# Current understanding of Pacific halibut migration patterns

**Juan L. Valero and Raymond A. Webster**

## Introduction

The Pacific halibut (*Hippoglossus stenolepis*) is distributed in the north Pacific Ocean from Hokkaido, Japan, to northern California, U.S.A. (Mecklenburg et al. 2002). The International Pacific Halibut Commission (IPHC) studies and manages halibut from the international border with Russia in the Bering Sea to northern California (Fig. 1). Halibut abundance distribution changes along its geographic range, with the current center of abundance located around Kodiak Island (Area 3A, Fig. 1) in the Gulf of Alaska (Clark and Hare 2006). There are also seasonal changes in halibut distribution resulting from spawning migrations as well as inter-annual changes resulting from ontogenetic migration of juveniles and adults. The goal of this report is to synthesize the current knowledge on Pacific halibut migration.

Several tagging programs that provide information on halibut migration patterns were implemented since the 1920s (Kaimmer 2000). Since objectives, methods, and spatial scope have changed through the years, the quality and relevance of the data to actual migration estimates have varied accordingly (Kaimmer 2000, Trumble et al. 1990). Previous work drew a clear distinction between juveniles and adults when analyzing halibut migration patterns (Hilborn et al. 1995, Clark and Hare 1998), at a time when it was assumed that most or all of the migration happened in smaller or younger halibut. Other studies made alternative definitions of juvenile or adult status, focusing on one of maturity, size, or age. Recent results from a coastwide passive integrated transponder (PIT) tagging study indicate that there is more of a continuum in halibut migration patterns and that although different factors may potentially influence migration (such as maturity, size, age), for most of those factors there is not enough information to evaluate their influence in a quantitatively rigorous manner. Therefore, the only distinction we make in this report is between spawning migration and ontogenetic migration without attempting to draw a finite distinction between juveniles and adults, although we discuss information on size and age effects on ontogenetic migration when available.

## 1. Migration and the life history of Pacific halibut

### Spawning migration

During summer, halibut are distributed on the continental shelf but during the winter mature halibut migrate to spawning grounds located in deeper waters. Most of the spatially and temporally consistent spawning grounds have been identified decades ago (Fig. 1), although spawning also probably occurs in most areas in deeper waters off the continental shelf (St. Pierre 1984). Recent archival tagging has identified winter spawning migrations as long as 1200 km (Loher and Seitz 2006), as well as some degree of site fidelity to summer areas (Loher 2008a). The current paradigm regarding seasonal spawning migration is that after spawning halibut return to the area they were in before the spawning migration, although this does not preclude ongoing ontogenetic migration.

**Ontogenetic migration**

After spawning, halibut eggs and larvae are carried by prevailing currents north and westward towards the western Gulf of Alaska and the Bering Sea. Juvenile halibut undertake an eastward-southward migration that counters the drift of eggs and larvae (Skud 1977, Hilborn et al. 1995). Analyses of tagging data show that this migration is ongoing for adult fish (see below). Analysis of traditional (Hoag et al. 1983, Quinn et al. 1985) and PIT tag (Webster and Clark 2007, Webster 2010) recoveries estimate that the fraction of fish migrating is a function of fish size/age; the general pattern indicates that smaller/younger fish are more likely to migrate out of area than larger/older fish. The counterclockwise (northward-westward) drift of eggs and larvae and the clockwise (eastward-southward) ontogenetic migration of juvenile and adult halibut has been described as a type of "compensatory emigration" (Dunlop et al. 1964, Best 1977, Skud 1977) or "migratory circuit" (Cushing 1976). This process is expected to have evolved along with other biological traits of Pacific halibut on an evolutionary time scale, and has strong implications for the population abundance and distribution.

Most of the knowledge of juvenile migration patterns originates from traditional tagging. Between 1963 and 1986 over 120,000 trawl-caught juvenile halibut from the Bering Sea and Gulf of Alaska were tagged as part of the "Trawl Recruitment Series" (Kaimmer 2000). A formal tag-recapture analysis of migration rates for juvenile halibut resulted from the peak tagging years of 1980 and 1981 (67,000 juveniles) and estimated migration rates between IPHC Regulatory Areas 2 and 3 (Hilborn et al. 1995). Although no formal tag-recapture analysis is available for juveniles < 65 cm tagged in Area 4, between 20% and 30% of juveniles tagged in Area 4 were recaptured out of area. Raw recovery proportions for halibut ages 2 to 6 and for halibut < 65 cm are listed in Tables 1 and 2 respectively. Table 3 shows recovery proportions and total numbers of halibut < 65 cm, when dividing combined Area 4 into Bering Sea and Gulf of Alaska components. Area 4 migration rate estimates are available for halibut 65 to 80 cm (Deriso et al. 1983) and suggest very similar emigration rates (around 23%) for Area 4 and Area 3B (Table 4).

## 2. Information sources

Tagging studies have been conducted by the IPHC since 1925. The first halibut tagged was a 12 lb, 34.5 in halibut caught on a hand line in northern Hecate Strait (current Regulatory Area 2B) on June 25, 1925 (Bell 1983). Over the next eighty years, more than 450,000 tagged halibut were released: 385,383 during historical tagging programs (Kaimmer 2000); 67,000 during a recent coastwide PIT program (Webster and Clark 2007), a smaller number (n = 327) of satellite-broadcasting electronic archival tags (e.g., Loher 2008a), and a recent conventional tag release (n = 773) in the Aleutian Islands (Loher 2011). Around 50,000 tags have been recovered to date.

**Historical tagging programs**

In the earliest days of the IPHC, understanding the amount of migration of halibut among fishing banks was identified as of primary importance for the development of regulations for the halibut fishery (Thompson and Herrington 1930). Tagging studies were selected as the most important means of answering questions regarding halibut movement. In this section, we review tagging programs that aimed to examine migration. There have been other tagging studies with different goals (e.g., estimation of mortality rates, Trumble et al. 1990) but these are outside the scope of this paper as they do not also provide useful information on migration. A summary of tag release and recoveries by tagging project and years of release is available in Table 3 of Kaimmer (2000). Also see Tables 5 and 6 of this report, which include both historical and recent tagging programs. The proportions of releases and recoveries by IPHC management area from historical and recent tag programs are presented in Tables 7 and 8.

As documented in Kaimmer (2000), the earliest programs relied on metal strap tags, which consisted of a small strip of metal fastened over the edge of the operculum on the halibut's dark side. There was some use of subcutaneous dart tags from 1959-1964, but strap tags predominated until external wire tags became the preferred tag type in the 1960s. External wire tags were subsequently used in all major tagging programs for the remainder of the 20$^{th}$ century.

The first tagged Pacific halibut were released in 1925 as part of a program examining movement among regions in present day Regulatory Areas 2B, 2C, and 3A (Thompson and Herrington 1930). A total of 9,289 tagged fish were released. In Area 3A, releases were concentrated in the major spawning area near Yakutat, in the Western Grounds southeast of Cape St Elias, and Portlock Bank, and were released in winter of both 1926 and 1927. In Areas 2B and 2C, localized sites in Queen Charlotte Sound, Hecate Strait, Dixon Entrance, and areas west of Prince of Wales Island were targeted for summer tagging in 1925 and 1926. The tagging program was publicized to commercial fishers, with a reward offered for returned tags. Further releases were made from 1929 to 1934 at these and other locations in the same present day regulatory areas, along with late April and early May 1929 releases of 928 tags around Shumagin Islands, and 687 tags around Unalaska Island in June 1930 (Kask 1935). The latter included the first releases of tagged halibut in the Bering Sea.

The Bering Sea became the focus of the next major halibut migration study. Over 11,000 tagged halibut were released from 1947 to 1963 in a series of releases at specific sites in the Bering Sea (Dunlop et al. 1964). Major releases (>300 tags per release) occurred in May-August of 1956 in Makushin Bay and on Polaris Ground (Bering Sea edge north of Unalaska Island), and in May-August of 1956 in the same areas and Clipper Ground (Bering Sea Edge, north of Polaris), and Slime Bank (north of Unimak Island). Smaller releases (<100 tags) occurred at several other Bering Sea sites in those years. In total, the 1956 releases comprised 3,183 tagged halibut. The 1959 releases included some fish marked with experimental subcutaneous dart tags, which were found to have a high shedding rate (Dunlop et al. 1964), and 4,106 fish marked with conventional strap tags. Other major releases in that period were 1,386 tagged fish released in May-August 1963 on the Bering Sea Flats and Edge, almost 1,000 of which were sublegal (<65 cm), and 1,070 halibut released on the Bering Sea Edge in November 1963. The former set of fish were mostly captured using trawl vessels, hence the large number of small fish. In the winter of 1963/64, 814 tags were released in Area 3B to examine whether there was winter movement from the Gulf to the Bering Sea (Dunlop et al. 1964).

A halibut setline survey grid began in 1976 in which tagged fish were released on a series of transects 24 nmile apart, on which setline stations were located with 6 nmile spacing (Hoag et al. 1980), and the data subsequently used for migration rate estimation. Tag release numbers are tabulated in Kaimmer (2000): from 1976 to 1986, 38,520 tagged halibut were released in Areas 2B, 2C, and 3A. Grids were initially located in the Charlotte region of Area 2B and the Kodiak region of Area 3A, and a third grid was added to Area 2C in 1982. The early years of this study are documented in Hoag et al. (1980), together with a previous setline survey conducted from 1963-1966 (on transects 12 nmile apart) that also included sets in Area 3B, on which around 10,000 tagged fish were released.

Around 51% of halibut have been tagged using trawl gear (Kaimmer 2000), which tends to catch smaller halibut than longline gear. The historical spatial distribution of tag releases of halibut caught by trawl gear is shown in Figure 2, and separately for the 1960s, 1970s and 1980s in Figures 3-5. Geographic coordinates for release locations were generally not recorded in IPHC databases prior to the 1960s, and there were few trawl releases in the 1990s. Trawl gear was first used to collect halibut for tagging in 1946, and between 1963 and 1986 a coastwide "Trawl Recruitment Series" was conducted (Figs. 3-5). The goals were to estimate year class abundance and subsequent recruitment to the commercial fishery. The peak tagging years in this program were 1980 and 1981 (Fig. 5), when around 67,000 juvenile fish were tagged (Hilborn et al. 1995). Over 99% of releases of tagged halibut caught with non-trawl gear have been from different types of hook and line or longline gear. For releases with available geographic coordinates, the historical spatial distribution of tag releases of halibut caught by non-trawl gear is shown in Figure 6, with Figures 7-10 giving releases by decade, from the 1960s to 1990s.

**Modern tagging programs**

In 2003 the IPHC staff marked with PIT (Passive Integrated Transponder) tags and released all fish caught on three skates of gear at all setline survey stations coastwide, totaling 43,999 fish (Kaimmer and Geernaert 2004). Tagged halibut were released in all regulatory areas except Area 4C, which had no survey stations until 2006, and Area 4E. The release was repeated in 2004 in Areas 2B and 3A, totaling another 23,437 fish (Williams et al. 2005). In each year from 2003 to 2009, samplers in major halibut ports scanned a substantial fraction of the landings to recover tagged fish, with an average of 43% of catch scanned during the course of the study. Fork length data were collected on release, and where possible, the length and age of recovered fish were measured. While the primary purpose of this project was to provide estimates of fishing mortality rates independent of the annual stock assessment, the data also permitted the estimation of rates of migration among regulatory areas.

Pop-up archival transmitting (PAT) tags have been employed in several studies of the movement of adult halibut since 2002 although with lower frequency than other tag types, due to their high cost. Prior to 2008, all fish in these studies (n = 200) were over 100 cm in length due to the large size of the tags and because holding experiments suggested erratic behavior if the tag's antenna contacted the tail. In 2008, modified tagging protocols and additional captive holding demonstrated that all O32 fish (those with fork length over 32 inches) can be successfully PAT tagged. Two types of study have been undertaken using these tags: those released in summer for winter or spring pop-ups that are designed to investigate spawning migration and seasonal dispersal; and those released in summer and recovered in the following summer, examining inter-annual migration of halibut. In 2002, the first summer-winter tags were released, with 12 fish tagged on setline surveys, three each in Areas 2B, 2C, 3A, and 3B (Loher and Seitz 2006). A second release in 2002 was of 12 tags around St. Paul Island, nine of which were timed to pop-up in winter, and three in summer the following year (Seitz et al. 2011). The central and western Aleutians were the subject of the next study, with 25 tags being released around Attu and Atka Islands in August 2004, timed to release in February 2005 (Seitz et al. 2011). Complementing these releases was the release of 24 tags in 2006 on the Bering Sea Edge (Areas 4A and 4D), which popped up in February 2007 (Loher and Seitz 2008a). A series of tags with staggered pop-ups in February and March 2007, from summer releases in Areas 2A (18 tags) and 2B in 2006 (60 tags), studied how movement from release location changes over time during late winter and early spring (Loher and Blood 2009). Close to 75% of tags were recovered with useful information on halibut movement from these studies.

The first summer to summer releases were three PAT tags in 2002 around St. Paul, but the first releases to provide useful data were in 2005 (Loher 2008b), when 49 tagged fish were released throughout the Gulf of Alaska (Areas 2B, 2C, 3A, and 3B). This was followed by 115 tags in the Bering Sea and Aleutian Islands in 2008 (Loher and Clark 2010) and a further 17 tags in 2009 around St. Matthew and St. Paul Islands (Loher and Clark 2011). Just under two thirds of the summer recoveries produced useful migration information.

In addition, 773 conventional opercular wire tags were deployed at four locations (near Sequam, Atka, Kanaga, and Attu Islands) in Area 4B in 2010 (Loher 2011). The primary purpose of this release was to identify future fishery-recaptured archival tagging sites.

## 3. Analysis of tag-recovery data

### Historical data

Little in the way of formal statistical analysis was conducted on tagging data until the 1980s, when data from earlier programs were revisited by IPHC staff. The lack of statistical analysis was no doubt largely because the modeling framework for multi-region tag-recovery data was not fully developed until relatively late in the 20th century, and instead, conclusions regarding migration patterns from the early tagging programs were drawn from the observed recovery data. We first summarize those earlier examinations of the data, and then describe the later formal analyses that were undertaken beginning in the 1980s.

The first IPHC tagging study, described in detail by Thompson and Herrington (1930), found that older fish in present day Area 3A could move large distances, but that younger fish in Area 2 tended to move far less. The Area 3 fish were winter releases in 1926-27, but were largely recovered in summer. Relatively few fish moved north or south of Cape Spencer, leading to the conclusion that there were two separate halibut populations. Based on these results, management Areas 2 and 3 were created, with the dividing boundary at Cape Spencer. Nevertheless, up to the end of 1928, over 5% of the tags released north and west of Cape Spencer were recovered in Area 2, including two fish in the southern part of present day Area 2A. Although Area 3B was not created until years later, 11% of tags released in Area 3A were recovered in the waters that now comprise this area (Table 4, Thompson and Herrington 1930). Western halibut recovered in summer were recovered much further from release locations than those recovered closer to winter. The authors interpreted this to be due to changes in fishing activity, with greater activity around spawning areas where fish were released during October and November, although we know that these results are also consistent with documented seasonal redistribution presumably associated with spawning (e.g., Loher and Seitz 2006, Loher and Clark 2010). Similarly, the Area 2 summer releases recovered in winter travelled further than those recovered in summer. The authors discussed factors that can influence recovery rates, including tag loss, capture-induced mortality, and natural mortality, but concluded that these did not seriously affect their results.

Kask (1935) updated this work to include further recoveries, including those from the additional releases described earlier in this report. The author supported the conclusions of Thompson and Herrington (1930) regarding the importance of Cape Spencer as a boundary, although noting again that some western fish do move south of the Cape. Recoveries of the April-May, 1929 Shumagin releases (in present day Area 3B) were widely distributed to the east and south, the southernmost recoveries being in Area 2B south of the Queen Charlotte Islands: to the end of 1934, 15% were recovered in Area 3A and 10% to Areas 2B and 2C, combined. Tags released near Unalaska, the majority of which (570 out of 687) were released on the Bering Sea side of the island, were also recovered long distances to the east: of the 43 recoveries with known locations, 20 were recovered to the east, mainly in Areas 3A and 2C. Kask also describes seasonal differences in the movement of halibut, with movement to deeper waters in fall and winter (associated with spawning), and a return to shallow waters in summer.

Dunlop et al. (1964) reported on the Bering Sea tag releases, beginning with an update of Kask's (1935) summary of the first Bering Sea releases discussed above: of the 61 recoveries until the end of 1939, only 25 were in the Bering Sea, the remainder having been recaptured in Area 3A (which extended to just east of the Shumagins at the time) and Area 2. From movement of tagged fish in the 1959 experiment in the southeastern Bering Sea, Dunlop et al. (1964) concluded that halibut on the fishing grounds of this region are interrelated. Despite the existence of what those authors describe as an intensive fishery in the western Bering Sea, only one fish was recovered there, off Cape Navarin, from the 1950s releases, leading to the conclusion that migration to the western Bering Sea was not significant. Otherwise, patterns of recoveries were similar to those obtained from earlier releases, with a large proportion of Bering Sea tags being recovered in Area 3A and Area 2. The authors note that previous tagging experiments, along with more recent studies such as the Shumagin releases of 1956, showed no evidence of a reverse migration into the Bering Sea from the Gulf. More generally, in discussing stock relationships, Dunlop et al. (1964) noted that the observed contranatant movement of larger fish must occur to counter larval drift and thus maintain the species in its habitat.

After 1955 a series of programs focused on juvenile halibut (< 65 cm, mostly ages 3 to 5, Skud 1977) trawl surveys from British Columbia to the Bering Sea and juvenile tagging in the Bering Sea and Gulf of Alaska (Trumble 1990). Best (1968) reported that most juveniles were found in the western Gulf of Alaska and Bering Sea, with very few along the coast of British Columbia and southeast Alaska. Although not providing an analysis of migration rates, Best (1968) showed extensive southerly and easterly movements of juvenile halibut based on inspection of out of area tag recoveries and an increase in juvenile age in the south to east direction. Skud (1977) further analyzed these data and noted some of their limitations, such as the inability at the time to incorporate the effect of different recovery rates due to differences in fishing effort or reporting rates among areas. Furthermore, the number of recoveries was relatively small and spanned several years during which juvenile natural mortality was assumed to be high (Skud 1977). In spite of these limitations, Skud's analysis of the age and size composition of juveniles, along with out of area recovery rates, led him to conclude that younger juvenile halibut migrated more extensively than older juveniles, and that the movement was mostly in an east-south direction, in agreement with what was reported in previous work.

The estimation of specific rates of ontogenetic migration from external tagging data was approached formally in the 1980s and 1990s. IPHC (1981), Deriso and Quinn (1983), Quinn et al. (1985), and Quinn et al. (1990) all present results from the analysis of historical external tagging data. The differences in the methods amount to the areas included, which areas were combined for analysis, and the years of data included in the analysis. In an attempt to exclude spawning migrants, all restricted their analysis to fish that were released and recovered during "summer" months The precise definition of summer in this work is unclear and recent analyses suggest that historical definitions of "summer" have likely encompassed the spring and fall migratory periods to some extent (Loher and Seitz 2008b). The results were not substantially different among the reports and papers, with all showing a general eastward migration of adult halibut, with greater movement rates from Areas 3B and 4. Deriso and Quinn (1983) present the only estimates from these analyses that separate Areas 3B and 4, although Area 3B at the time extended as far west as Samalga Pass in present day Area 4A. These authors used data from external tagging studies from 1950 to 1969 to estimate migration rates among six regulatory areas, from Area 2A north and east through 3B, and a combined Area 4. They estimated separate movement matrices for three length groups, 65-80 cm, 80-120 cm, and >120 cm, and found that for all areas, migration rates decreased with increasing size. Estimates from their analysis for 80-120 cm fish, which represents the majority of tagged halibut, are reproduced in Table 9, for comparison with PIT tagging results detailed below.

A formal tag-recapture analysis of migration rates for juvenile halibut resulted from the peak tagging years of 1980 and 1981 (67,000 juveniles) from the "Trawl Recruitment Series" data was undertaken by Hilborn et al. (1995), who estimated migration rates between IPHC Regulatory Areas 2 and 3. The authors produced seven alternative models depending on varying assumptions on movement and natural mortality, tag loss, size dependent movement and survival, and gear selectivity. Migration rate estimates for the best model as considered by the original authors are shown in Table 10. Although no formal tag-recapture analysis is available for juveniles tagged in Area 4 as part of this program, the proportion of juveniles tagged in Area 4 and Area 3 and recovered out of area is similar (around 30%, Clark and Hare 1998).

Potential problems with interpreting historical tagging data have been discussed since the earliest studies (Thompson and Herrington 1930), and are summarized in Trumble et al. (1990). These include releases that are not spatially distributed in proportion to abundance, unknown reporting rates that likely differ across the coast, tag mortality and tag shedding, and difficulty separating seasonal spawning and ontogenetic movements. As mentioned, the 1980s analyses of tag-recovery data attempted to separate spawning from ontogenetic migration by including only summer releases and recoveries, although the precise definitions of summer are unclear. Particularly problematic for parameter estimation is the non-reporting of tags by commercial fishers, as estimates can be highly sensitive to incorrect specification of reporting rates in the models. The patchy nature of the historical external tagging releases is also a significant problem for the analyses. The historical studies involved the release of tags in relatively small areas over many years, and so were not distributed in proportion to the spatial abundance of halibut. If tagged fish are not representative of the population of interest, estimated migration rates may be biased. Similarly, if recapture effort does not fully represent underlying demographic and geographic population structure, then results will better define the dynamics of fishable biomass than overall population dynamics, *per se*. Authors also found it necessary to aggregate data over time, and therefore no estimation of temporal trends in migration was possible. Nevertheless, despite their limitations, data from external tagging programs have been essential in determining the general pattern of both ontogenetic and spawning migrations (Bell 1983, Trumble et al. 1990).

**PIT tags**

A total of 3,190 PIT tagged fish from summer releases were recovered during the portside scanning program from 2003-2009. Webster (2010) and earlier reports detail the analysis of the PIT tagging data using tag-recovery models of the kind developed by Brownie et al. (1993). Only data from Areas 2B, 2C, 3A, 3B, and 4A were included due to sparse (sometimes zero) recoveries for most length groups from other areas (Table 11). The probability of migration was modeled as a function of halibut length (Fig. 11). Estimates of annual migration rates for 100 cm fish are given in Table 12 (100cm was approximately the average length of O32 fish upon capture and was used as the reference length when parameterizing the models). Rates of migration were estimated to be highest for Area 4A and lower for other areas, although it should be noted that the majority of 4A emigrants had been tagged south of the Aleutian Ridge (Table 13). The general pattern was of a west-to-east migration, with Area 4A being a significant net exporter of O32 biomass, and Area 2B a net importer of biomass (Webster 2010). The only substantial westward movement among areas was from Area 3A into Area 3B, although these fish tended to be recovered just west of the Area 3A/3B boundary, while fish moving in the reverse direction were far more widely distributed to the east; 0.67 of all Area 3A recoveries in Area 3B were in the statistical area adjacent to Area 3A, whereas the reverse was true for only 0.15 of fish.

For western areas, the estimated probability a fish moves in a given year declines with increasing length (Fig. 11). Estimated annual emigration probabilities are very high for smaller Area 4A fish, over 0.5 per year for halibut under 70 cm, and remaining over 0.2 for fish up to 95 cm. For Area 3B, halibut under 80 cm have at least a 0.15 probability of moving each year, a rate that declines to around 0.1 for a 100 cm fish. For Areas 2B, 2C, and 3A, the relationship between emigration rates and fish length is less clear: although a positive relationship is estimated in some cases, these results are based on relatively little recovery data for large fish and the relationships are very imprecisely estimated (Fig. 11). For Area 2C, the annual probability of emigration of a halibut is estimated to be around 0.1, and closer to 0.05 for Area 3A (Table 12 for 100 cm fish and Table 14 for all lengths combined).

The model estimates of emigration rates only tell part of the story, as the impact of outward migration on receiving areas depends on the relative population abundance or biomass between areas. Table 15 (reproduced from Webster 2010) presents estimates of net annual migration of O32 biomass at the beginning of 2010, based on a combination of length-specific migration estimates from the PIT tag modeling, and biomass estimates from the 2009 IPHC stock assessment. By far the largest net outward migration is from Area 4A, for which 21% of the O32 biomass was estimated to migrate to other areas each year. The greatest net recipient of biomass migration from all areas is Area 2B, for which annual net migration represents an 8% gain to the biomass. The estimates in Table 15 are broken down by source and destination of migration in Tables 16 and 17. For example, Area 2B receives the most biomass from Area 2C, 5.4% per year, and a total of a further 4% each year from areas to the west (Table 6). In the other direction, Area 2B sends 0.9% of its biomass back to Area 2C and 0.7% to western areas each year (Table 17). The importance of considering the size of the biomass in an area on understanding the impact of migration between areas is best illustrated by considering Area 3A. While Area 3A is estimated to export only 0.4% of its biomass to Area 2B and 0.3% to Area 2C (Table 17), these each represent an annual gain of 1.2% to those areas (Table 16), because Areas 2B and 2C currently have much smaller biomass than Area 3A. These figures include only the estimates of movement of fish that are part of the exploitable biomass. If fish of all sizes were to be considered, the movement rates of biomass would be even higher.

Bering Sea recovery data, although largely excluded from the statistical analysis (except for Area 4A) followed the patterns described in earlier IPHC reports, with a relatively large fraction of tags being recovered south and east in the Gulf of Alaska (Table 13), while only two fish released in the Gulf were recovered in the Bering Sea.

While the primary tagging analyses excluded data from Areas 2A, 4B, and 4D because of sparse recoveries, a supplementary analysis which did not include length as a migration rate covariate was undertaken using data from all areas (Table 14). In addition to the results of the main analysis, it is estimated that there is relatively little movement out of Area 4B, significant movement from Area 4D to Area 4A, a small amount of migration from Area 4D to the Gulf, and an annual movement rate of over 10% from Area 2A to Area 2B. These values, especially those for Areas 4B and 2A, are based on very little data, and should be treated with caution. They are presented here mainly because the Area 4 results complement those obtained from the PAT tags described below better than the raw data presented in Table 11, as they account for differential observed recovery rates among areas.

Tag-recoveries in most areas were much lower than expected in this study, leading to estimates of fishing mortality rates for larger fish that Commission staff believed to be unrealistically low (Webster et al., in prep). We have considered a number of factors that may have affected tag-recovery rates, including hook shyness, emigration out of the study area, and additional release mortality due to injuries sustained upon capture. Hook shyness occurs when the initial capture process leads to subsequent capture probabilities that are lower than those for fish that have not previously been captured. If hook shyness is present, then fishing mortality will be lower for tagged fish than untagged fish, and model estimates of mortality will not be applicable to the entire halibut population. There would be no effect, however, on estimates of migration rates. Emigrants out of the entire IPHC regulatory area have zero capture probability, and therefore such emigration also leads to lower recovery rates and reduced estimates of fishing mortality when natural mortality is fixed. The only influence on migration estimation would be to miss a component of movement, and from the PAT data, this may only apply to Area 4. Data on injuries received on initial capture imply that there may be unaccounted for release mortality in the tag-recovery models we have fitted to date, and that this may be somewhat greater for Area 4B than other areas. However, this would again affect mortality estimation, not estimation of migration rates. Of greater concern are areas in which tagged fish were not released in proportion to the spatial distribution of halibut abundance. Areas 4B and the southeast Bering Sea, in particular, had large gaps in survey coverage, while the Gulf of Alaska regulatory areas had smaller regions not covered by the survey. The tagged fish may therefore be unrepresentative of an area's population to some degree, which could bias migration estimates if their behaviour differs from unsampled fish. Nevertheless, in most of the areas included in the main analysis, gaps in coverage are relatively small, and any bias in movement rates estimated among areas within the Gulf of Alaska is likely to be minor. Another issue is that the tag recovery period included times when spawning migration was ongoing, and so migration estimates may be affected by recoveries of fish that were temporarily out of release area due to spawning movement. However, a re-analysis of the data using only recoveries from May to September led to migration rate estimates that had only very minor differences from those presented here, and therefore spawning movement was not a significant source of bias in the PIT tag analysis. There were also limits on the complexity of the models: with only two release groups (2003 and 2004), there was insufficient information for the estimation of temporal changes in movement rates, and the only data on halibut sex for estimating how migration rates differ between male and female fish came from a far smaller set of recoveries on the setline survey from 2006-08.

**PAT tags**

The first summer release/winter pop-up PAT releases had small samples sizes, making it difficult to reach meaningful conclusions. However, the majority of recoveries (8/10) in the Gulf of Alaska study showed movement consistent with a seasonal spawning migration to deep slope waters and northward redistribution during winter (Loher and Seitz 2006). Winter pop-ups in the 2002 St. Paul releases also showed movement to deeper waters for spawning, with all seven fish with recovered tags remaining in the Bering Sea (Seitz et al. 2011). The larger set of 2004 releases in the western Aleutians yielded 16 recoveries, all in the vicinity of the islands near which they were released (Seitz et al. 2011). The authors note this is consistent with there being a distinct spawning group in that region. The 2006 Area 4A/4D Edge summer release/winter reporting had 19/24 successful pop-ups, which also remained in the Bering Sea, with most again being recovered in the vicinity of their release location (Seitz et al. 2011). The Area 4D releases and recoveries were in Middle Canyon, which the authors conclude is likely to be an important spawning ground, one which lies much further north than grounds previously investigated. In the 2006/07 study of fish released in Areas 2A and 2B during the summer, a large proportion of successful Area 2A winter pop-ups (5/13 fish) occurred in areas to the north at known spawning locations, with four recoveries in Area 2B and one in Area 2C (Loher and Blood 2009). Fish tagged off Cape Johnson in Washington tended to be recovered there (4/5 fish), indicating that this may be a previously undocumented spawning location. Of the successful Area 2B tags, almost all (41/44) were recovered around spawning areas in Area 2B, the remaining three moving north to Area 2C. The expectation from earlier external tagging data was that more fish would move north to spawn, and the authors postulate that size and sex differences may be factors in the inconsistent findings, with PAT tags fitted to larger fish than average, which are also more likely to be female. However, it is also possible that the tag transmitting dates (February) were after the typical spawning period (January), and spawning fish may have already returned from moving out of the tagging areas, or that fish maintained a deepwater habitat even following a spawning migration. Alternatively, similar disparities could result from differences in study design, including the inability of the conventional tag analysis to resolve seasonal and ontogenetic dispersal, or from temporal variance in dispersal patterns.

The summer-summer PAT tag releases in the Gulf of Alaska and Area 4 had the potential to provide information on ontogenetic migration of halibut as a supplement to the results of the PIT tag study. In the Gulf study, a total of 25 out of 48 tags provided useful recovery locations, and of those, 20 were recovered less than 20 km from their site of release, demonstrating either a high degree of site fidelity or homing behaviour (Loher 2008b). The remaining five fish had moved 40-393 km from their release location; only one moved out-of-area, from Area 3A to 3B.

In the 2008/09 Area 4 summer releases, 33 of the 40 Area 4B tags produced useful migration information, and as with the earlier winter recoveries, all fish were located within the island group at which they were released (Loher and Clark 2010). The authors conclude that there is no evidence for significant adult emigration out of Area 4B, and hypothesize that low recovery probabilities in that area may have been the cause of the relatively high rate of out-of-area recoveries of Area 4B PIT tag releases. This is supported by the supplementary PIT analysis results described previously and presented in Table 14, which gives an estimate of 97% of 4B fish remaining in that area each year. Nevertheless, almost all Area 4B PAT tags moved some distance from the release location (Loher and Clark 2010), and therefore did not exhibit the same degree of site fidelity as Gulf releases noted above. This could explain why Area 4B PIT tags were not recovered by the IPHC setline survey, while many Gulf of Alaska tags were recovered on the station of release (Forsberg 2008, 2009). The fish PAT tagged in Areas 4C, 4D, and the Bering Sea side of Area 4A showed a range of migratory behaviour (Loher and Clark 2009, 2010), although in contrast to the PIT tags (Table 13) none of the 40 pop-ups in these areas occurred in the Gulf of Alaska. Two out of 21 Area 4D and one out of seven Area 4C fish moved across the contiguous northern Bering Sea continental shelf into Russian waters, and three of seven northern Area 4A fish moved into the Closed Area, implying a proportion of the PIT tags could also have been unrecoverable because of movement out of the region subject to commercial fishing. One of the 2009 Area 4D tags also moved into Area 4E, where little fishing occurs, and one Area 4D fish moved south to Area 4A. Of the 13 recovered southern Area 4A tags, one moved north into the Closed Area, three moved into Area 3B and one moved into Area 2A. With low sample sizes in the PAT study and likely higher recovery rates in eastern areas in the PIT study, none of these results is inconsistent with the PIT tag data and analyses.

## 4. Conclusions from tagging studies

Perhaps the clearest picture of ontogenetic migration patterns of larger halibut comes from the recent coastwide PIT tagging study, in which 67,000 halibut, mostly of adult size, were tagged and released over a two year period (2003-04), and recovered from 2003-09. The results show that ontogenetic halibut migration continues beyond age eight (Webster and Clark 2007), with annual migration rates that decrease with increasing size. Rates of movement are greatest for western regulatory areas in the Gulf of Alaska, resulting in a large net emigration of biomass out of Area 4A, and net immigration into Area 2B (Webster 2010). These results are consistent with earlier analyses of external tagging studies (Quinn et al. 1985, Quinn II et al. 1990). Reports from the 1930s to the 1970s also describe the movement of fish among present day regulatory areas in a manner consistent with the pattern of results of the more recent analyses. There is less information from the margins of the stock, particularly Areas 2A and 4B. The data we do have from these areas, particularly from recent PIT and PAT studies, shows that there is some movement from Area 4B eastward, although fewer fish appear to migrate than other parts of Area 4, and that there is significant movement from Area 2A northward. Further work will be required if we are to more precisely determine the degree of migration into and out of these areas.

The focus of some of the earliest IPHC tagging studies was to determine if the halibut population could be divided into essentially closed subpopulations for the purposes of management (Thompson and Herrington 1930). Of particular interest has been whether or not the Bering Sea constitutes a distinct subpopulation of halibut, with no significant mixing with Gulf of Alaska fish. While no statistical estimates of migration rates into and out of the Bering Sea have been made, recovered tags from the recent PIT study and earlier external tag studies show that there is significant movement of halibut of all sizes/ages from the Bering Sea into the Gulf (Dunlop et al. 1964, Bell 1981, Webster and Clark 2007). Tags from Bering Sea releases have been recovered throughout the Gulf of Alaska, including as far south as Area 2A. The reverse is not true, that is, very few fish tagged in the Gulf have been recovered in the Bering Sea. This pattern is consistent with the compensatory migration pattern described previously. Results from recent studies using PAT tags have used relatively small sample sizes, and the lack of observed movement of these tags from the Bering Sea to the Gulf does not contradict the observations from other tagging studies.

**Movement of juveniles**

As mentioned before, most of the knowledge of juvenile migration patterns originates from traditional tagging conducted between 1963 and 1986. Over 120,000 trawl-caught juvenile halibut from the Bering Sea and Gulf of Alaska were tagged as part of the "Trawl Recruitment Series" (Kaimmer 2000). A formal tag-recapture analysis of migration rates for juvenile halibut resulted from the peak tagging years of 1980 and 1981 (67,000 juveniles) and estimated migration rates between IPHC Regulatory Areas 2 and 3 (Hilborn et al. 1995). Although no formal tag-recapture analysis is available for juveniles < 65 cm tagged in Area 4, between 20% and 30% of juveniles tagged in Area 4 were recaptured out of area. Raw recovery proportions for halibut ages 2 to 6 and for halibut < 65 cm are listed in Tables 1 and 2 respectively. Between 50% to 60% of U32 halibut tag releases occurred in the proximity of the Aleutian islands between Unimak and Unalaska islands, with the remaining releases spread along the Bering Sea edge, flats, and what corresponds to the Bering Sea Closed Area (Fig. 1). Table 3 shows recovery proportions and total numbers of halibut < 65 cm, when dividing combined Area 4 into Bering Sea and Gulf of Alaska components. Area 4 migration rate estimates are available for halibut 65 to 80 cm (Deriso et al. 1983) and suggest very similar emigration rates (around 23%) for Area 4 and Area 3B (Table 4), although they do not differentiate between Bering Sea and Gulf of Alaska components.

**Conclusions**

The consistency among results of previous historical tagging programs has been noted in earlier IPHC staff work (Skud 1977, Bell 1981). Historical and modern tagging methods have common and particular limitations for each study. In spite of this, the raw out of area recovery proportions are very similar (Tables 7 and 8), excepting Area 2A, for which data are sparse, and to a lesser extent Area 4. The estimation of migration rates from historical and modern tagging programs has relied on different tag-recapture methods and produced migration rates summarized by different criteria (either age or length classes) that make comparison of estimated rates less straightforward. However migration rates estimated by historical tags and methods for halibut 80-120 cm (Table 9) are similar to those estimated by modern PIT tags and analytic methods for halibut 100 cm (Table 12). For migration estimation, the shortcomings of the PIT tag study are minor compared with those of the historical tagging studies. With known tag reporting rates, and tags distributed over a short period of time in approximate proportion to abundance, the migration estimates from the PIT study should be regarded as the most reliable estimates available for larger halibut.

## 5. Evaluation and application of information on halibut migration

Historically, the IPHC staff has undertaken evaluations of the quality of information and conclusions derived from past tagging studies, resulting in the discontinuation of past tagging experiments (e.g., tagging of juveniles) and techniques (e.g., strap and wire tags) and implementation of new techniques and tagging experiments (e.g., PIT and PAT tagging programs). The application of the information and conclusions regarding halibut migration derived from the analyses has varied through time. The decision to establish separate regulatory areas relied extensively on tagging studies done during the 1920s (Skud 1977). The initial belief of stock independence between Areas 2 and 3 (Thompson and Herrington 1930, Babcock et al. 1931) was used to justify the separation of these areas into management units (Skud 1977). During the late

1950s and the mid 1960s, information from tagging experiments was crucial in showing extensive halibut migrations from the Bering Sea to the rest of the management areas, at a time when Japan was required to abstain from fishing halibut in the Bering Sea provided that the stocks were fully utilized (Skud 1977, Bell 1981).

During the 1980s, migration rates were estimated formally (Deriso and Quinn 1983, Quinn et al. 1985, 1990) and were applied in stock assessment work. Three stock assessment approaches were used (concurrently in some years) during the 1980s: coastwide models (1982-1988), migratory models using migration rates estimated external to the model from tag-recovery data (1984-1988), and closed-area models (1986-1988). In 1989, coastwide stock assessment models and those that included halibut migration were discontinued in favor of closed-area assessments (Sullivan et al. 1990). Closed-area assessments assumed that halibut older than age 8 had completed their ontogenetic migration. A formal analysis and estimation of migration rates from juvenile tag-recovery data from the 1980s was conducted in the mid-1990s (Hilborn et al. 1995). However, migration rates were considered to be poorly determined and not applied in analyses of bycatch impacts at the time, which instead used a range of migration speeds for ages 2 and 8 between nursery areas and home areas, assuming that halibut older than age 8 did not migrate (Clark and Hare 1998). Data from the recent PIT tag experiment did not support the assumption that adult halibut do not migrate (a critical assumption of closed-area models), leading to the conclusion that closed-area assessments were likely biased due to migration. Closed-area assessments were rejected by IPHC staff in favor of a coastwide model (Clark and Hare 2007). An independent review (IPHC 2007) supported the rejection of closed-area assessments and agreed with the use of a coastwide assessment for the 2006 assessment, further recommending the development of a spatially structured coastwide model incorporating migration (Francis 2008, Medley 2008). The IPHC staff agreed that the spatially structured approach was feasible, but did not believe that sufficient data were available to create a reliable alternative to the coastwide approach (Clark et al. 2008), which has been used since its adoption in 2007.

Although migration rate estimates and tag-recovery data are not currently being used directly in halibut stock assessment, estimates from both PIT and historical tagging of adults and juveniles are being used for harvest strategy work. This includes exploring the relative effect of fishing and migration on halibut distribution and population dynamics (Valero and Hare 2009, 2010a), evaluating alternative biomass apportionment methods (Valero and Hare 2010b), and evaluating the effect of migration on the distribution of bycatch impacts (Valero and Hare 2011). Results from the PAT and archival tagging experiments involve a much smaller number of fish tagged and focus on restricted areas of the coast, with a higher resolution of information per fish. In that sense, their results are not as straightforward to extrapolate to the whole halibut population, but they provide invaluable information for understanding processes such as the spatial extent and timing of the spawning migration (applicable to questions regarding commercial season length), fidelity to and from spawning locations, among others.  Additionally, they represent the only source of fishery-independent migration data available, which can shed light on potential biases associated with conventional tag data.

## 6. A conceptual model of halibut migrations

The conceptual model of halibut migration detailed below summarizes key findings from IPHC tagging and survey programs extending more than eight decades. Most of the general concepts and major results have already been described in earlier IPHC reports and other related works (Thompson and Herrington 1930, Kask 1935, Thompson and Van Cleve 1936, Dunlop et al. 1964, Skud 1977, Bell 1981). These previous concepts have been refined by recent tagging programs such as the PAT and PIT experiments, whose results have been largely consistent with those of historical tagging programs. However, the evolution of the understanding of halibut migration patterns has not been gradual or consistent through time. As noted by Skud (1977), during the 1930s to 1950s IPHC publications emphasized the independence of halibut stocks between Areas 2 and 3, however by the late 1950s the emphasis was on interrelationships between halibut of Areas 2, 3, and the Bering Sea. In a similar way, during the 1990s and mid-2000s halibut were assumed to have completed their ontogenetic migration after becoming available to the commercial fishery (around age 8 at the time) and to remain in one regulatory area, except during spawning migrations.

The following conceptual model follows the halibut life history starting from the production of eggs and larvae during spawning. Our knowledge of spawning locations is still incomplete. Spawning has been reported to occur along the edge of continental shelf from November to March and it is assumed that mature halibut spawn annually, although the possibility of skip reproduction on mature fish has not been discounted (Loher and Seitz 2008b). The current paradigm regarding seasonal spawning migration is that after spawning halibut return to the general area they were in before the spawning migration. Main spawning areas have been identified several decades ago (St. Pierre 1984) and are shown in Fig. 1. Spawning concentrations have also been reported in the Bering Sea and along the continental shelf (Skud 1977). Past emphasis on the identification of major spawning areas may have implied that these were the only spawning grounds; in fact, there is reason to conclude that spawning is widespread and occurs in many areas, although not in as dense concentrations as those discussed in previous reports. Recent work using PAT tags supports this conclusion and has been reported to be consistent with local spawning areas in Areas 4B and 4D (Seitz et al. 2007), further north than previously investigated spawning areas (Fig. 1). In a similar way, PAT tag work indicated that fish tagged in Areas 2A and 2B may be more restricted in spawning movement than would have been expected based on historical tagging work, suggesting the possibility of local reproduction as far south as Cape Johnson, WA (Loher and Blood 2009). The current paradigm regarding the winter spawning migration is that after spawning, halibut return to the area they were before the spawning migration, and recent PAT tag results (Loher 2008a) seem consistent with this pattern. As noted, this does not preclude ongoing ontogenetic migration.

After spawning, halibut eggs and larvae are carried by prevailing currents north and westward towards the western Gulf of Alaska and the Bering Sea. Our understanding of processes responsible for general patterns or larval advection has not advanced beyond our state of knowledge dating more than three decades ago (Thompson and Van Cleve 1935, Bell and St-Pierre 1970, Skud 1977). After metamorphosis from the larval stage to the characteristic juvenile-adult form, halibut commence their bottom existence. Juvenile halibut undertake an eastward-southward migration that counters the drift of eggs and larvae. As halibut grow older and larger, the fraction of fish migrating decreases, but there is ample evidence both from historical and recent tagging programs that halibut continue to migrate throughout their life, even as adults.

## 7. Future research

As noted in previous sections there are limitations of historical tagging studies such as uncertainty in reporting rates, changing designs, and differences in the scope of tagging programs, depending on objectives. Modern tagging studies also have limitations and our understanding of the migratory behaviour of Pacific halibut is still incomplete. While the PIT tag study has produced estimates of ontogenetic migration rates with fewer sources of bias than previous data, limited information was collected on areas at the margins of the halibut range and these data were necessarily fishery-dependent. Fishery-dependent data cannot fully capture dispersal to or from regions that are relatively unfished, and will therefore always contain some level of spatial bias that is correlated to effort patterns. While these data may provide accurate representations of stock dynamics within the fishable portion of the stock, uncharacterized population components may still be important in governing observed patterns of fishery recruitment or responses to higher-than-target exploitation. Thus, there is a need for better data on movement rates to and from Areas 2A, 4B, and 4C, as well as a need to increase the amount of fully fishery-independent data available for analysis. The PAT and historical tag data show there is at least some movement out of the region open to fishing within IPHC waters, including movement to Russia and the Bering Sea Closed Area. Quantifying the degree of such movement would help in understanding relationships among different components of the entire halibut stock, as well as potentially shedding light upon whether movement out of the system was a significant factor in low tag-recovery rates in some western areas in the PIT study.

Regarding the low-recovery rates of PIT tagged halibut, while these alone may not significantly bias migration rate estimation, understanding their causes would be important for any future work using such tags for migration and mortality rate estimation. Along with emigration out of the region open to fishing discussed above, the possibility of some long-term hook shyness of previously captured halibut has been considered (Webster et al., in prep.), i.e., the initial capture process reduces the chances that a fish is recaptured in the future. As yet we have no direct evidence for or against the existence of hook shyness in Pacific halibut, and it is an extremely difficult factor to study scientifically for fish species: in a tagging study, we would require multiple recaptures per fish and an assumption of population closure (Pollock et al. 1990), which is unreasonable even for short periods of time over small areas for Pacific halibut (Webster 2009). Further, models fitted to the PIT data assumed negligible release mortality of tagged fish based on holding tank studies. Data on injury severity at release imply non-zero mortality rates that vary somewhat among areas. Additional modeling is planned to account for such mortality. There is also potential for using the PIT data to estimate migration rates as a function of age rather than length: around two thirds of recovered fish were aged, although of course no ages are available for unrecovered halibut, and these would have to be estimated as part of the modeling.

New techniques are becoming available and are under study by IPHC staff, including the use of geomagnetic tags and the ability to determine sex of released halibut (Loher and Stephens, in press). Geomagnetic tags have the potential for providing more detailed location information of tagged halibut between release and recapture than that available with previously deployed archival tags that relied on light information. More detailed location information would be useful to refine our understanding of the spatial extent and timing of seasonal migrations (applicable to questions regarding commercial season length) and fidelity to and from spawning locations, among others. A pilot study to evaluate the feasibility of using geomagnetic tags is currently underway (IPHC

2011). With respect to the ability to determine sex of tagged halibut at release, considerable scope might be added to migration analyses if we were able to conduct them in a sex-specific manner. Sex-biased dispersal has been observed across taxa, and may occur for halibut. If so, migration analyses conducted according to fish size could be confounded with sex-specific movement rates, because sex ratios are expected to be biased towards females among larger size classes. Furthermore, changes in sex ratio and/or age structure within the population over time, or among regulatory areas, could result in variance in apparent dispersal rates that are unrelated to mean length, *per se*. To date, none of the IPHC's tag recovery data have been amenable to sex-specific formal analysis.

Other potential future research includes a re-evaluation of the available historical tagging data that have not yet being analyzed by modern modeling methods, including tag releases from < 65 cm halibut from Area 4. Additionally, smaller "miniPATs" are also now available that would be suitable for tagging U32 fish, allowing a better understanding of movement of fish which generally show the greatest degree of migration. Designing studies for understanding the migration of smaller halibut presents its own challenges, and evaluating the feasibility of such research depends greatly on tag type, tag release methods (most likely involving trawl-captured halibut), tag retrieval method, and the goals of the study. Whereas PIT tags and external tags may require very intensive recovery effort from commercial catches due to low selectivity of small halibut to commercial gear, miniPAT tags could provide an alternative independent of the commercial fishery for tag recovery but would not provide data sufficient for population-level inferences. While individual miniPAT tags are more expensive than PIT or external tags, far fewer would be need to be released to achieve comparable recovery numbers to PIT or external tags, and the recovery costs could be much lower. The feasibility of any potential tagging study would have to be studied very carefully before informed decisions could be made, as was certainly the case for the PIT tag study (Leaman et al. 2003, Parker et al. 2003).

The aforementioned newer tagging techniques also have the potential to refine our understanding of seasonal migrations in particular. The current paradigm regarding spawning migrations is that mature halibut spawn every year and that they return to their feeding area after the spawning season is over. However, there is no conclusive evidence to date to support or reject the former, and the degree to which the latter is true cannot presently be quantified. Furthermore, it is not clear if halibut return to the same spawning locations every year. We have stressed the importance of screening tag recovery data to reduce the possibility of confounding seasonal dispersal with ontogenetic migration, but our present understanding of seasonal dispersal is only rudimentary. Obtaining data that would allow us to quantify the proportion of individuals expected to be either on their summer or winter grounds, or in a state of migration between them, by date and area, would aid future analyses.

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**Table 1. Raw recovery rates of externally-tagged halibut ages 2 to 6 tagged in Area 4 (from Clark and Hare, 1998).**

| Recovery Area | | | | |
|---|---|---|---|---|
| **4** | **3** | **2C** | **2B** | **2A** |
| 0.704 | 0.177 | 0.038 | 0.062 | 0.020 |

**Table 2. Raw recovery rates of halibut < 65cm tagged externally in Area 4, summarized from IPHC database.**

| Recovery Area | | | | |
|---|---|---|---|---|
| **4** | **3** | **2C** | **2B** | **2A** |
| 0.763 | 0.142 | 0.027 | 0.050 | 0.018 |

**Table 3. Recovery proportions by release and recovery areas of externally-tagged halibut < 65 cm. Total numbers are provided in the last column. Area 4 is presented as separate Bering Sea (BS) and Gulf of Alaska (GOA) components.**

| | Recovery Area | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Release Area** | **4 BS** | **4 GOA** | **3B** | **3A** | **2C** | **2B** | **2A** | **Total recovered** |
| **4 BS** | **0.748** | 0.047 | 0.038 | 0.085 | 0.011 | 0.049 | 0.021 | 527 |
| **4 GOA** | 0.225 | **0.250** | 0.100 | 0.275 | 0.025 | 0.125 | - | 40 |
| **3B** | 0.014 | 0.007 | **0.452** | 0.290 | 0.071 | 0.148 | 0.017 | 714 |
| **3A** | 0.001 | - | 0.020 | **0.699** | 0.063 | 0.192 | 0.025 | 1,625 |
| **2C** | - | - | - | 0.022 | **0.816** | 0.160 | 0.002 | 463 |
| **2B** | - | 0.000 | - | 0.004 | 0.025 | **0.967** | 0.005 | 3,077 |
| **2A** | - | - | - | 0.053 | - | 0.105 | **0.842** | 19 |
| | | | | | | | | 6,465 |

**Table 4. Estimated annual migration rates of 65-80 cm fish from each regulatory area using data from the 1950-1969 external tagging programs. Adapted from Deriso and Quinn (1983).**

| Area in year i | Area in year i+1 | | | | | |
|---|---|---|---|---|---|---|
| | **4** | **3B** | **3A** | **2C** | **2B** | **2A** |
| **4** | **0.773** | 0.033 | 0.137 | 0.038 | 0.019 | 0.000 |
| **3B** | 0.000 | **0.773** | 0.160 | 0.046 | 0.020 | 0.000 |
| **3A** | 0.000 | 0.025 | **0.934** | 0.022 | 0.018 | 0.001 |
| **2C** | 0.000 | 0.000 | 0.007 | **0.953** | 0.040 | 0.000 |
| **2B** | 0.000 | 0.000 | 0.001 | 0.003 | **0.996** | 0.000 |

**Table 5. IPHC tag types used 1925 through 2010 (modified from Kaimmer 2000).**

| Tag type code | Description | Experiment numbers | Years | Total tags released[1] |
|---|---|---|---|---|
| 1 | Large strap | 1-469 | 1925-1970 | 62,703 |
| 2 | Small strap | 1-245 | 1925-1962 | 9,407 |
| 3 | Large dart | 171-363 | 1959-1964 | 10,518 |
| 4 | Small dart | 203-351 | 1961-1964 | 7,065 |
| 5 | Large Orange Wire | 181-624 | 1960,1965-1981 | 68,835 |
| 6 | Loop wire | 286-413 | 1963-1967 | 5,189 |
| 7 | Lock on | 542-859 | 1979-1995 | 540 |
| 8 | Dennison | 549-584 | 1979-1980 | 1,040 |
| A | Large yellow wire | 589-759 | 1980-1984 | 59,760 |
| B | Small yellow wire | 583-757 | 1980-1984 | 34,743 |
| C | Large pink wire | 747-863 | 1984-1996 | 56,047 |
| D | Light orange wire | 858 only | 1995 | 4,852 |
| E | Homer Derby orange wire[2] | 860 only | 1996 | 50 |
| F | Homer Derby orange wire[2] | 864 only | 1997 | 76 |
| G | Homer Derby orange wire[2] | 865 only | 1998 | 67 |
| P | PIT | | 2003-2004 | 67,436 |
| S | PAT | | 2003-2010 | 327 |

[1] Totals do not include almost 65,000 tag releases prior to 1960 which were recorded as tag type 1 but which included both Type 1 and Type 2 tags.

[2] E, F and G tags are same description but carry xxxx for years 1996, 1997 or 1998.

**Table 6. IPHC tag releases and recoveries by tagging project from 1925 to 2010 (modified from Kaimmer 2000).**

| | Years | Releases | Recoveries | % Recoveries |
|---|---|---|---|---|
| **Stock Assessment Studies** | 1925 to 1992 | 59,799 | 8,637 | 14.4% |
| Banks tagging | 1946 to 1968 | 86,642 | 18,202 | 21.0% |
| Coastwide marking program | 1961 to 1963 | 7,219 | 133 | 1.8% |
| Gulf groundfish trawl survey | 1963 to 1966 | 10,698 | 1,395 | 13.0% |
| Setline grid | 1963 to 1986 | 121,657 | 4,290 | 3.5% |
| Trawl recruitment series | 1976 to 1986 | 42,160 | 6,507 | 15.4% |
| Setline grids | 1983 to 1984 | 954 | 45 | 4.7% |
| Japan Cooperative research | 1956 to 1987 | 3,799 | 119 | 3.1% |
| US Cooperative research | 1975 to 1978 | 521 | 6 | 1.2% |
| USSR Cooperative research | | | | |
| Total | 1925 to 1992 | 333,449 | 39,334 | 11.8% |
| **Bycatch and Survival** | | | | |
| Troll bycatch and survival | 1950 to 1972 | 512 | 176 | 34.4% |
| Domestic trawler observer program | 1962 to1971 | 11,588 | 2,523 | 21.8% |
| Trawl/setline size and survival | 1966 | 2,347 | 786 | 33.5% |
| comparison | 1969 to 1995 | 5,846 | 220 | 3.8% |
| Trawl bycatch and survival | 1970 to 1971 | 153 | 1 | 0.7% |
| Foreign trawl catch comparison | 1980 | 185 | 16 | 8.6% |
| Crab pot survival | 1986 | 2,099 | 170 | 8.1% |
| Hook stripper study | 1988 | 174 | 18 | 10.3% |
| Multiple recapture by trawlers | 1989 | 219 | 24 | 11.0% |
| Oil spill impact | 1993 to 1994 | 13,096 | 861 | 6.6% |
| Careful release from cod style hooks | | | | |
| Total | 1950 to 1995 | 36,219 | 4,795 | 13.2% |
| **Gear Design** | 1958 | 222 | 3 | 1.4% |
| Tagging mortality | 1966 | 1,804 | 615 | 34.1% |
| Grid/spot tagging comparison | 1979 | 202 | 44 | 21.8% |
| Tag design | | | | |
| Total | 1958 to 1979 | 2,228 | 662 | 29.7% |
| **Miscellaneous Tagging** | | | | |
| Hand-lined fish during grid survey | 1961 | 52 | 2 | 3.8% |
| Gear and vessel effectiveness | 1962 | 1,113 | 31 | 2.8% |
| Hook spacing | 1972 to 1985 | 4,364 | 745 | 17.1% |
| Snap conventional gear study | 1982 | 1,448 | 149 | 10.3% |
| J/Circle hook comparison | 1983 | 528 | 81 | 15.3% |
| Setline catchability study | 1983 to 1987 | 3,814 | 617 | 16.2% |
| Tag release for fishing derby | 1984 to 1998 | 1,764 | 205 | 11.6% |
| Depletion fishing experiment | 1987 | 168 | 15 | 8.9% |
| Hook size study | 1988 | 77 | 8 | 10.4% |
| Incidental to movie production | 1988 | 159 | 17 | 10.7% |
| Total | 1961 to 1998 | 13,487 | 1,870 | 13.9% |
| **PIT** | 2003-to 2004 | 67,436 | 3,190 | 4.7% |
| **PAT** | 2002-to 2010 | 327 | | |
| **Grand total** | 1925 to 2010 | 452,710 | 49,851 | 11.1% |

**Table 7. Proportion of releases and recoveries by IPHC management area from historical tagging programs between 1925 and 1998. (From Kaimmer 2000).**

| | 4 | 3B | 3A | 2C | 2B | 2A |
|---|---|---|---|---|---|---|
| **4** | **0.63** | 0.07 | 0.19 | 0.05 | 0.05 | 0.01 |
| **3B** | 0.01 | **0.61** | 0.26 | 0.04 | 0.06 | 0.01 |
| **3A** | 0.00 | 0.04 | **0.88** | 0.02 | 0.05 | 0.01 |
| **2C** | 0.00 | 0.00 | 0.02 | **0.88** | 0.10 | 0.00 |
| **2B** | 0.00 | 0.00 | 0.00 | 0.01 | **0.98** | 0.00 |
| **2A** | 0.00 | 0.00 | 0.01 | 0.02 | 0.19 | **0.78** |

**Table 8. Proportion of releases and recoveries by IPHC management area from the PIT tagging program (From Webster 2010).**

| | 4 | 3B | 3A | 2C | 2B | 2A |
|---|---|---|---|---|---|---|
| **4** | **0.55** | 0.07 | 0.23 | 0.08 | 0.08 | 0.01 |
| **3B** | 0.00 | **0.61** | 0.32 | 0.04 | 0.02 | 0.00 |
| **3A** | 0.00 | 0.07 | **0.90** | 0.02 | 0.01 | 0.00 |
| **2C** | 0.00 | 0.00 | 0.03 | **0.84** | 0.12 | 0.01 |
| **2B** | 0.00 | 0.00 | 0.01 | 0.03 | **0.94** | 0.02 |
| **2A** | 0.00 | 0.00 | 0.00 | 0.08 | 0.46 | **0.46** |

**Table 9. Estimated annual migration rates of 80-120 cm fish from each regulatory area using data from the 1950-1969 external tagging programs. Adapted from Deriso and Quinn (1983).**

| **Area in** | **Area in year i+1** | | | | | |
|---|---|---|---|---|---|---|
| **year i** | **4** | **3B** | **3A** | **2C** | **2B** | **2A** |
| **4** | **0.853** | 0.016 | 0.068 | 0.019 | 0.010 | 0.000 |
| **3B** | 0.000 | **0.853** | 0.104 | 0.030 | 0.013 | 0.001 |
| **3A** | 0.000 | 0.016 | **0.958** | 0.014 | 0.001 | 0.001 |
| **2C** | 0.000 | 0.000 | 0.004 | **0.972** | 0.024 | 0.000 |
| **2B** | 0.000 | 0.000 | 0.002 | 0.006 | **0.991** | 0.001 |

**Table 10. Annual juvenile migration rates estimated by Hilborn et al. (1995). Their work estimated 7 alternative models, the table corresponds to the best model as considered by the original authors.**

| Area in year i | Area in year i+1 | | | | |
|---|---|---|---|---|---|
| | **3B** | **3A** | **2C** | **2B** | **2A** |
| **3B** | **0.708** | 0.231 | 0.061 | | |
| **3A** | | **0.894** | 0.080 | 0.026 | |
| **2C** | | | **0.698** | 0.302 | |
| **2B** | | | | **0.942** | 0.058 |
| **2A** | | | | | **1.000** |

**Table 11. Numbers of PIT releases and recoveries by release area and release length class. Fish with no release length recorded are excluded from the totals.**

| | | Length class (cm) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Release Area | | <60 | 60-70 | 70-80 | 80-90 | 90-100 | 100-110 | 110-120 | 120-130 | 130-140 | 140-150 | >150 | Total |
| 4D | releases | 2 | 31 | 76 | 127 | 192 | 265 | 149 | 60 | 38 | 20 | 19 | 979 |
| | recoveries | 0 | 0 | 2 | 8 | 16 | 20 | 7 | 5 | 4 | 0 | 1 | 63 |
| 4B | releases | 9 | 49 | 155 | 206 | 270 | 157 | 100 | 81 | 44 | 21 | 38 | 1130 |
| | recoveries | 0 | 1 | 2 | 3 | 4 | 5 | 1 | 0 | 0 | 0 | 0 | 16 |
| 4A | releases | 41 | 336 | 733 | 811 | 610 | 381 | 237 | 148 | 78 | 37 | 40 | 3452 |
| | recoveries | 0 | 5 | 29 | 34 | 29 | 15 | 4 | 4 | 0 | 0 | 1 | 121 |
| 3B | releases | 156 | 1639 | 4288 | 3783 | 2576 | 1464 | 744 | 328 | 163 | 68 | 69 | 15278 |
| | recoveries | 1 | 28 | 118 | 184 | 119 | 73 | 20 | 13 | 4 | 1 | 0 | 561 |
| 3A | releases | 184 | 1815 | 7847 | 12109 | 6416 | 3485 | 2100 | 1250 | 785 | 370 | 311 | 36672 |
| | recoveries | 0 | 9 | 111 | 506 | 455 | 258 | 151 | 92 | 56 | 26 | 13 | 1677 |
| 2C | releases | 14 | 228 | 769 | 865 | 538 | 371 | 302 | 223 | 160 | 111 | 92 | 3673 |
| | recoveries | 0 | 4 | 54 | 72 | 72 | 55 | 38 | 26 | 11 | 9 | 8 | 349 |
| 2B | releases | 51 | 529 | 1564 | 1489 | 811 | 462 | 337 | 283 | 147 | 63 | 64 | 5800 |
| | recoveries | 0 | 10 | 82 | 130 | 68 | 33 | 23 | 22 | 9 | 4 | 3 | 384 |
| 2A | releases | 0 | 21 | 87 | 85 | 42 | 34 | 13 | 13 | 2 | 2 | 0 | 299 |
| | recoveries | 0 | 1 | 5 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 13 |

**Table 12. Estimated annual migration rates with 95% Bayesian credible intervals for 100 cm fish from each regulatory area using data from the 2003-09 PIT tag study.**

| Area in year i | Area in year i+1 | | | | |
|---|---|---|---|---|---|
| | 4A | 3B | 3A | 2C | 2B |
| 4A | **0.833** (0.759, 0.890) | 0.041 (0.014, 0.087) | 0.093 (0.058, 0.141) | 0.013 (0.006, 0.024) | 0.019 (0.008, 0.034) |
| 3B | 0.002 (0.000, 0.006) | **0.907** (0.887, 0.925) | 0.084 (0.067, 0.102) | 0.004 (0.003, 0.007) | 0.003 (0.001, 0.005) |
| 3A | 0.000 (0.000, 0.002) | 0.059 (0.045, 0.076) | **0.934** (0.917, 0.948) | 0.003 (0.002, 0.004) | 0.004 (0.002, 0.006) |
| 2C | 0.000 (0.000, 0.002) | 0.000 (0.000, 0.002) | 0.025 (0.012, 0.043) | **0.895** (0.858, 0.927) | 0.080 (0.053, 0.112) |
| 2B | 0.006 (0.000, 0.022) | 0.000 (0.000, 0.003) | 0.002 (0.000, 0.008) | 0.008 (0.004, 0.014) | **0.984** (0.968, 0.992) |

**Table 13. Recovery areas of PIT tag releases in Area 4, 2003-09.**

| Release Area | Recovery Area | | | | | | |
|---|---|---|---|---|---|---|---|
| | 4D | 4C | 4B:BS | 4A:BS | 4B:GOA | 4A:GOA | 3+2 |
| 4D | **55** | 0 | 0 | 3 | 0 | 1 | 4 |
| 4B:BS | 1 | 0 | **4** | 0 | 0 | 0 | 3 |
| 4A:BS | 0 | 1 | 1 | **19** | 1 | 1 | 8 |
| 4B:GOA | 0 | 0 | 0 | 0 | **4** | 0 | 4 |
| 4A:GOA | 0 | 0 | 0 | 1 | 1 | **16** | 68 |

**Table 14. Estimated annual migration rates from the PIT tag study for all release areas from a model in which migration is not a function of length. Note that estimates for Areas 2A and 4B are based on very little data, and should be treated with caution.**

| Area in year i | Area in year i+1 | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 4D | 4B | 4A | 3B | 3A | 2C | 2B | 2A |
| 4D | **0.924** | 0.000 | 0.062 | 0.000 | 0.003 | 0.001 | 0.010 | 0.000 |
| 4B | 0.002 | **0.967** | 0.000 | 0.000 | 0.021 | 0.005 | 0.005 | 0.000 |
| 4A | 0.000 | 0.014 | **0.792** | 0.053 | 0.097 | 0.016 | 0.025 | 0.003 |
| 3B | 0.000 | 0.000 | 0.003 | **0.887** | 0.101 | 0.005 | 0.004 | 0.000 |
| 3A | 0.000 | 0.000 | 0.000 | 0.046 | **0.947** | 0.003 | 0.003 | 0.000 |
| 2C | 0.000 | 0.000 | 0.000 | 0.000 | 0.024 | **0.898** | 0.067 | 0.012 |
| 2B | 0.000 | 0.000 | 0.004 | 0.000 | 0.004 | 0.009 | **0.970** | 0.014 |
| 2A | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.008 | 0.110 | **0.882** |

**Table 15. Estimates of net annual migration rates (%) of O32 halibut biomass[1] (from Webster 2010).**

| Area | Immigration | Emigration | Net migration |
|---|---|---|---|
| **4A** | 1.4 | 22.6 | -21.3 |
| **3B** | 11.1 | 12.4 | -1.3 |
| **3A** | 9.9 | 5.9 | 3.9 |
| **2C** | 6.3 | 9.8 | -3.4 |
| **2B** | 9.4 | 1.6 | 7.8 |

[1]Calculated from estimates of annual emigration rates from tag-recovery modelling for 2004-09 and population numbers for January 1 2010 estimated using the coastwide stock assessment.

**Table 16. Annual immigration rates (%) of O32 halibut biomass into each area broken down by source of immigration (from Webster 2010).**

| | Source of immigration | | | | | |
|---|---|---|---|---|---|---|
| **Area** | **4A** | **3B** | **3A** | **2C** | **2B** | **Total** |
| **4A** | | 0.6 | 0.3 | 0.0 | 0.5 | 1.4 |
| **3B** | 2.1 | | 9.1 | 0.0 | 0.0 | 11.1 |
| **3A** | 2.8 | 6.5 | | 0.5 | 0.1 | 9.9 |
| **2C** | 2.2 | 1.8 | 1.2 | | 1.2 | 6.3 |
| **2B** | 2.0 | 0.8 | 1.2 | 5.4 | | 9.4 |

**Table 17. Annual emigration rates (%) of O32 halibut biomass out of each area broken down by destination of emigration (from Webster 2010).**

| | Destination of emigration | | | | | |
|---|---|---|---|---|---|---|
| **Area** | **4A** | **3B** | **3A** | **2C** | **2B** | **Total** |
| **4A** | | 5.4 | 12.6 | 2.0 | 2.6 | 22.6 |
| **3B** | 0.2 | | 11.1 | 0.6 | 0.4 | 12.4 |
| **3A** | 0.1 | 5.3 | | 0.3 | 0.4 | 5.9 |
| **2C** | 0.0 | 0.0 | 2.2 | | 7.6 | 9.8 |
| **2B** | 0.4 | 0.0 | 0.3 | 0.9 | | 1.6 |

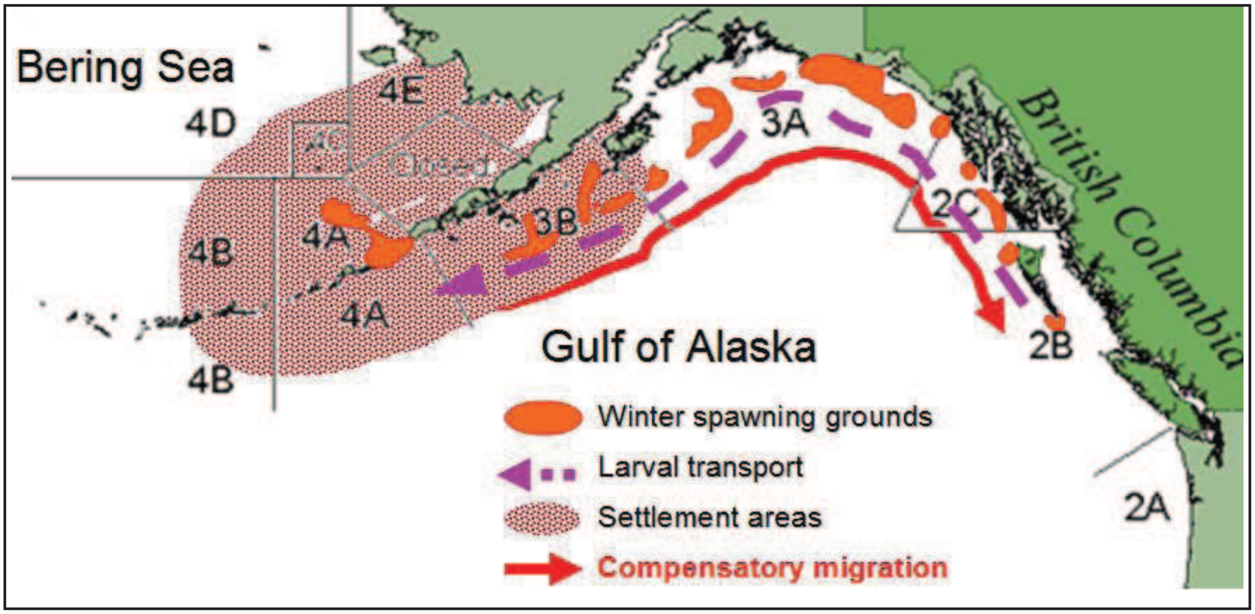


**Figure 1. Conceptual model of Pacific halibut migration patterns.**

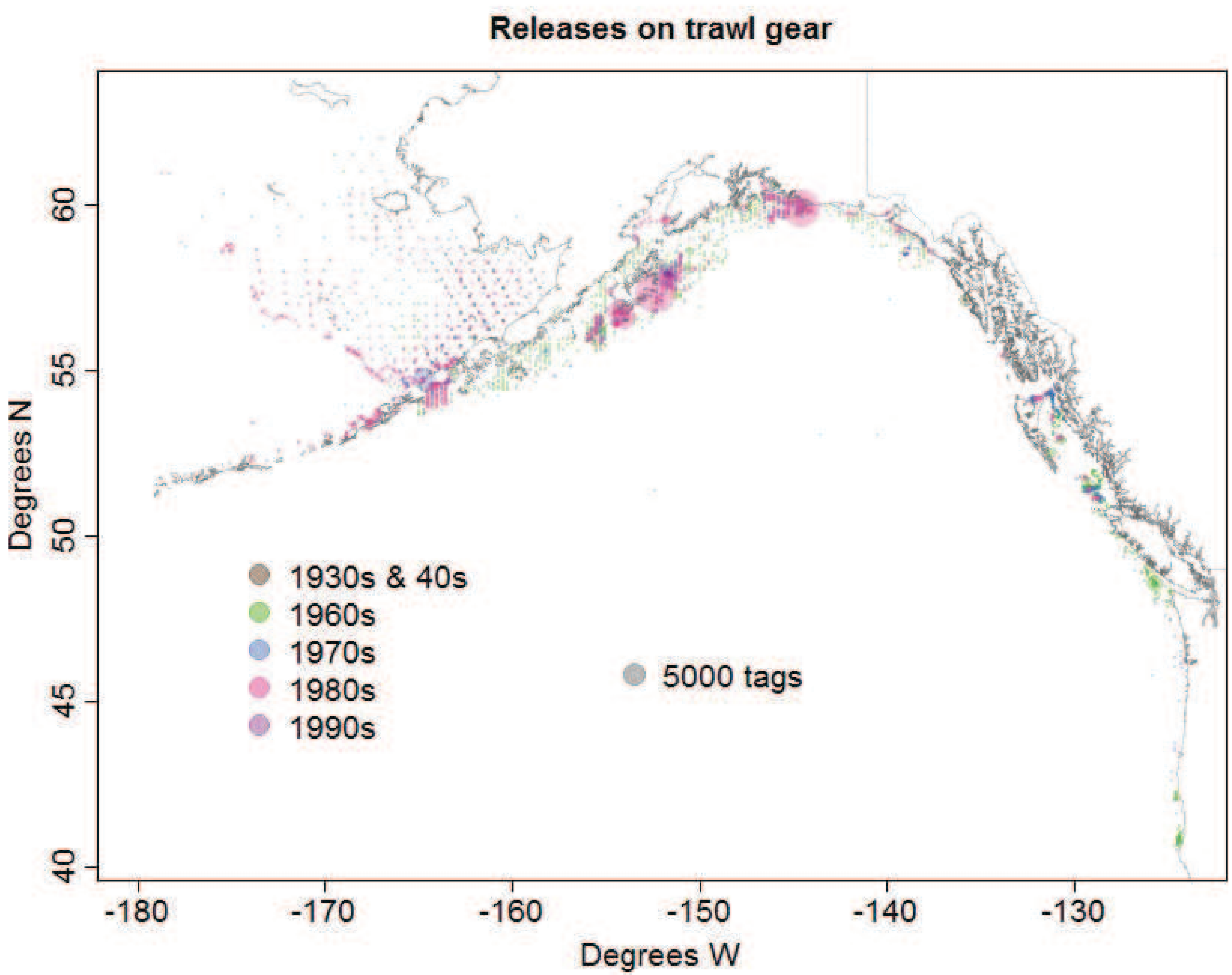


**Figure 2. Geographic location of historical tag releases of trawl captured halibut. Please see electronic version for colours.**

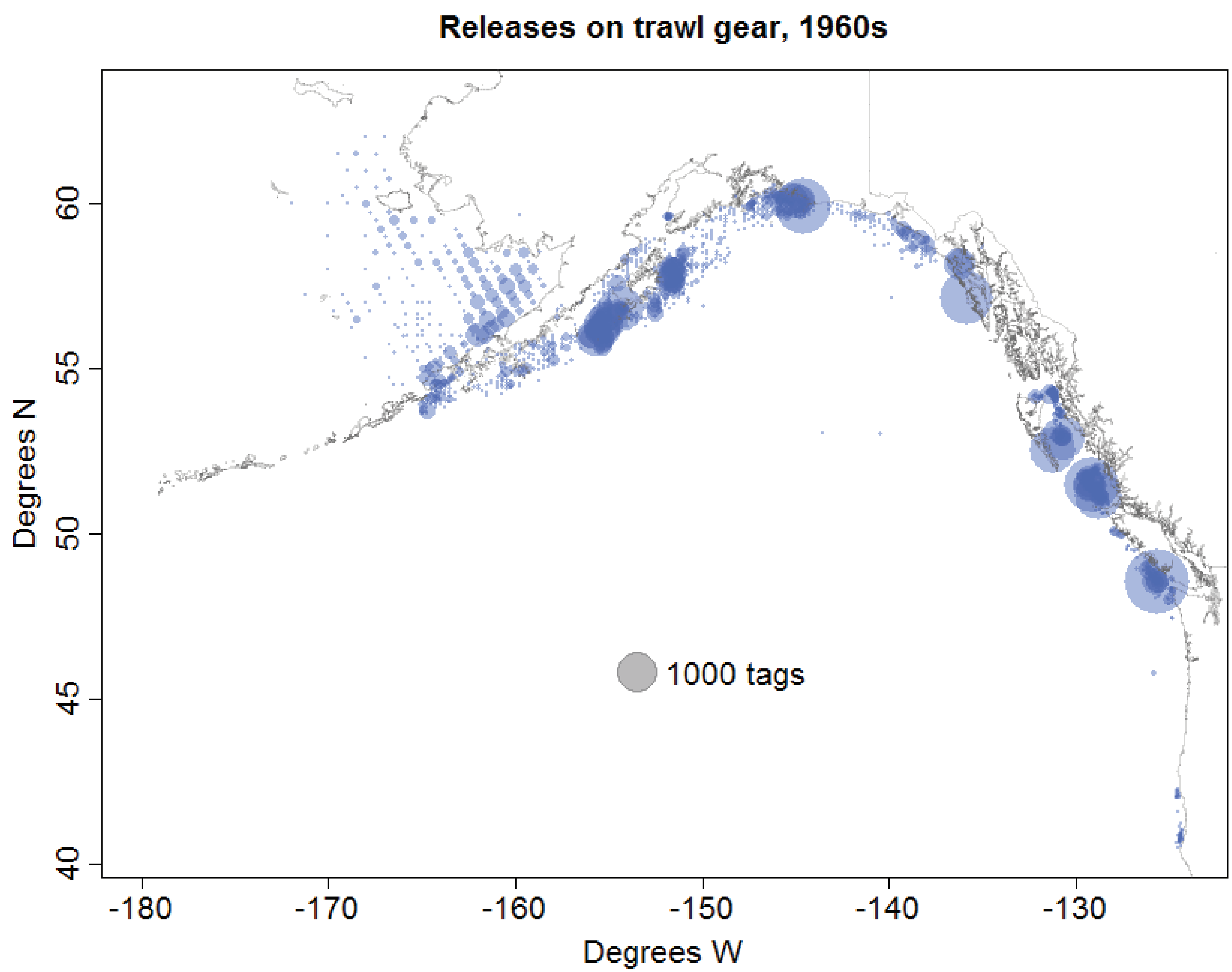


**Figure 3. Geographic location of historical tag releases of trawl captured halibut in the 1960s.**

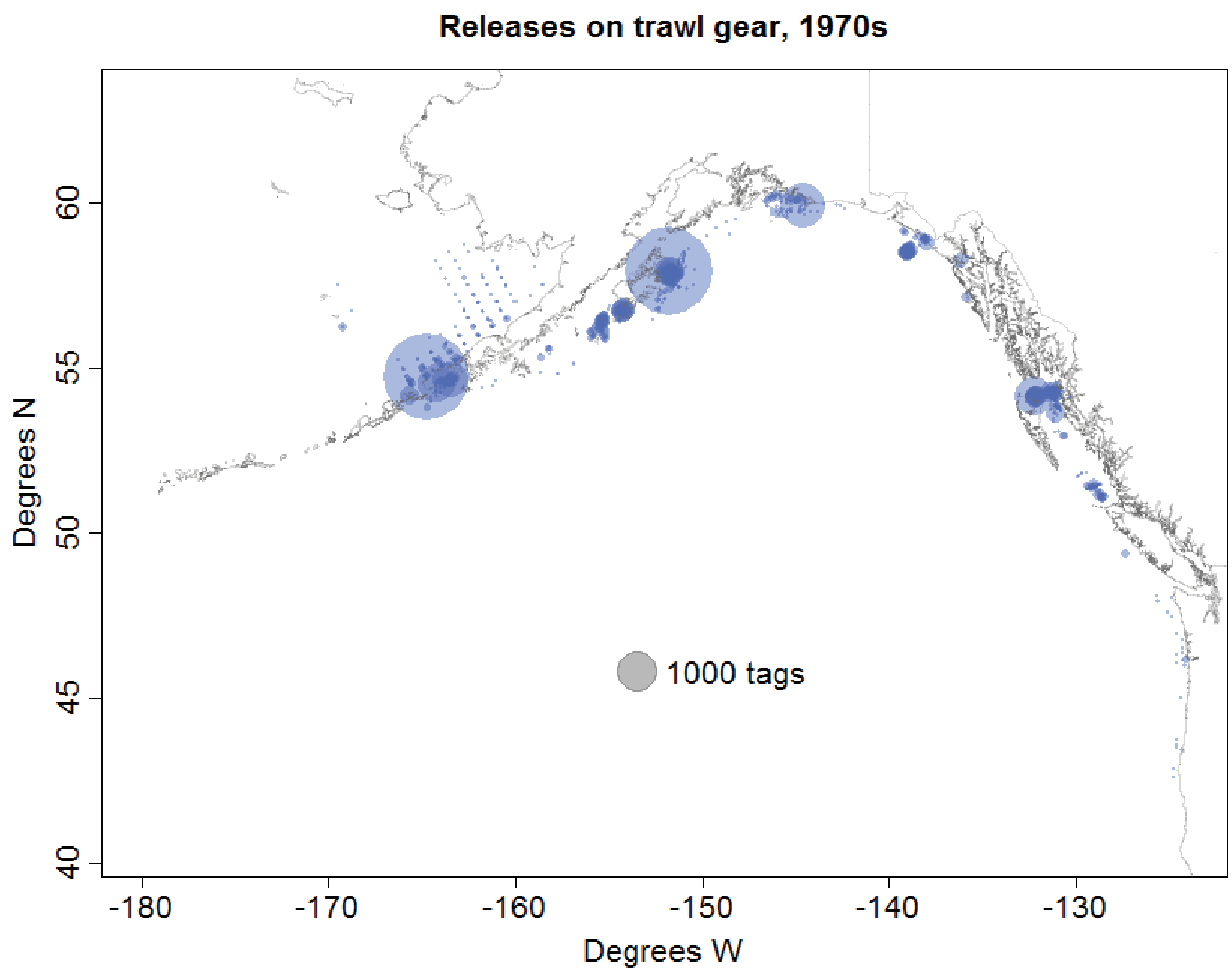


**Figure 4. Geographic location of historical tag releases of trawl captured halibut in the 1970s.**

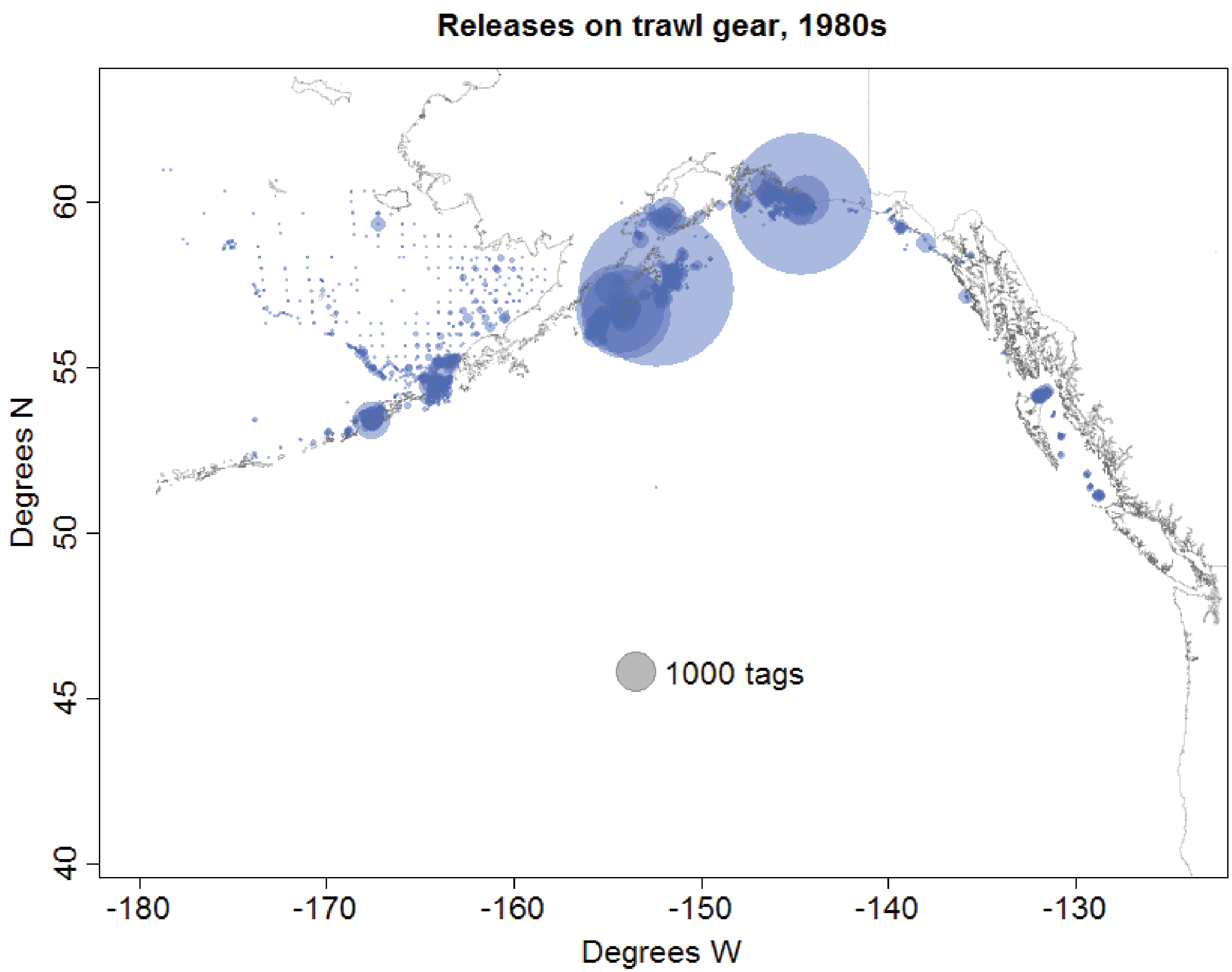


**Figure 5. Geographic location of historical tag releases of trawl captured halibut in the 1980s.**

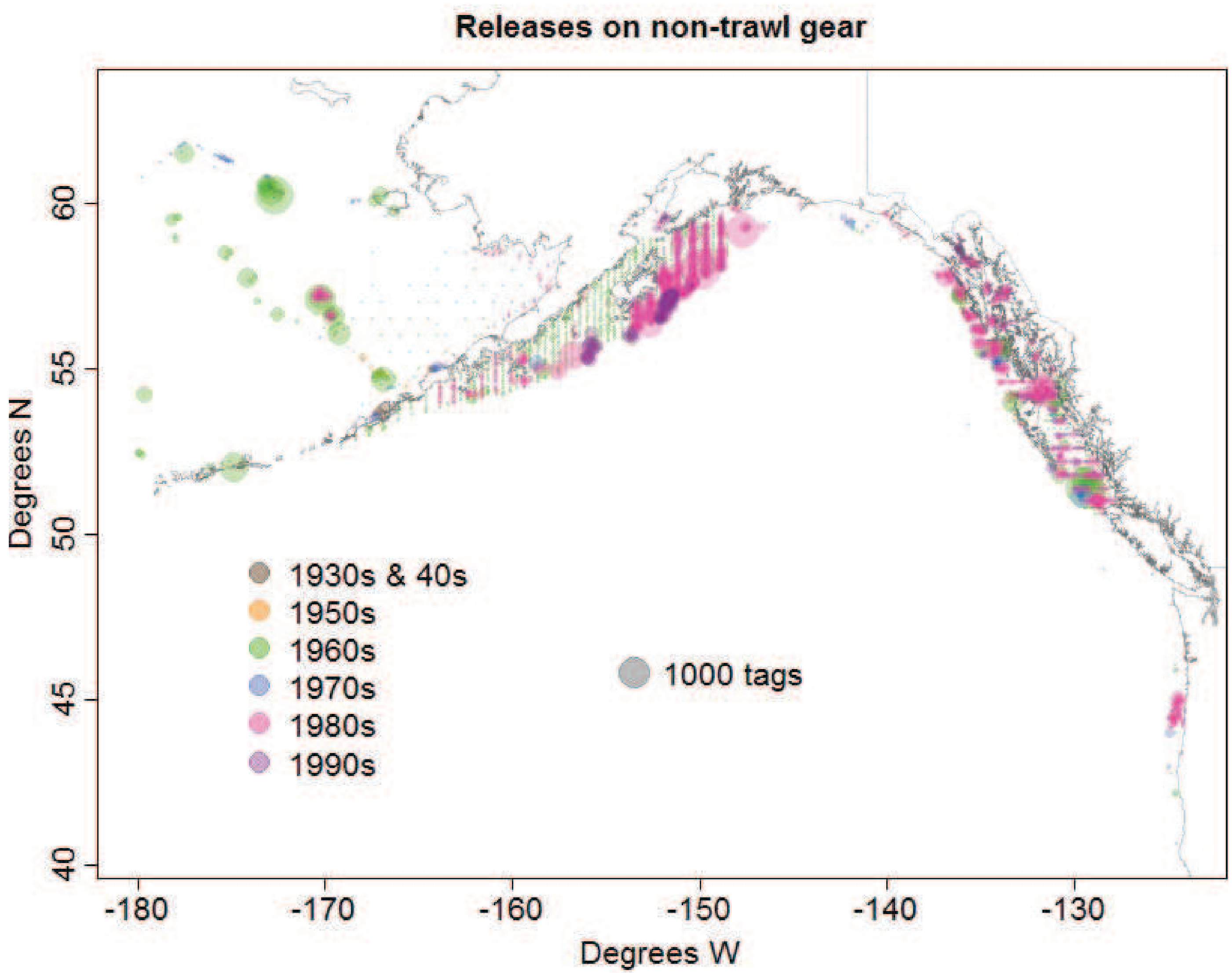


**Figure 6. Geographic location of historical tag releases of halibut captured from non-trawl gear (over 99% longline or hook and line gear). Please see electronic version for colours.**

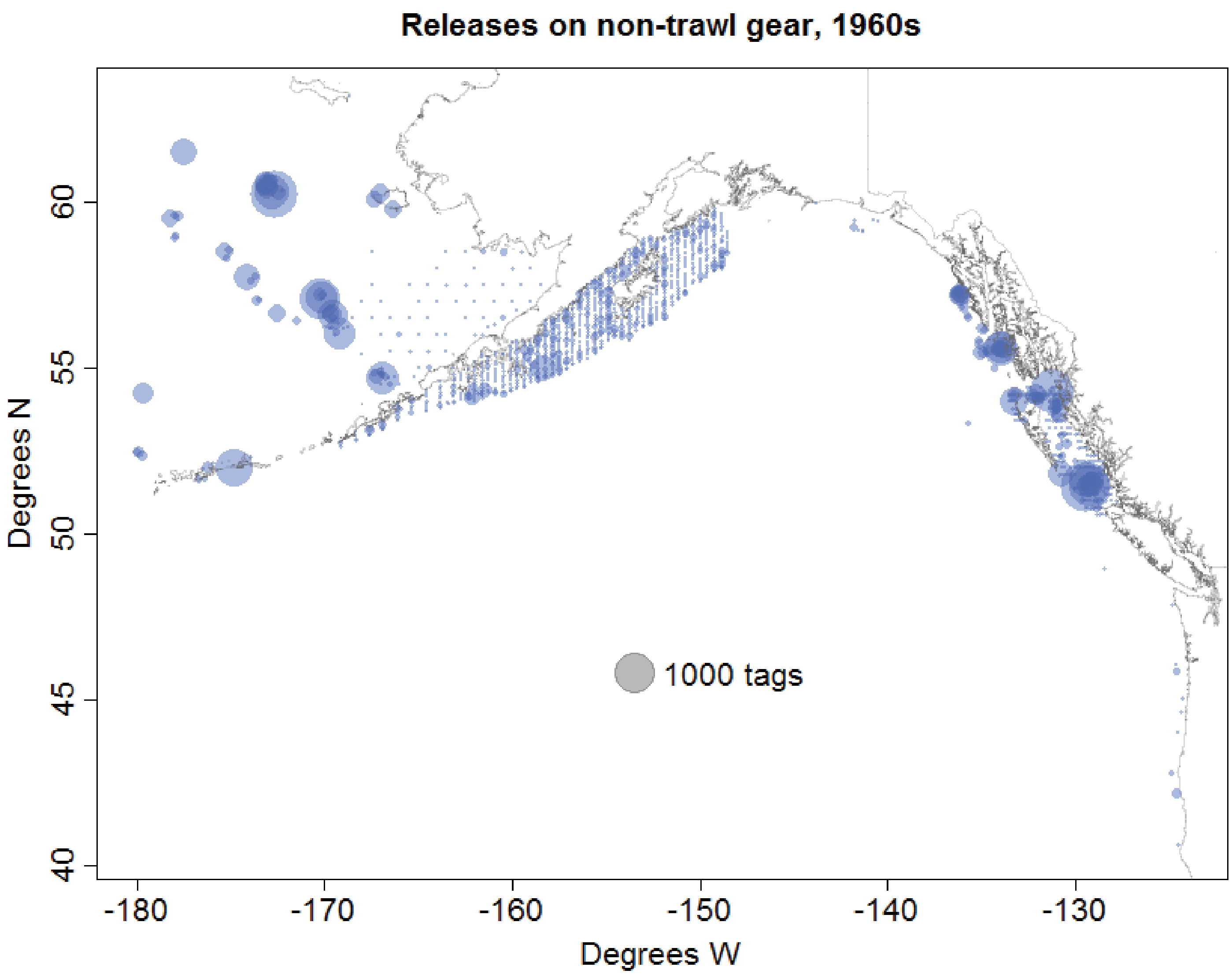


**Figure 7. Geographic location of historical tag releases of halibut captured from non-trawl gear (over 99% longline or hook and line gear) in the 1960s.**

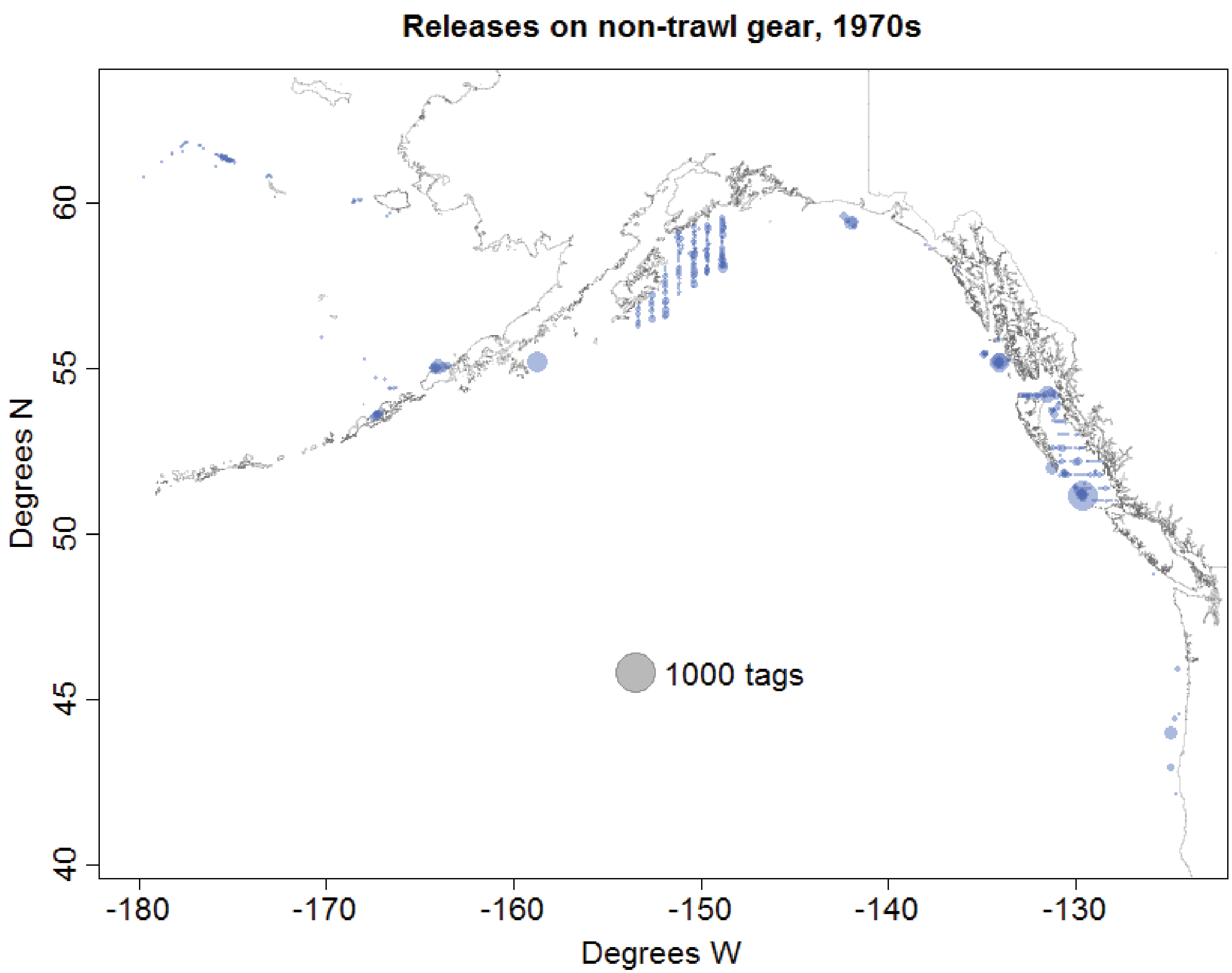


**Figure 8. Geographic location of historical tag releases of halibut captured from non-trawl gear (over 99% longline or hook and line gear) in the 1970s.**

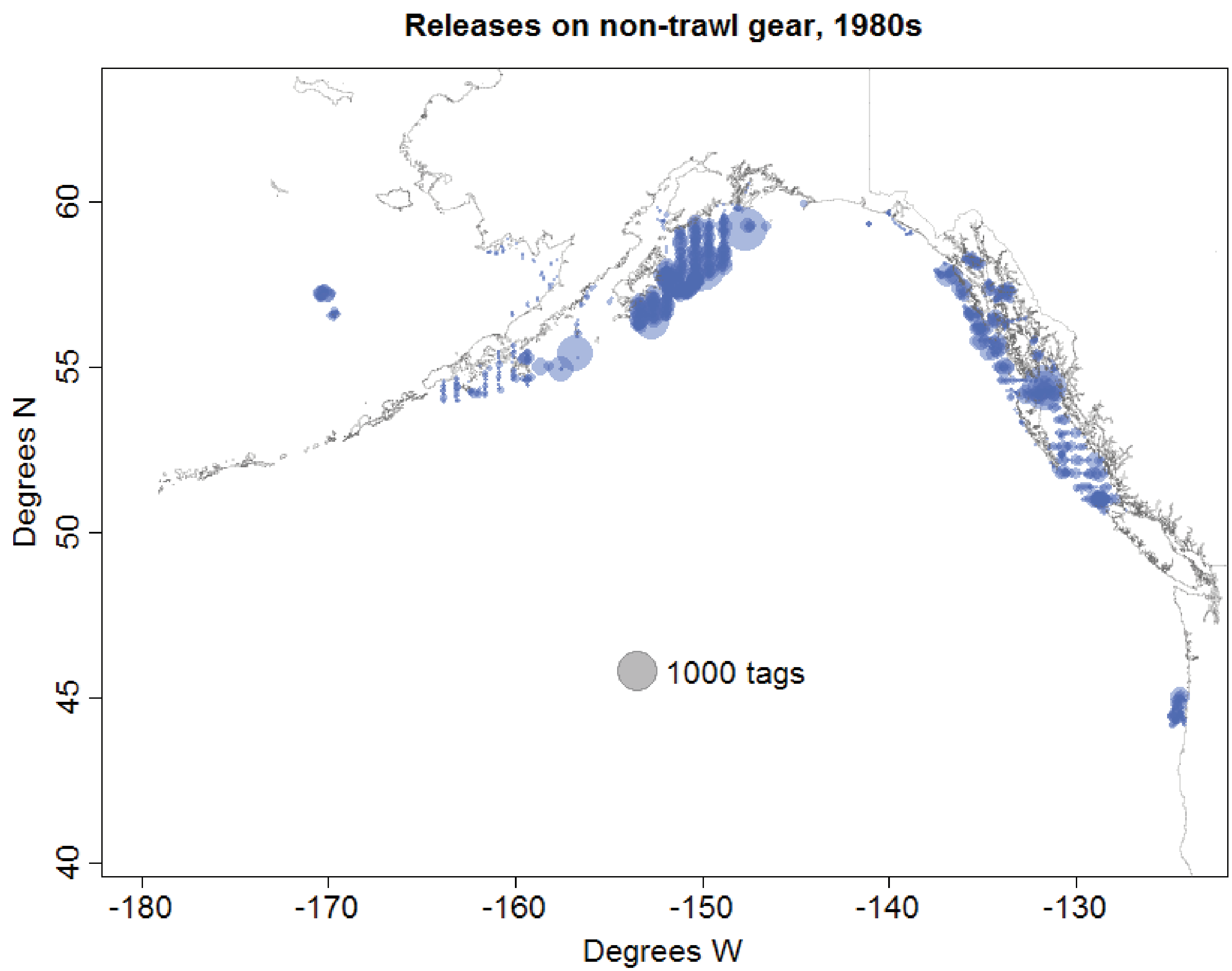


**Figure 9. Geographic location of historical tag releases of halibut captured from non-trawl gear (over 99% longline or hook and line gear) in the 1980s.**

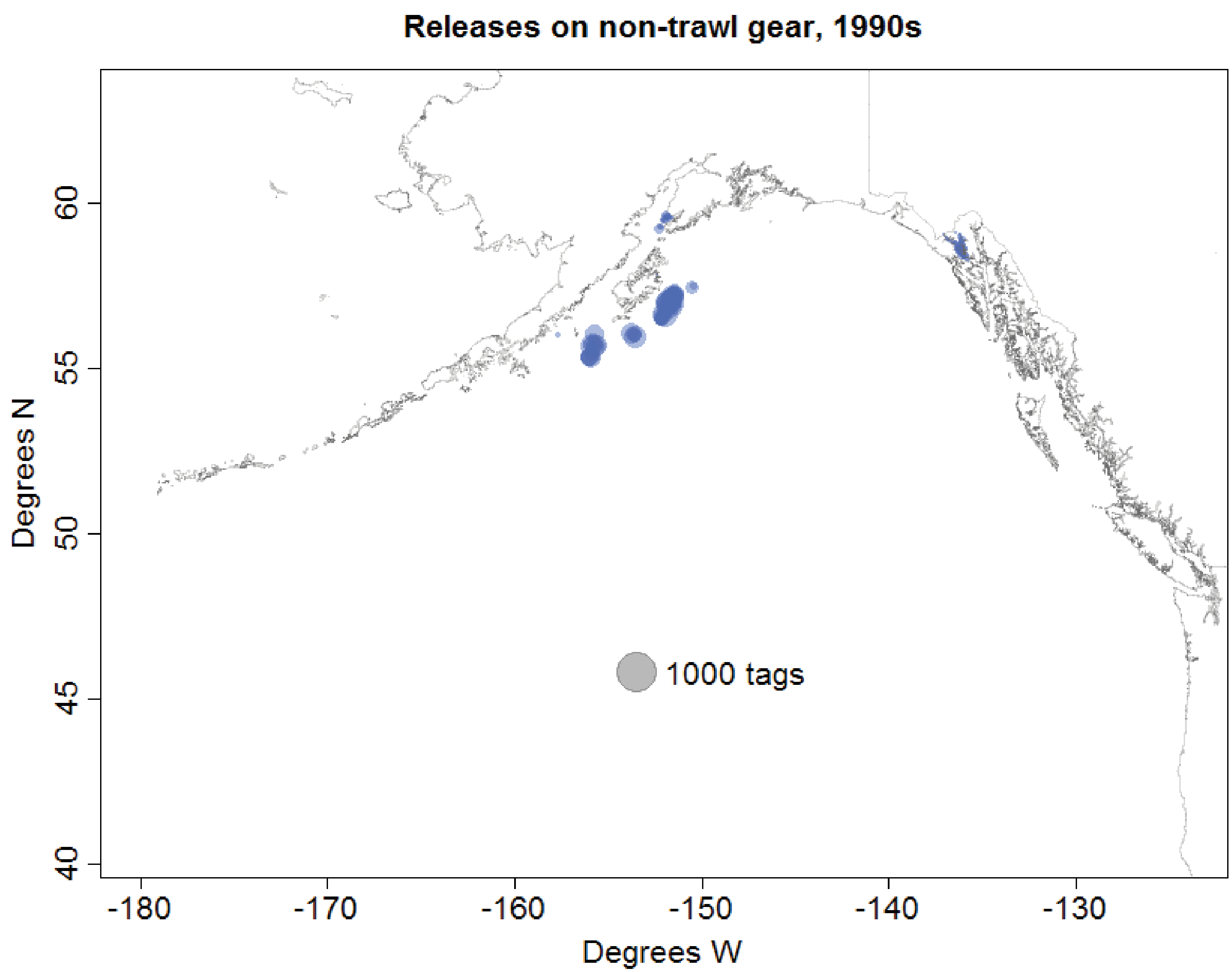


**Figure 10. Geographic location of historical tag releases of halibut captured from non-trawl gear (over 99% longline or hook and line gear) in the 1990s.**

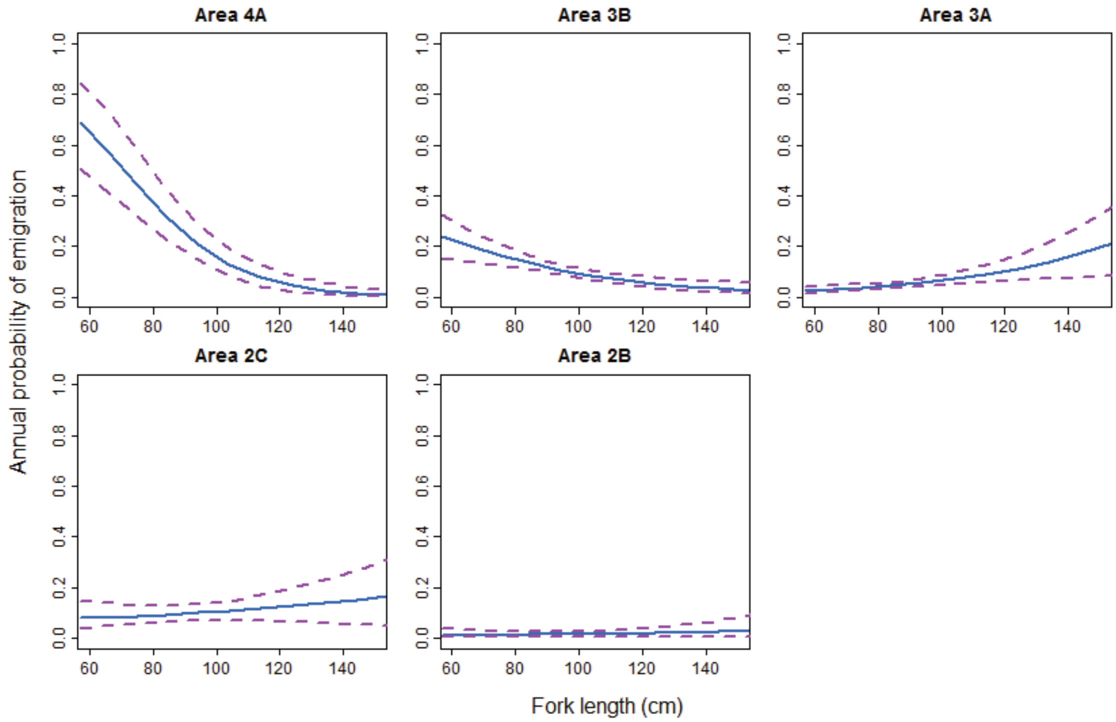


**Figure 11. Estimated relationship between annual emigration probability and halibut length from modelling of the PIT tag data. Dashed lines are upper and lower 95% Bayesian credible interval bounds.**