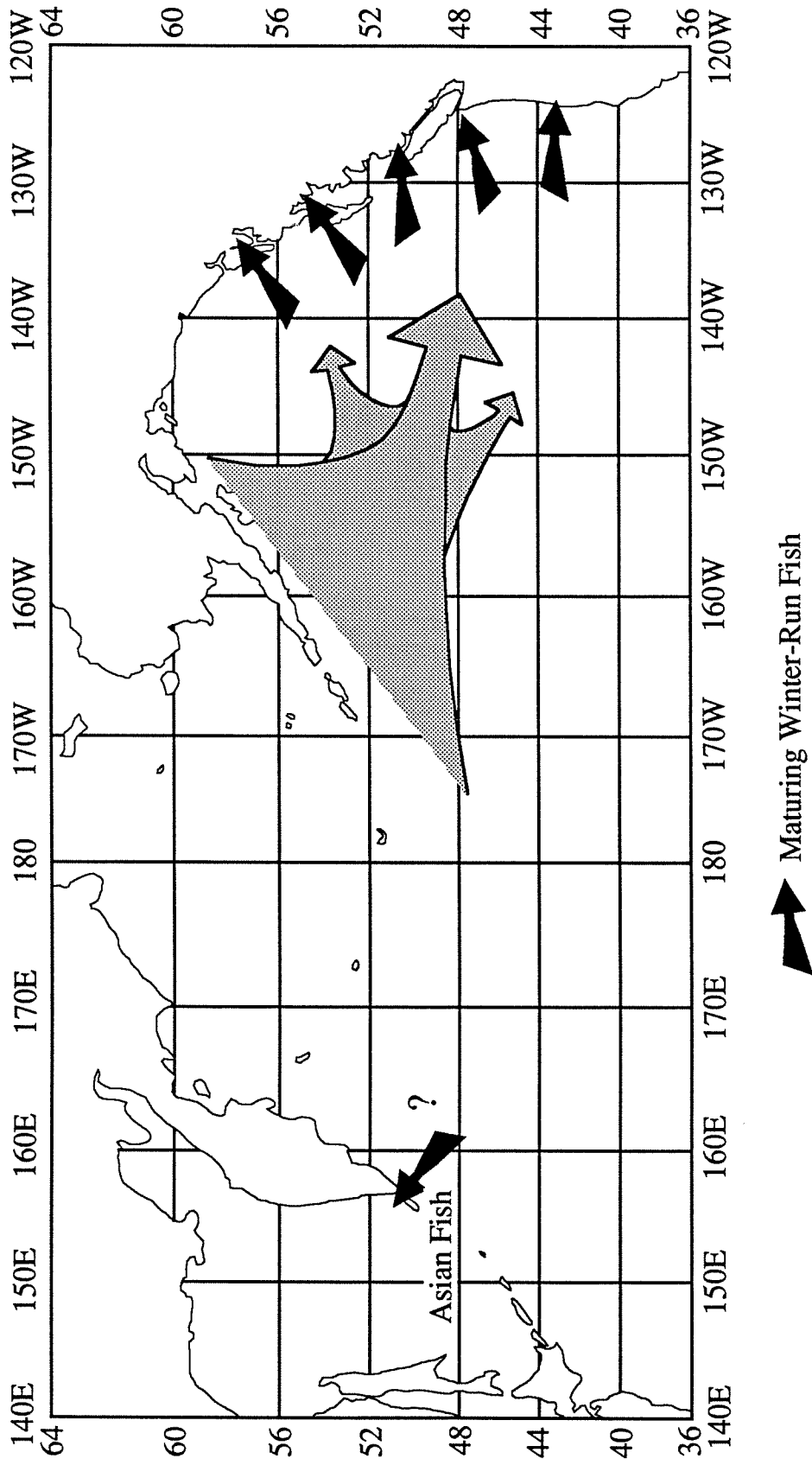


Figure 29. Model of steelhead oceanic migrations from November through February of their third year at sea (ocean age .2). This same pattern would be followed by fish during all subsequent years at sea.

Appendix A. Ranges of steelhead catch-per-unit-effort (CPUE) values for each of three gear types used during fishing operations of U.S. and Canadian (1955-1985), U.S.S.R. (1983-1985), and Japanese (1972-1985) research vessels in the North Pacific Ocean.

ANALYSIS 1: All fish (ages and spawning histories combined).

GEAR	CPUE QUARTILE			
	1	2	3	4
Purse Seines ¹	0.0357-0.0698	0.0811-0.1327	0.1538-0.3810	0.4468-17.0000
Gillnets ²	0.0001-0.0048	0.0055-0.0194	0.0200-0.0482	0.0492-0.2453
Longlines ³	0.0014-0.0125	0.0129-0.0300	0.0310-0.0706	0.0710-0.4500

ANALYSIS 2: By ocean age (all spawning histories combined).

GEAR	CPUE QUARTILE			
	1	2	3	4
Purse Seines ¹	0.0022-0.0455	0.0465-0.1039	0.1064-0.2727	0.2742-14.0000
Gillnets ²	0.0001-0.0051	0.0052-0.0126	0.0127-0.0278	0.0297-0.2050
Longlines ³	0.0009-0.0081	0.0084-0.0203	0.0213-0.0387	0.0390-0.2667

ANALYSIS 3: By spawning history (all ages combined).

GEAR	CPUE QUARTILE			
	1	2	3	4
Purse Seines ¹	0.0022-0.0426	0.0455-0.1111	0.1132-0.3000	0.3333-14.0000
Gillnets ²	0.0002-0.0047	0.0051-0.0146	0.0152-0.0396	0.0399-0.2348
Longlines ³	0.0005-0.0098	0.0099-0.0214	0.0216-0.0438	0.0447-0.2793

¹CPUE = steelhead per set.

²CPUE = steelhead per 50-m tan.

³CPUE = steelhead per 49-hook hachi.