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The mysterious sei whale: Its distribution, movements and population decline in the North Pacific revealed by whaling data and recoveries of Discovery-type marks

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ABSTRACT

We explore the distribution, movements and population structure of sei whales (*Balaenoptera borealis*) in the North Pacific by analyzing 20th century whaling data, data from recoveries of Discovery-type marks and data from systematic sightings surveys. Analysis of whaling and Discovery mark data suggest a division between pelagic and coastal stocks, as well the possibility of multiple stocks of sei whales that appear to feed within known ocean current systems.

1) A pelagic migratory stock appears to feed south of the North Pacific Current.
2) An Aleutians/Gulf of Alaska stock appears feed to along the Aleutian Trench south of the Alaska Stream, north of the North Pacific Current and likely moves eastward into the Alaska Current as it mixes in the Gulf of Alaska ,
3) An eastern North Pacific migratory stock that appears to migrate within the California Current north into the Alaska Current,
4) A southern North American coastal stock which was caught by land-based whalers off Central California within the California Current whose boundaries are unclear, and
5) A Japanese coastal stock which appears to be a resident, non-migratory stock that is bounded to the east by the Kuroshio and bounded to the north by the Oyashio where the Oyashio coincides with the Kuroshio.

Although pelagic and land station whaling data showed concentrations of sei whales both in coastal waters and on the high seas, systematic sighting surveys indicate that sei whales are now rarely seen in coastal areas where large numbers had been taken by whalers. Bayesian analyses of catch and Discovery mark data show that whaling mortality greatly exceeded what would have been sustainable for such a long-lived species. Analyses indicate that the pelagic migratory stock, which had already been depleted by 1972 to approximately 11,000 individuals, was likely reduced by a further 65% (95% CI 30-86%) to approximately 4,000 individuals in 1975, after which sei whale catches were prohibited.

Key words: *Balaenoptera borealis,* abundance, depletion, whaling, Discovery mark, pelagic stock, migratory

INTRODUCTION

In many ways, the sei whale (*Balaenoptera borealis* Lesson, 1828) could be said to be the most mysterious and poorly understood of the large baleen whales. Pelagic throughout much of its range, and known for sudden appearances followed by long absences in certain coastal waters, the factors governing the occurrence and distribution of sei whales remain unclear, and little is known regarding their population structure. Sei whales occur in all the world's oceans but are generally found in a narrower range of latitudes than their larger balaenopterid relatives the blue whale (*B. musculus*) and the fin whale (*B. physalus*). The species remains mainly in more temperate mid-latitudes, rarely entering tropical or polar waters.

In this paper, we seek to achieve a greater understanding of the life history and historical changes in population structure of sei whales in the North Pacific, both by reviewing existing literature and analyzing historical data from whaling data and marking records. To start, we review historical records and reported life history information for sei whales. Next, we explore the distribution and movements of sei whales in the North Pacific by analyzing mid-20th century whaling data as well as location data from recoveries of 106 Discovery-type marks, as well as additional information from sighting surveys dating back to 1980. From this, we examine existing ideas about the population structure of this species, and suggest that, while there may a single stock of sei whales in the pelagic North Pacific that appear to feed in the Subarctic Frontal Zone, additional coastal stocks may have existed that were either extirpated or remain depleted almost 40 years after whaling ceased. Finally, we conduct an integrated analysis of sei whale mark-recovery data to estimate population size and trend in the last few years of commercial whaling from 1972 through 1975.

Background

The sei whale was first made known to science when an individual stranded on the German coast of the North Sea in 1819. This animal was described by Karl Asmund Rudolphi (Rudolphi 1822), who named it *Balaena rostrata*. For a long time thereafter it was called "Rudolphi's rorqual". Rudolphi's scientific name turned out to be preoccupied, so it was replaced by *Balaenoptera borealis* Lesson, 1828. The common name of the species is an anglicized version of the Norwegian *Sejhval* (*or Seihval*), meaning pollock or coal-fish whale, because the whales appeared seasonally when the pollock (*Pollachius virens*) became available to the Norwegian fishing fleets (Allen 1916). However, sei whales were never known to feed on pollock.

Few sei whales were examined by scientists until Svend Foyn (the inventor of the harpoon cannon) killed one off Varangerfjord, Finnmark, Norway in 1881 (Andrews 1916).

The first attempt to learn more about the biology of the sei whale was made by Collett (1886), a Norwegian zoologist. In July 1885 he visited the Norwegian whaling stations on Varangerfjord. Although he examined only 6 specimens of sei whales, he provided the first information on food habits, parasites, fetuses, and other topics (Collett 1886). Little more was learned about the species until 1910, when Andrews (1916) made a study of sei whales landed at Japanese shore stations.

In the Southern Ocean, few sei whales were taken in the early decades of Antarctic whaling, but Matthews (1938) reported on 220 sei whales examined at the shore stations on the island of South Georgia and in South Africa during the course of the British Discovery Investigations from 1926 to 1931.

Although sei whales had been exploited to some extent by Japanese coastal whalers beginning in the late 19th century (Mizroch *et al.* 1984; Kasuya 2009), the intensity of hunting by pelagic whalers increased markedly in the second half of the 20th century after stocks of other large whales had been depleted (Mizroch 1984). Whaling for sei whales was most intense in the mid-1960s and sei whale stocks in both the North Pacific and Antarctic were at such low levels by the early 1970s that catches were banned in 1975; the ban went into effect in the 1976 whaling season in the North Pacific (Anonymous 1975) and in the 1978/79 whaling season in the Antarctic (Anonymous 1979).

Food habits

Like all species of rorquals, sei whales employ a unique method of filter-feeding called "gulping", "engulfing", or "lunge-feeding". Their possession of a huge ventral pouch enormously increases the capacity of the mouth cavity, and allows them to engulf a large volume of prey-laden water.

However, unlike all other species of rorquals, the sei whale also engages in skim-feeding (Ingebrigtsen 1929; Nemoto 1970). This involves swimming forward with the mouth continuously open, allowing them to take in larger quantities of sparsely distributed prey such as copepods. Another unique feature of sei whales is the extremely fine, "silky" fringe on their baleen, which allows them to capture smaller prey (primarily calanoid copepods).

Because of these features, sei whales, as a species, are more generally more euryphagous than the larger species of rorquals, which feed largely or exclusively on dense swarms of krill (Mizroch *et al.* 1984). At any given time and place, sei whales have been found to be stenophagous (Prieto *et al.* 2011). However, Nemoto and Kawamura (1977) noted that these categories are dependent on both the behavioral habits of the whales and also the availability of prey.

Japanese whalers called the sei whale *Iwashi Kujira* (“sardine whale”), named after their presumed prey in those waters at the time (Andrews 1916). Andrews (1916) noted that although the Japanese whalers believed that sei whales preferred small schooling fishes, his analyses at the “Aikawa” (Ayukawa) whaling station showed that only a few sei whales consumed sardines (Andrews presumed the species to be *Eugraulis japonicus,* which is actually an anchovy), but all the other whales he examined had consumed euphausiids. Andrews therefore concluded that euphausiids were preferred in this locality if available.

Later studies by Omura (1950) and Mizue (1951) confirmed that sei whales around Hokkaido and the Sanriku coast of Honshu depended mainly on euphausiids (*Euphausia pacifica, Thysanoessa inermis,* and *T. longipes*), but they did take significant numbers of fishes. In the more northerly waters of the North Pacific they feed almost exclusively on copepods (*Neocalanus cristatus* and *N. plumchrus*).

Whale researchers have noted annual variability in prey preferences. For example, from 1963 to 1965, more than 90% of the stomachs of sei whales killed off Vancouver Island, Canada contained copepods. Those killed in 1966 contained mostly euphausiids, and those killed in 1967 contained mainly fishes—primarily sauries (*Cololabis saira*) (Ford 2014).

Off the coast of California during the 1960s, sei whales preyed on substantial numbers of krill (*E. pacifica*), anchovies (*Engraulis mordax*), and sauries (*C. saira*); only a few had eaten copepods (*Calanus pacificus*) (Rice 1977).

Distribution

Because sei whales are often distributed in pelagic waters far from land, the distribution of sei whales is hard to analyze in the absence of offshore surveys. Andrews (1916) noted the "sudden appearance in 1885 of great numbers of Sei Whales (*sic*) east of the North Cape, Norway, where previously they had only been seen as stragglers, and of similar invasions of the waters about Scotland; also their arrival at Newfoundland in 1902 and at the South Georgia Islands in 1913-1914 where before they were quite unknown, indicate that *B. borealis* has a roving disposition and sometimes travels great distances in its wanderings".

Nasu (1966) found strong links between sei whale distribution and oceanic fronts and noted that they tend to "move along the oceanic front and the current which develops in this region [of the front]". He also noted that as whalers transitioned from targeting fin whales to targeting sei whales along the Aleutians and Gulf of Alaska in the 1960s, areas of sei whale concentration differed from areas of fin whale concentration. His data showed that sei whales were more likely to be found in the boundary zone between the Alaska Stream and the "Central Subarctic Water"; that is., the North Pacific Current. In the western Aleutians, sei whales were found south of the Alaska Stream and the northern extension of the Kuroshio Current and the North Pacific Current (see Fig. 1 for a broad schematic of ocean currents in the North Pacific (Stabeno, pers. comm.))

Gregr (2000) also found that sei whale seasonality and distribution was linked to changes in oceanographic conditions off the western coast of Canada. He noted that the pattern of seasonal abundance of sei whales was much different than the other baleen whale species taken by Canadian whalers at the Coal Harbour whaling station during years of high exploitation in the 1960s. He also remarked that sei whales showed "significant offshore movement" in July and found that models of sei whale distribution indicated that sei whales were more likely to be associated with deep water than other balaenopterids.

Possible morbidity and mortality factors

Possible morbidity and mortality factors include diseases and parasites. Rice (1977) reported that 20 (7%) of sei whales examined at the California whaling stations from 1959 to 1971 were infected with a disease that causes loss of baleen plates. Twelve of these infected whales had been feeding on fishes (sauries, anchovies, and jack mackerel (*Trachurus symmetricus)*), and one had been feeding on euphausiids. However, although direct evidence is lacking, it seems likely that this baleen disease could result in significant mortality.

He also noted that sei whales were more heavily infested with parasitic helminths than were the other baleen whale species ((Rice 1974). However only two species of helminths regularly showed pathogenic effects: liver flukes (*Brachycladium goliath*) and kidney worms (*Crassicauda boopis*).

Most sei whales killed off California carried a heavy load of stomach nematodes (*Anisakis simplex*), but they had no obvious pathogenic effects except for one individual, a 14.9 m pregnant female (age 17 based on counts of growth layer groups) killed on 14 September 1961. Hundreds of nematodes had invaded the bulk of her liver, the parenchyma of which was very soft and pale, and probably necrotic. Her liver was also infested with liver flukes. We assume that such a massive infestation of nematodes would have eventually led to her death. None of the others species of helminths observed in other whales at the California whaling stations had any obvious pathogenic effects.

Sei whales are also noted for often having extensive scarring on the skin, apparently caused by ectoparasites. Andrews (1916) had noted “All the specimens brought to the stations in Japan were thickly covered with scars” which he attributed to “the action of parasitic cirripeds, probably Coronula, and the Copepod Penella [sic] Antarctica Quidor, but very few of the parasites remained attached to their hosts. Collett (1886) discusses at length the peculiar scars left by the Penella [sic],-but did not suspect they were due to parasites”.

However, *Pennella* is not common on sei whales, and the barnacles of the genus *Coronula* are host-specific epizoites of the humpback whale with only rare adventitious occurrences on other cetaceans (Scarff 1986).

We believe that at least some of the scars described by Andrews (1916) and shown in the photograph on plate XXXV of that publication were caused by bites of cookiecutter sharks (*Isistius brasiliensis*) (Jones 1971; Walker and Hanson 1999).

On the California whaling stations, the only fresh bites observed on sei whales (by Rice) were caused by Pacific lampreys (*Entosphenus tridentate*) (Pike 1951).

The only predator known to take sei whales is the killer whale (*Orcinus orca*), but such attacks have rarely been observed (Mizroch and Rice 2006).

MATERIALS AND METHODS

We first describe available data for North Pacific sei whales (whaling, marking, sightings and acoustics data), and then describe methods for analyzing these records.

Data sources

Whaling data

Starting in 1929, whaling data from the modern whaling era were collected and collated by the Bureau of International Whaling Statistics (BIWS) in Sandefjord, Norway (Anonymous 1930). Management responsibility for those data was transferred to the International Whaling Commission (IWC) in Cambridge, U.K. in 1981. Since that time, the IWC has been responsible for managing and archiving all current whaling data. As time has permitted, they have been entering historical whaling data that pre-dates the BIWS. The catch data analyzed here were distributed by the IWC in December 2012, and include catch records of 2,373,175 whales hunted in the North Atlantic since 1883, in the Southern Hemisphere starting in the early 20th century and in the North Pacific starting in 1908, as well as records of catches in the South Atlantic, South Pacific and Indian Ocean.

The total catch of sei whales in the North Pacific as reported to the BIWS was 62,413. Reported land station catches totaled 22,516 (Table 1) and reported pelagic catches totaled 39,897 (Table 2).

However, sei whale catch data reported prior to the enactment of International Convention for the Regulation of Whaling in 1946 (Anonymous 1950) are incomplete and often erroneous. Also, in the years before the Second World War (WW II), catches of sei whales were rare, sporadic and highly localized in the eastern North Pacific (Webb 1988). Therefore the pre-war catch data will not be analyzed in this paper.

Although the BIWS/IWC catch statistics are a valuable source of data on whale distribution because of their great volume, they should be analyzed with caution because the Soviet fleets were known to have submitted falsified catch statistics to conceal their extensive violations of the IWC regulations that prescribed protected species, catch quotas, and length limits. These violations extended from 1948 until at least 1972 (see Berzin (2008) for an overview and Ivashchenko *et al.* (2013) and Ivashchenko and Clapham (2014) for specific details about Soviet mis-reporting in the North Pacific).

For analyses of the broad distribution of sei whales, we will analyze and plot the Japanese pelagic catch data which had been reported with actual location data for each sei whale caught. Ivashchenko (*in litt*.) provided summaries of the raw corrected Soviet catch data, but these totals lack location data, so annual catch summary tables and charts where appropriate will show the Japanese catch as reported to the BIWS as well as the corrected Soviet catch as described by Ivashchenko *et al.* (2013). The corrected Soviet data (Table 2) show that there was some small-scale under-reporting of sei whale catches starting in 1962, then extreme over-reporting of sei whale catches between 1966 and 1969 (reporting catches of other species as sei whales to mask catches of illegal species) and some continued over-reporting on a small scale until 1972, when an international observer program was initiated to monitor catch reporting. All catch maps will show the Japanese pelagic catch data and Soviet data will only be presented in summary form.

Marking

From 1949 through 1975, 620 sei whales were marked with Discovery marks during marking expeditions which operated independently of whaling vessels. Of these, 110 marks were recovered (Fig. 2).

Discovery marks were named after the British Discovery Committee and are steel tubes approximately 23.5 cm long tipped with a conical lead point 38 mm long. Each Discovery mark was inscribed with a unique number. Discovery marks were fired into a whale from a 12-gauge shotgun. The geographic location of each marking event was recorded. When a marked whale was killed by whalers, the recovery location was recorded. Rayner (1940) describes the evolution of the Discovery mark and Brown (1977) provides an overview of whale marking studies.

The Japanese marked a total of 557 sei whales (102 recoveries) (Table 3), the Soviets marked 43 (6 recoveries) the US marked 11 sei whales (2 recoveries), and Canada marked 9 sei whales (0 recoveries). Data sources included: Omura and Ohsumi (1964) (mark recoveries through the 1962 season); Ohsumi and Masaki (1975) (mark recoveries through the 1972 season); Ivashin and Rovnin (1967) (mark recoveries through the 1966 season); IWC Japanese Progress Report SC/26/4 (reporting the 1973 season); IWC Japanese Progress Report SC/27/2 (reporting the 1974 season); IWC Japanese Progress Report SC/28/6 (reporting in 1975 season); and Rice, unpublished data).

Sighting surveys

Systematic sighting surveys to assess cetacean abundance were conducted in the following areas and periods: in the Gulf of Alaska in June and August 1980 (Rice and Wolman 1982), near the Aleutian Islands in August 1994 (K. Forney and R. Brownell, SWFSC, unpublished data), along the coasts of California, Oregon and Washington in the summer and fall from 1991 through 2008 (Carretta *et al.* 2014), as well as additional unpublished data from summer and fall of 2014 (J. Barlow, SWFSC, pers. comm.), in Alaskan waters, Bering Sea and Arctic from in spring, summer and fall from 1999 through 2012 (Zerbini *et al.* 2006; Friday *et al.* 2012; Friday *et al.* 2013) as well as additional unpublished data (National Marine Mammal Laboratory, unpublished data, see Table 4), in Canadian Pacific waters year-round from 2002 through 2012 (Ford *et al.* 2010) including additional data through 2012 (Ford, DFO Canada, pers. comm.), in Hawaiian waters in summer and fall of 2002 and 2010 (Carretta *et al.* 2014), in Alaskan coastal areas and the pelagic North Pacific in July and August from 2010 through 2013 (Matsuoka *et al.* 2011; Matsuoka *et al.* 2012; Matsuoka *et al.* 2013; Matsuoka *et al.* 2014) and in the western North Pacific from 1964 through 1990 (Miyashita *et al.* 1995) and from 2002 through 2007 (Hakamada *et al.* 2009; Kiwada *et al.* 2009).

Acoustics

Passive acoustic data on the distribution of sei whales in the North Pacific are sparse: few confirmed sei whale recordings have been collected, thus call characteristics remain uncertain and are often difficult to discern from fin whales. Sei whale call data have been reported in Rankin and Barlow (2007) and various papers by Baumgartner and colleagues (Baumgartner *et al.* 2008; Baumgartner and Mussoline 2011; Baumgartner *et al.* 2013).

Rankin and Barlow (2007) documented 107 sei whale vocalizations during a survey near the Hawaiian Islands in November 2002 and noted that the calls they recorded appeared to be different than sei whales calls recorded in other oceans. However, Baumgartner *et al.* (2008) documented similar calls while recording sei whales in the Atlantic and the Antarctic and suggested that some aspect of sei whale calls may be present calls across regions. Further work is ongoing to refine detection of sei whale calls (Baumgartner and Mussoline 2011; Baumgartner *et al.* 2013) but as of now, verified acoustic recordings of sei whales are not available in sufficient quantities to enable us to draw conclusions about the extent of their distribution.

Analysis methods

We used a combination of synthetic reasoning and data analysis to interpret historical sei whale records.

Synthetic reasoning

In many cases, the available data were simply not amenable to modern statistical analysis methods (e.g., movement modeling, cluster analysis or genetic procedures for stock delineation). For instance, there is a dearth of historical biopsy records and effort information (both regarding marking and whaling effort), precluding definitive quantitative analysis of movement rates and stock structure. Nevertheless, taken as a whole, the palette of available data can help paint a compelling picture of the historical distribution and population structure of sei whales in the North Pacific.

Mark-recovery and integrated population analysis

We fit two conceptually different models to historical sei whale marking and recovery (whaling) records. The first uses a modified Lincoln-Petersen estimator, while the second incorporates prior distributions for recruitment and survival processes within a state-space modeling framework. Here, we describe the principal features of the data and each modeling approach. A more detailed description is provided in the Appendix.

Mark-recovery models make a number of assumptions about data collection and the target population (Brownie *et al.* 1985), and it is worth addressing several of these at the outset since many of the decisions we made regarding data and models were to limit the effects of assumption violations. First, mark-recovery models assume that marked animals completely mix with unmarked animals, such that marked and unmarked animals have the same hunting and natural mortality rates. Essentially, we want the marked cohort to be "representative" (with respect to natural mortality and exploitation) of the entire population of sei whales for which we wish to make inference. Due to data sparseness, it was not possible to test this assumption definitively (e.g., with models permitting incomplete mixing of animals; see Hoenig *et al.* (1998)). However, examination of marking and recovery records obtained between 1972 and 1975 indicated that a large difference in the number of recoveries depending on where marking was conducted. For instance, 25 out of 73 whales marked during winter research cruises in the central and western Pacific were subsequently recovered, but 0 out of 38 marked in coastal areas were recovered. We conducted a post hoc likelihood ratio test for binomial proportions to evaluate that the null hypothesis that recovery probabilities associated with pelagic marking events (p_{pelagic}) was equal to recovery probabilities associated with coastal marking events (p_{coastal}). Since marking areas were temporally and spatially distanced from areas where whaling occurred during these years, this test can help assess whether wintering areas overlap between coastally and pelagically marked whales.

In particular, it appeared that whales marked pelagically on wintering grounds were highly exploited, but that whales marked in coastal areas were not subject to whaling effort during this time period. As such, our primary mode of inference was to estimate abundance for the pelagic stock only, limiting analysis to whales marked pelagically in winter only and assuming that all catches came from this stock. However, in the Appendix we also report estimates from an analysis of all marking records (assuming that all marked whales were members of a single stock and were all exposed to similar levels of whaling effort). To our mind, this latter assumption is probably a poor one, but results are still presented for completeness. Bayesian analyses of whaling and Discovery mark data to estimate survival and abundance

We conducted a hierarchical, Bayesian analysis of mark-recovery data for whales marked and recovered between 1972 and 1975 in order to estimate life history, exploitation, and abundance parameters. We constrained analysis to this relatively short time frame for several reasons. First, marking in this time period occurred primarily during scientific winter surveys and were temporally and spatially decoupled from whaling operations. This disaggregation serves to increase the level of mixing of marked and unmarked animals relative to earlier surveys, which largely occurred at the same time as whaling operations. Second, limiting analysis to this time period helped to eliminate issues with heterogeneity in hunting and marking efforts, whereby the spatial locations targeted for marking and whaling could vary considerably from one year to the next. In contrast, the Japanese increased their marking research program starting in 1972, and sei whales were the primary target species of wide-ranging whaling efforts in these final years of commercial whaling. A total of 111 sei whales had been marked during or after 1972 (61 in 1972, 27 in 1973, 15 in 1974 and 8 in 1975 (Table 3).

Of those, 73 (50 in 1972, 17 in 1973 and 6 in 1974) were marked in low latitudes, all but one in Areas V C (160-180° E, 20-40° N) and VI C (140-160° E, 0-30° N). The remaining 38 (11 in 1972, 10 in 1973, 9 in 1974 and 8 in 1975) were marked in former whaling grounds including the Aleutian Islands, Gulf of Alaska and the west coast of North America (Table 3).

For the full analysis presented in the Appendix, data were analyzed for 111 whales marked through 1975 (Table 5). The recovery of nearly 25% of these marked whales over such a short time span suggested that the whalers were catching an extremely large proportion of a rapidly dwindling population of sei whales, which is supported by our analyses (below).

For analyses reported in the body of this paper, we restrict analysis to the 73 marks that were placed during winter months in the lower latitude areas V C and VI C (see Table 3), under the assumption that the "pelagic migratory stock" was the primary stock subject to whaling efforts between 1972 and 1975. As, such, estimates pertain only to the pelagic stock wintering in the lower latitudes of the North Pacific. In the Appendix, we also report on analyses where we assume that all marked whales (both pelagic and coastal marking events) were subject to whaling effort.

We used two conceptually different approaches to estimate abundance, depending on whether or not a sei whale population dynamics model was integrated into the estimation procedure. In particular, we used a Lincoln-Petersen-like estimator using the fraction of marked whales recovered in the harvest (Diefenbach *et al.* 2004) to generate snapshot estimates of abundance, as well as a state-space model (e.g. see Meyer and Millar (1999) and Besbeas *et al.* (2002)) to incorporate auxiliary information on survival and recruitment to help link latent abundance estimates. The former approach requires fewer assumptions, but tends to result in lower precision than state-space models fit to a combination of mark-recovery and whaling data (Conn *et al.* 2008). In both cases, we used the same underlying probability structure for mark-recovery data, and conduct inference under a hierarchical, Bayesian framework. Data, assumptions, and procedures used in these analyses are fully described in the Appendix.

RESULTS

Whaling

Eastern North Pacific Coastal whaling

In the eastern North Pacific, the earliest catches of sei whales occurred in 1913 when three individuals were landed at the Port Armstrong whaling station in southeastern Alaska but these catches are not in the BIWS/IWC catch database.

The earliest eastern North Pacific catches of sei whales recorded the BIWS/IWC catch database occurred at whaling stations off the Canadian Pacific coast and date back to 1916 (Nichol *et al.* 2002). They were reported as “UK” catches of whales, presumably because the whaling companies in Canada were operated by a company based in the United Kingdom (UK) (Table 1). Sei whales were hunted at Kyoquot, Sechart and Rose Harbour land stations on the Canadian Pacific coast during this time period (Table 6). The BIWS/IWC database shows a total of 329 sei whales caught by the “UK” from 1916 to 1919.

The earliest U. S. land station catches of sei whales in the BIWS/IWC database date back to 1919. In total, only 35 sei whales were taken at U. S. land stations in the years before the Second World War (Table 1).

Whalers at the Canadian land station at Coal Harbour began hunting sei whales in the years after the Second World War, while they were also hunting other species. Catches of sei whales began to increase in 1954 and 1955, and increased again starting in 1959. From 1948 to 1959, a total of 697 sei whales were caught.

In the early 1960s, the Japanese whaling industry developed a partnership with the Canadian whaling industry to convert their market from whale oil-based products to edible fresh/frozen meat for human consumption (Webb 1988). Because the other large whales were depleted, and because the market had shifted to meat for human consumption, catches of sei whales began to overtake catches of other species in 1962 (Fig. 3a). By 1964, sei whales were the primary target species because they were preferred in the Japanese markets. Sei whales dominated in the catches at the Coal Harbour land station from 1962 to 1966 during which time 2,153 sei whales were caught. By 1967, the population of sei whales off Canada was so depleted that whalers caught only 89 whales. The whaling station closed after the 1967 season (Fig. 3a).

Whalers at US land stations did not start hunting sei whales in large numbers until the late 1950s (Table 1). Whaling had started at Fields Landing in northern California in 1940 and continued through 1951 (except for 1945, 1946 and 1950) but only 8 sei whales were taken: 1 in 1942, 2 each in 1943 and 1944, and 3 in 1947 (Rice, NMML library, unpublished data submitted to US Bureau of Commercial Fisheries).

Two whaling stations opened at Point San Pablo on San Francisco Bay: the Del Monte Fishing Company in 1956 and the Golden Gate Fishing Company in 1958. In their early years, humpback and fin whales were the preferred species. Catches of sei whales increased starting in 1959 and peaked in 1963 (Table 1). After a large catch in 1966, sei whales catches declined and whalers reported that sei whales were scarce (Fig. 3b). The stations final years of operation were 1971 and 1966, respectively.

Along the west coast of Mexico, five floating factories operated in 1913 and 1914, from 1924 through 1930, and 1935. These were old-style factory ships that lacked a stern slipway, and they operated from protected anchorages as mobile shore stations. They killed mostly blue whales and gray whales, but they did take a total of 121 small rorquals which they listed indiscriminately as “sei” or “sei (Bryde’s)” whales (Rice, unpublished data provided by the BIWS). Our field observations off Mexico suggest that they were probably mostly Bryde’s whales, and we do not consider them further here.

Western North Pacific coastal whaling

Land stations were first set up in Japan starting in 1898 and western North Pacific land station catches of sei whales date back to the late 19th century (Kasuya 2009). Andrews (1911) stated that Japanese “Island Empire shore-whaling developed during the last 15 years”. However, none of these early Japanese land station catches have as yet been entered into the BIWS/IWC catch database. The only pre-WW II land station catch records reported as sei whales in the database are 364 whales caught in 1929 (Table 1).

Even though sei whales were a preferred species at Japanese land stations over the all the years they were hunted, until the early 1950s, catches of Bryde’s whales at Japanese land stations had been reported as sei whales. Based on analyses presented in Omura *et al.* (1952), the Japanese whaling stations began reporting “sei” whale catches with greater specificity starting in 1955 (S. Ohsumi, Institute of Cetacean Research, pers. comm.). For example, catches were reported in the whaling log books as “southern” sei whales (i.e., Bryde’s whales) or “northern” sei whales (i.e., sei whales).

Although the BIWS/IWC database shows substantial numbers of “sei” whales taken at Japanese land stations in the years after the Second World War (Table 1), these catches are actually a mix of Bryde’s and sei whales (C. Allison, IWC, pers. comm.). Therefore, this paper does not include analyses of Japanese land station catches of sei whales because it is impossible to separate sei whale and Bryde's whale catches with any degree of certainty. However, the logbooks contain additional data and distribution, seasonality and abundance of sei whales (as well as Bryde's whales). These data can and should be analyzed once the original log books data are evaluated and reconciled.

Reported catches of sei whales from Soviet land stations in the Kuril Islands from 1949 through 1965 totaled 1,759 whales. It is assumed that most of the whales reported as sei whales along the Kuril Island chain were actually sei whales and not a mix of sei and Bryde's whales, because Bryde's whales are generally restricted to warmer waters and are seldom encountered north of the island of Honshu, Japan (Rice 1998, C. Allison, IWC, pers. comm.). It is possible that the sei whale catch numbers reported for the Kuril Islands are accurate (see Ivashchenko *et al.* (2013)). However, because the Kuril Island chain is just north of the northernmost Japanese land stations, analyses of the Kuril Islands sei whale catch data will be deferred until the Japanese land station data are reconciled and analyzed.

Pelagic whaling

Pelagic whaling began in the North Pacific in 1933 with the Soviet floating factory *Aleut*, the first "modern" factory ship with a stern slipway that allowed whales to be hauled aboard for processing (Zenkovich 1954).

Sei whales were not the primary target species during the early years of pelagic whaling as modern whaling techniques (harpoon-cannon and fast catcher boat) were employed. The early modern whalers (mostly Europeans) preferred blue, humpback, and fin whales because they were heavier and yielded more oil, and were therefore more profitable for an industry that focused mainly on whale oil and whale meal production. This difference in value between different species of whales was reflected in the old Blue Whale Unit (BWU) that was used to set catch limits. One BWU equaled 1 blue whale, 2 fin whales, 2.5 humpback whales, or 6 sei whales.

Because of the lack of effective regulation of the numbers of whales being killed in the North Pacific, populations of the preferred species began to disappear one by one as stock after stock was overexploited. As the populations of other whales began to show signs of depletion by the late 1950s, the whaling industry began to pursue sei whales in greater numbers. Worldwide catches of sei whales had averaged less than 20 per year until 1904, and less than 400 per year from 1904 through 1946, then began an extreme increase to a high of over 27,000 in 1965 (BIWS/IWC catch database).

The International Whaling Commission banned the killing of humpback whales after the 1962/63 season in the Southern Ocean and after the 1966 season in the North Pacific Ocean. The Commission banned the taking of blue whales worldwide after 1966. Fin whale stocks continued to decline.

The European whaling industry, which had been based on selling whale oil and whale meal, began winding down their operations as the populations of the larger whales (i.e., those yielding more oil per individual) dwindled. The Asian and eastern European whaling industry (mainly Japan and the Soviet Union) preferred selling whale meat as the main product so they were able to continue to be profitable because sei whales provided a sufficient quantity of whale meat per individual caught.

In the Southern Ocean, where catch limits were still based on the BWU, reported catches of sei jumped from ca. 8,000 in the 1963/64 season to ca. 20,000 in the 1964/65 season, because whalers could catch 6 sei whales for each BWU.

In the North Pacific, there were no formal limits on the numbers of whales that could be killed until the 1971 season (Anonymous 1970). This was well after the sei whale catches had peaked and long after the major species were already depleted (Figs 4 and 5).

As pelagic whaling developed in the North Pacific in the first years after the Second World War (1946-1951), pelagic catches were concentrated in waters near the Japanese mainland and off the Kamchatka Peninsula (see Mizroch and Rice (2006) for more details about the development of pelagic whaling in the North Pacific). Until 1952, sei whales were largely ignored by the pelagic whaling fleets.

From 1952 to 1962, the pelagic fleets expanded to the Aleutians, Bering Sea, and, to a small degree, the Gulf of Alaska. Catches near the Japanese mainland also remained high during this period as fleet capacity expanded. The fin whale had been the dominant species taken in the North Pacific as whaling developed during the post-WW II years. Because of its large size and availability, it was preferred by whalers from all nations because yields of both oil and meat were sufficiently high to be profitable. During this period, even though the larger preferred species were available in profitable numbers, small numbers of sei whales were taken, virtually all north of 50ºN and south of the Aleutian Islands (Fig. 6a), mostly north of the North Pacific Current bounded on the east off Kamchatka by the Oyashio

From 1963 to 1967, whaling expanded across the northern North Pacific and into the Bering Sea (Mizroch and Rice 2006). During this time period some of the more egregious illegal whaling activities of the Soviet Union commenced (Berzin 2008; Ivashchenko *et al.* 2013). Catches were high throughout the northern North Pacific, off Kamchatka, the Aleutians, the Bering Sea and the Gulf of Alaska, as well as near the Japanese mainland. However, as fin whales were becoming harder to find by the early 1960s, catches of sei whales began to increase. There was a major increase in sei whale catches in 1963 and more sei whales than fin whales were caught starting in 1966 (Fig. 4). During this period, most sei whales were taken north of 50º N, although substantial numbers began to be killed south to 40º N, and a few as far south as 30º N (Fig. 6b). Most of the catches were north of the North Pacific Current south of the Aleutian Islands and extended eastward into the Alaska Current where it mixes in the Gulf of Alaska. There were also substantial catches west of the Aleutians near Kamchatka bounded to the north by the Commander Current.

Thereafter, the sei whale was the preferred balaenopterid in the North Pacific, and Japan was the dominant whaling nation hunting this species. From 1968 until 1975 (after which commercial hunting of sei whales was banned, the whaling fleets began moving southward into waters south of the North Pacific Current (Fig. 6c). Catches were concentrated in the area where the Kuroshio Extension mixes with the North Pacific Current, as well as in the Subarctic Frontal Zone south of the North Pacific Current.

Analysis of the Japanese pelagic catches of sei whales from 1966 through 1972 show the expansion of whaling areas both across the North Pacific and into areas where sei whales had not been caught before.

Figs. 7a-7j illustrate the changes in catch numbers and areas of exploitation. In 1966, as the catches of the other balaenopterids were declining (Fig. 4), sei whales were caught all along the

Aleutians and into the Gulf of Alaska, in and along the edges of the Alaska Stream (see Nasu 1966) (Fig. 7a, total catch of sei whales = 2,207).

By 1967, whalers were exploring areas at the extremes of the Aleutians near Kamchatka, but also moving farther south (Fig. 7b, total catch of sei whales = 3,473) to try to find unexploited stocks of sei whales. This was the first year that whalers took more sei whales than fin whales.

From 1968 onward, when hunting of blue and humpback whales was banned and the fin whale population was severely depleted, the pelagic fleets shifted their operations south and began to hunt large numbers of sperm and sei whales in the rich grounds along the Subarctic Frontal Zone (Fig. 7c, total catch of sei whales = 3,821).

By 1969, whalers were expanding catches along the Subarctic Frontal Zone across the North Pacific (Fig. 7d, total catch of sei whales = 3,589).

In 1970, whalers expanded to the eastern North Pacific near the Canadian coasts (areas near where the Canadian land station whalers had hunted with some success from 1962 to 1966, Fig. 3b) and also continued to work in the Subarctic Frontal Zone (Fig. 7e, total catch of sei whales = 3,253).

By 1971, whalers had moved even farther south and catches were spread along the Subarctic Frontal Zone (Fig. 7f, total catch of sei whales = 2,420). By 1972, the last year of large (>2,000) sei whale catches in the North Pacific, the whalers had moved even farther south to an area that encompassed both the Subarctic Frontal Zone and the Subtropical Frontal Zone (Fig. 7g, total catch of sei whales = 2,041).

In 1973, whalers were hunting in roughly the same areas in the western North Pacific that they had been hunting in 1972, but were also exploring areas in the eastern North Pacific across the Subarctic Frontal Zone (Fig. 7h, total catch of sei whales = 1,710). In 1974, whalers were hunting in similar areas as in 1973 but catches were much reduced, from 1,710 whales in 1974 to fewer than 1,190 whales in 1974 (Fig. 7i, total catch of sei whales = 1,190).

By 1975, the last year of commercial sei whale hunting, fewer than 500 sei whales were caught. Whaling was scattered along the Subarctic Frontal Zone although a few sei whales were caught in the Gulf of Alaska and well offshore of the North American coast (Fig. 7j, total catch of sei whales = 454).

Commercial whaling for sei whales was banned in 1975 for the 1976 whaling season (Anonymous 1975). The bulk of the reported sei whale catch during this era was taken in the Subarctic Frontal Zone (Fig. 6c).

Marking

In all, 110 Discovery marks were recovered between 1950 and 1974, but location data were missing for 4 mark recoveries. Therefore, movement data were analyzed for 106 marks (45 males, 41 females and 20 where the sex was not recorded) (Fig. 2). The number of marks placed each year as well as the number of marks recovered shows that a large number of marks were placed in the early post-war years (1949-1953) and again in the last few years of commercial whaling (1972 onwards) (Fig. 8).

Based on information first noted by Ohsumi and Masaki (1975), it is likely that the Soviets under-reported Discovery mark recovery data for sei whales. They reported that Discovery mark recovery efficiency was extremely high (42.1%) for humpbacks whale and very low for the sei whale (3.6%) when they compared recovery data with other whale species.

The longest time between marking and recovery was 11 years, for a whale marked south of Kodiak Island on 7 July 1954 and recovered in the Gulf of Alaska on 27 June 1965 approximately 658 km from the place where it was marked. The longest distance between marking and recovery was 6,774 km, for a whale marked on in the southwestern North Pacific in the Subtropical Frontal Zone on 6 February 1972 and recovered on the eastern edge of the Subarctic Frontal Zone on 7 August 1973 (Fig. 2).

In the earliest years of sei whale marking (1949-1953), almost all sei whales were marked near the coast of Japan, in area VI B, Sanriku-Hokkaido (140-160° E, 30° N to Kuril Islands), or in an area southeast of Japan near Ogasawara, area VI C (140-160° E, 0-30° N) (Table 3). Of the 160 sei whales marked from 1949 through 1953, only 3 were marked elsewhere. There were only 15 recoveries of these marked whales, all from a relatively small area bounded between 25-43° N and 142-150° E (Fig. 9, 6 males and 9 females). There were no mark recoveries of any of these whales after 1961 and no mark recoveries in the pelagic high seas, even though there were substantial catches in the Subarctic Frontal Zone starting in the late 1960s. All the mark and recovery data during this period were near coastal Japan west of the Kuroshio and south of the Oyashio except for one whale which had been marked east of 160° E and recovered along the Japan Trench.

Between 1954 and 1962, 73 sei whales were marked by the Japanese and 17 were recovered. During this time period, whalers preferred fin whales and the pelagic fleets were beginning to expand across the North Pacific (Fig. 10a, 6 males, 3 females and 8 of unknown sex). Of the 17 recoveries, one shows a long-distance (4,411 km) seasonal movement of a whale marked in July 1962 well south of the Aleutians and recovered in May 1969 off the coast of Japan. Another shows a long-distance (1,736 km) seasonal movement of a whale marked in November 1962 off the central coast of California and recovered in August 1966 near Vancouver Island, Canada.

By 1963, as catches of sei whales began to increase, the Japanese sei whale marking program also began to increase. Between 1963 and 1971, 213 sei whales were marked and 49 were recovered (Fig. 10b, 24 males, 17 females and 8 of unknown sex).

Until 1972, whale marking was conducted during the whaling season on research cruises that operated independently of the whaling ships. However, starting in 1972, the Japanese expanded their sei marking program to lower-latitude waters during the winter months. Marking during the winter months had rarely been conducted except by the U. S. under the supervision of Dale Rice (see Mizroch *et al.* (2009) Mizroch and Rice (2013) who describe winter marking projects for fin and sperm whales).

A total of 111 sei whales were marked during or after 1972 (Table 3, Fig. 11a). Of these, 73 (50 in 1972, 17 in 1973 and 6 in 1974) were marked in low latitudes, all but one in Areas V C (160-180° E, 20-40° N) and VI C (140-160° E, 0-30° N). The remaining 38 (11 in 1972, 10 in 1973, 9 in 1974 and 8 in 1975) were marked in former whaling grounds including the Aleutian Islands, Gulf of Alaska and the west coast of North America (Table 3).

There was a large increase in mark recoveries of whales marked in 1972 (Fig. 8). Of the 61 sei whales marked in 1972, 19 were recovered. All of these 19 recoveries were from the 50 whales marked in 1972 during winter in lower latitudes. None of the 11 marks placed in higher latitudes during 1972 were ever recovered by whalers.

In subsequent years, this pattern of recoveries continued. All 25 recoveries of whales marked between 1972 and 1975 were from the 73 whales marked between 1972 and 1974 in lower latitudes (9 males and 12 females and 4 of unknown sex). None of the 38 whales marked in higher latitudes were ever killed by whalers.

For perspective, there were only 110 recoveries (106 with location data) over all the years of whaling in the North Pacific (1949-1975). Of those, 19 were recoveries of 61 whales (actually of the 50 marked in wintering areas in 1972 (see Table 5)) and another 6 whales of the 23 whales marked in wintering areas after 1972 (Table 5, Fig. 8). This high rate of recovery of whales marked in 1972 is clearly shown in the data (Fig. 8).

Recoveries of whales marked in winter months show migratory movements into the Subarctic Frontal Zone in June and July, although a few moved into the Aleutian Trench area in late June and July. One whale marked in winter during this time period moved from the Subtropical Frontal Zone in the western North Pacific to the Subarctic Frontal Zone in the eastern North Pacific, which is the longest movement recorded for sei whales.

Based on the winter marking data and summer recovery data, sei whales were found between 15° and 25° N during winter months and migrated northwards to between 35°to near 50°N in the summer months of June, July and August (Fig. 11a).

However, analysis of movements of 25 whales marked or recovered in the month of May (which is early in the feeding season as migratory whales head north to preferred feeding areas) show animals in different areas of the North Pacific during this month (Fig. 12). Some of these sei whales were marked or recovered near the coast of Japan, some were marked or recovered south of the Aleutian Islands, and one was marked in the Gulf of Alaska offshore of southeastern Alaska.

Movements of 11 whales marked or recovered in the month of September (which is late in the feeding season for a migratory baleen whale) were mostly in the vicinity of Japan except for one whale that had been marked in May and recovered September near the Aleutians (Fig. 13).

Movements of 11 whales marked or recovered in the near-coastal areas of the eastern North Pacific (east of 140° W) (Fig. 14) between 1960 and 1971 were analyzed. Some whales moved long distances but none were recovered west of 156° W.

One whale was marked off southern California in November 1962 and killed near Vancouver Island in August 1966. Another whale was marked off southern California in June 1965 and killed well offshore in July 1969. Another whale was marked offshore very early in the season, in April 1964 (near the Mendocino Fracture Zone) and killed in August 1964 offshore south of Vancouver Island. One whale was marked south of Kodiak Island in June 1960 and killed offshore Vancouver Island in July 1962.

Rates of travel based on Discovery mark recoveries

There was a total of 33 marks that were recovered within one year of marking. The fastest rate of travel recorded was 56.5 km/day of a whale marked in August 1956 and recovered 2 days later. The second fastest rate recorded was 49.8 km/day of a whale marked in July 1953 and recovered one day later.

Of the whales that showed extensive long distance movements shortly after marking, the fastest rate of travel recorded was 44.86 km/day of a whale marked in May 1974 and recovered in July (51 days later) after traveling 2,288 km.

A number of whales were marked in the winter and recovered in summer feeding areas, and the fastest winter-summer migration recorded was 32.4 km/day of a whale marked in January 1972 and recovered in June (138 days later) after traveling 4,467 km.

Sighting surveys

Gulf of Alaska

A research cruise was conducted across the Gulf of Alaska from 17 June to 28 August 1980 (Rice and Wolman 1982). The census area covered 221,915 km^2. and the surveys were conducted over the continental shelf, continental slope and offshore waters between 138° W and 156° W (Rice and Wolman 1982). This cruise was conducted just 5 years after sei whales were protected in the North Pacific. The authors noted that all the species of large whales appeared to be "severely depleted" and they reported that no sei whales had been seen during the entire survey. They also noted the absence of any sightings of blue whales, right whales and gray whales.

Aleutians Islands and Aleutian Trench

A research cruise was conducted south of the Aleutian Islands from 6 to 31 August 1994 (Fig. 15). The survey was conducted over the continental shelf, the Aleutian Trench and south to the northern portion of the abyssal plains of the Gulf of Alaska approximately 200 nautical miles south of the Aleutian Islands chain. (K. Forney and R. Brownell, SWFSC, unpublished data). The purpose of the cruise was to assess whale abundance in areas that had been noted as historical whaling grounds. They encountered eight cetacean species, but reported that no sei whales or blue whales had been seen, even though the area surveyed had been an area of concentration for those species during the years of commercial whaling.

California, Oregon and Washington

Summer and fall surveys conducted off the coasts of California, Oregon and Washington from 1991 to 2008 were summarized in the U. S. Pacific Marine Stock Assessment reports (Carretta *et al.* 2014). Despite extensive survey effort, there were only 9 confirmed sightings of sei whales during this time period. However, as many as 11 sei whales were sighted during a series of surveys conducted by NOAA's Southwest Fisheries Science Center off the coasts of California and Oregon from August through October 2014 (J. Barlow, SWFSC, pers. comm.).

Alaskan waters, including the Gulf of Alaska, Aleutian Islands, Bering Sea and Arctic

Researchers from the National Marine Mammal Laboratory conducted systematic shipboard and aerial surveys to assess distribution and abundance of cetaceans in Alaskan waters between 1999 and 2012 (Zerbini *et al.* 2006; Friday *et al.* 2012; Friday *et al.* 2013). These surveys were conducted in the Gulf of Alaska, along the Aleutian Islands, in the Bering Sea (most often in June, July and August) and as far north as the Chukchi and Beaufort Seas (most often in August through September or October) (see Table 4 for location and timing, Fig. 16 for all tracklines and sei whale sightings).

In spite of many years of systematic cetacean survey effort, a total of 9 sei whale groups (total 13 individuals) were seen during these surveys, mostly along the shelf break in the Bering Sea, although one was sighted south of the Aleutians (Fig. 16). Three groups were seen during the month of June and six groups were seen during the month of July.

Canada

A total of 21 systematic surveys were conducted off the Pacific coast of Canada including coastal waters from southern Vancouver Island to north of Haida Gwai between 2002 and 2008 (Ford *et al.* 2010) and two additional surveys were conducted through 2012 (Ford, pers. comm.).

Three surveys were conducted during the winter (January –March) from 2006 through 2008, seven surveys were conducted during spring (April-June) from. 2002 through 2008, seven surveys were conducted during summer (July-September) from 2002 through 2008 and four surveys were conducted in fall (October-December) in 2003, 2004, 2006 and 2007. No sei whales were sighted during any of these surveys.

Systematic surveys were conducted in inshore coastal waters of Canada during the summers of 2004 and 2005 and one sei whale was seen (Williams and Thomas 2007).

Hawaii

Surveys were conducted in the summer and fall in the vicinity of the Hawaiian Islands in 2002 and 2010 (Carretta *et al.* 2014). Four sei whales were sighted in 2002 and three sei whales were sighted in 2010.

IWC POWER (Pacific Ocean Whales and Ecosystem Research)

Large-scale pelagic research cruises were conducted in the northern North Pacific from 29 June to 2 September 2010 (Matsuoka *et al.* 2011), from 11 July to 8 September 2011 (Matsuoka *et al.* 2012), from 13 July to 10 September 2012 (Matsuoka *et al.* 2013) and from 12 July to 9 September 2013 (Matsuoka *et al.* 2014). In 2010, systematic surveys were conducted from 8 July to 23 August between 170° E and 170° W, north of 40° N and south of the Aleutian Islands.

The surveys were stratified into northern and southern strata, delineated by the U. S. EEZ boundary. The northern stratum was generally within the Aleutian Trench, and the southern stratum was south of 47° N. Four individual sei whales were seen in the northern stratum (Aleutians Trench area), but survey coverage in this zone was reduced due to poor weather conditions. A total of 49 groups of sei whales comprising 97 individuals (including 4 calves) were observed in the southern stratum along the Subarctic Frontal Zone.

In 2011, systematic surveys were conducted from 21 July to 31 August between 170° W and 150° W, north of 40° N and south of the Alaska Peninsula. The surveys were stratified into northern and southern strata, delineated by the U. S. EEZ boundary. The northern stratum included the easternmost section of the Aleutian Trench, Unimak Pass, and the area between Unimak Pass and Kodiak Island. The southern stratum was south of the U. S. EEZ boundary. No sei whales were observed in the northern stratum. Survey coverage in the Aleutian Trench and Unimak Pass area was reduced due to poor weather conditions, but survey coverage was excellent between Unimak Pass and Kodiak Island. A total of 38 groups of sei whales made up of 73 individuals (including 2 calves) were observed in the southern stratum along the Subarctic Frontal Zone.

In 2012, systematic surveys were conducted from 24 July to 30 August 2012 between 150° W and 135° W, north of 40° N and south of Alaska. The surveys were stratified into northern and southern strata, delineated by the U. S. and Canadian EEZ boundaries. The northern stratum included the Gulf of Alaska east of Kodiak Island and west of southeastern Alaska. The southern stratum was south of the U. S. and Canadian EEZ boundaries. Even though survey coverage was quite extensive due to excellent weather conditions, only 2 groups comprising 4 individual sei whales were observed in the northern stratum (within the Canadian EEZ). A total of 79 groups of sei whales comprising 147 individuals (including 6 calves) were observed in the southern stratum along the Subarctic Frontal Zone.

In 2013, systematic surveys were conducted from 23 July to 23 August between 160° W and 135° W, north of 30° N and south of 40° N in the pelagic high seas. Although survey coverage was quite extensive due to excellent weather conditions, no sei whales were seen during this cruise, which was conducted well south of the Subarctic Frontal Zone.

Western North Pacific

Sightings surveys were conducted by whale scouting vessels in the North Pacific starting in 1964 (Miyashita *et al.* 1995). Sei whale sightings were reported by month pooled over the years 1964 through 1990 but it is likely that the surveys became infrequent after whaling ceased in 1975. Sei whales had been seen in the western North Pacific in April and across the North Pacific from May through August, and in the eastern and western North Pacific in September (Miyashita *et al.* 1995).

Sighting surveys were conducted in the western North Pacific west of 170° E from 2002 to 2007 (Hakamada *et al.* 2009; Kiwada *et al.* 2009). Surveys were conducted from May through September from 2002 through 2004, from May through August in 2005 and 2006 and from May through July in 2007.

Sei whales were observed throughout most of the western North Pacific survey area with the exception of the coastal areas near Japan, where Masaki (1977) had reported large catches during the years of commercial whaling (Konishi *et al.* 2009).

Hakamada *et al.* (2009) suggested that the sei whales that had been seen in the lower latitudes (south of 41° N) early in the survey season (May and June) had likely migrated north and were available to be surveyed in the northern surveys (north of 41° N) later in the season (July through September).

Post hoc likelihood ratio test for stock composition

It is worth noting that marking and recovery events for pelagically marked sei whales were temporally and spatially disassociated (Fig. 11a), and that recovery events for marked whales had a similar spatial distribution to those of all whales killed (compare Figs. 10b and 11a). These observations suggest that the level of mixing was likely sufficient for us to treat marked whales as representative of the pelagic stock as a whole.

A likelihood ratio test for binomial proportions suggested that recovery probabilities for coastally and pelagically marked whales were statistically different ($\chi^2 = 20.3$, df = 1, $p < 0.00001$) in years where research marking operations occurred during the winter. This suggests that summer feeding distributions were spatially distinct between the two populations.

Mark-recovery estimates of abundance and survival

Posterior summaries for abundance for both models (Lincoln-Petersen, state-space) indicated that the abundance of North Pacific pelagic migratory sei whales was likely in the 10,000-11,000 range in 1972 (Table 7, Fig. 17).

Lincoln-Petersen posterior predictions of abundance were right-skewed and indicated considerable uncertainty about abundance, particularly for the final year (1975). By contrast, state-space estimates were considerably more precise, reflecting the additional information provided by prior distributions on natural mortality and per capita recruitment. Although it was difficult to discern a temporal trend in Lincoln-Petersen estimates owing to poor precision, state space estimates suggested that the pelagic population of North Pacific sei whales decreased by approximately 65% from 1972 to 1975, with an estimate just above 11,000 in 1972 and an estimate close to 4,000 by 1975 (Table 7). Marginal posterior densities for natural mortality (Fig. 18) are shifted to the right when compared to prior distributions, and indicate that large values are plausible given the data. However, estimated values of natural mortality much greater than 0.06 (e.g., as reported by Masaki (1976)) are likely biased high due to unreported Soviet Discovery mark recoveries.

The posterior distribution for per capita recruitment was almost identical to the prior distribution (Fig. 19), indicating that there is no real information in the catch data to help estimate recruitment. Estimates of the number of new recruits each year (Table 7) suggest 190-400 new recruits each year, though these numbers are quite imprecise. Regardless, estimates from the state space model suggest that many more whales were being removed than were being replaced, from 1972 to 1975.

DISCUSSION

Effects of whaling

Sei whales were the victim of overexploitation at an extreme level that greatly surpassed the depletion levels of the other species starting in the 1960s, with the exception of the illegal whaling of sperm and right whales (Berzin 2008; Ivashchenko *et al.* 2013; Ivashchenko and Clapham 2014). The overexploitation of sei whales occurred in plain sight. Most, if not all, of the sei whales were caught legally, and our strong presumption is - in contrast to the Soviet whaling data - that all Japanese catches of sei whales were reported accurately to the Bureau of International Whaling Statistics each year.

As the stocks of the larger whales became depleted, the northern European whaling companies that marketed whale oil products ceased whaling operations and began to switch to other commercial (non-whaling) ventures. However, the non-European whaling nations, especially Japan, preferred products such as whale meat. Sei whales provided sufficient meat per animal to remain profitable, so they began to be preferred by nations operating in the 1960s. In the Southern Ocean, whale quotas had been based on the BWU. Although the oil production from a sei whale may have been only one sixth or one-third that of a blue or fin whale, sei whale meat production amounted to a much larger proportion. Since a sei whale represented only one-sixth of a BWU, Southern Ocean catch limits of 2,000-4,000 BWU in the late 1960s meant that catches of sei whales were virtually uncontrolled, potentially as many as 12,000-24,000 sei whales per year.

There were no catch limits in the North Pacific until the 1971 season, which meant that sei whale catches remained unregulated long after the catches of sei whales peaked in 1968 and began to decline due to depletion.

Some whale scientists, most notably Mackintosh (1942), Laws (1961) and Gambell (1973), had assumed, erroneously, that whale reproductive rates had increased substantially over time due to presumed unrealistically positive "density-dependent" effects from the extreme sequential depletions of the large whale species. The prevailing wisdom at the time was that sei whale pregnancy rates had increased from 25% in 1946 to over 50% in the 1970s (Gambell 1973; Anonymous 1977). Sei whale stock assessments conducted during a special meeting on sei and

Bryde’s whales in 1974 (Anonymous 1977) had been based upon these inflated but erroneous pregnancy rate estimates.

This erroneous assumption led whale researchers to conclude that the sei whale population was robust and increasing at the time that whalers switched from targeting fin whales to targeting sei whales (Fig. 4). Whale assessment models were based on assumptions about single-species density dependence, specifically that fin then sei whale populations had shown marked increases in recruitment over the years because of an increase in food availability as abundance of the larger whales decreased.

In reality, there had been no measurable increase in sei whale pregnancy rates and the early analyses were based on spurious assumptions (Mizroch 1980; Mizroch 1983). Proper statistical analyses demonstrated that there was no basis for such a density-dependent increase in baleen whale reproductive rates (Mizroch 1983). However, by the time these analyses had been conducted, sei whales stocks had long been depleted and commercial whaling for sei whales had long been prohibited.

In order to estimate the rate of decline in the final years of commercial hunting for sei whales, we fit several different types of models (see Appendix).

Posterior predictive Lincoln-Petersen estimates required fewer assumptions to be made (e.g., we did not need to specify a prior distribution for recruitment), but resulted in highly variable estimates. By embedding a state space model for population dynamics model into the estimation process, we were able to obtain much higher levels of precision and to obtain a much clearer picture of the decline of the North Pacific sei whale population, at least over a relatively short time period in the early to mid-1970s. Although this analysis required more assumptions (see

Appendix), our analysis suggests that whaling effort and mortality greatly exceeded what could have been sustainable for such a long-lived and low fecund species, and that the abundance of the pelagic migratory stock was likely reduced by 65% (95% CI 30-86%) from 1972 through 1975, the last few years of commercial exploitation, to perhaps only 4,000 animals.

Although estimates of the entire population of sei whales, i. e., assuming a single stock in the North Pacific rather than a separate pelagic stock as reported above, required several assumptions that are not well-supported (see more details in the Appendix), those estimates are similar to those produced by alternative methods. For instance Tillman (1977), fit population models to catch-effort data and suggested that sei whale abundance had declined from approximately 42,000 whales in 1963 to approximately 8,600 whales in 1974. By comparison, our "single stock" (coastal and pelagic) state space analysis produced an estimate of close to 7,000 in 1974 (Appendix). By the time catch regulations were instituted in 1975, sei whales had already become so severely depleted that it was difficult for the whalers to find enough whales to meet their catch quotas. That is, whaling was halted only after whalers could not find enough whales to sustain the industry.

Stock identity and stock boundaries

Historically, there has been much uncertainty about stock identity of North Pacific sei whales (Mizroch *et al.* 1984). According to Masaki (1976), Fujino (1964, in Japanese, not seen) suggested that sei whales caught in the Gulf of Alaska and sei whales caught near the Canadian west coast were from different stocks based on frequencies of different blood types. (Masaki 1976, 1977) analyzed catch data, Discovery mark recoveries, sightings data and baleen plate proportions and proposed that there were three stocks of sei whales in the North Pacific, with longitudinal boundaries at 175° W and 155°W.

Donovan (1991), in his comprehensive review of whale stock boundaries used by the IWC, reported that the IWC Scientific Committee did not consider Masaki's results "conclusive" (Anonymous 1977). The Scientific Committee had also discussed delineating an "Eastern" and "Western" stock with the boundary set arbitrarily at 180°. After sei whales became protected from commercial whaling at the end of the 1975 whaling season, the IWC began to manage the North Pacific sei whales as a single management unit (i.e., one stock). Donovan (1991) noted that when sei whales became protected from commercial hunting, there was "little further work on stock identification".

Kanda *et al.* (2009) compared microsatellites and mitochondrial DNA from samples from whales caught by commercial whalers in 1972 and 1973 in the pelagic high seas from 165° E to 139° W to samples from whales caught during JARPNII (Japanese Whale Research Program under Special Permit in the North Pacific) surveys from 2002 to 2007 in the pelagic high seas from 143° E and 170° E. Kanda *et al.* (2015b) extended the analysis to included biopsy samples collected from sei whales during the IWC-POWER cruises in 2010 through 2012 (Matsuoka *et al.* 2011; Matsuoka *et al.* 2012; Matsuoka *et al.* 2013) and found no apparent stock differences.

Per the U. S. Marine Mammal Protection Act, the U. S. is required to assess all endangered cetacean species, including North Pacific sei whales. For reporting purposes, the U. S. has produced separate stock assessment reports for sei whales in the vicinity of the Hawaiian Islands and for sei whales in the eastern North Pacific (Carretta *et al.* 2014), but these stock assessment reports are simply based upon where sei whales have been observed in the U. S. EEZ and do not purport to represent biological stock boundaries.

Our examination of marking and recovery records indicates that there is a distinct North Pacific pelagic migratory pelagic stock which migrates between the Subtropical Frontal Zone and the Subarctic Frontal Zone bounded to the north by the North Pacific Current.

We propose that there had been four other stocks—Aleutian Islands/Gulf of Alaska, coastal Japan, eastern North Pacific migratory (California to Canada to the offshore Gulf of Alaska), and southern coastal North America (California coastal).

North Pacific pelagic migratory stock

Discovery mark recovery data show extensive seasonal movements across all putative boundaries that had been suggested by Masaki and others (Masaki 1976, 1977; Donovan 1991) (Figs. 2 and 11a). These movements suggest one pelagic stock which migrates between the Subtropical Frontal Zone in the winter and the Subarctic Frontal Zone in the summer and is bounded to the north by the North Pacific Current. Genetics data (Kanda *et al.* 2009; Kanda *et al.* 2015a; Kanda *et al.* 2015b) also support the theory that sei whales caught in pelagic mid-latitudes of the North Pacific all come from one stock.

Mark recovery data show migrations from lower latitude areas in the winter to the Subarctic Frontal Zone, a known area of high productivity, as the season progresses in May, June and August. These movements are in agreement with Hakamada *et al.* (2009) who suggest that sei whales migrate from south to north as the spring and summer season progresses. There seems to be little basis for previously proposed sei whale management areas (i.e., stock boundaries) that divide North Pacific sei whale stocks by arbitrary longitudinal bands.

Mostly strongly, analysis of mark recovery data shows that recovery probabilities for “coastally” and “pelagically” marked whales are entirely different, as shown by a statistically significant

($p<0.00001$) likelihood ratio test. That is, sei whales which had been marked in coastal areas were not "available" to whalers operating in pelagic areas.

Aleutians/Gulf of Alaska stock based on Nasu (1966)

The movements of a single whale marked in May and recovered in September may represent limited evidence that there had been an Aleutian Islands stock of sei whales (Figs. 12 and 13). The Aleutian Islands area was formerly a dense sei whale ground (Figs. 6a and 6b) and whaling was closely associated with the oceanic front formed at the conjunction of the Alaska Stream and the northern extension of the Kuroshio Current and the North Pacific Current (Nasu 1966)).

Mark recovery data suggest the possibility of an Aleutian stock which may have fed in the highly productive Alaska Stream along the Aleutian Trench during summer months. Statistical analyses have demonstrated that whales marked in the Aleutians and Gulf of Alaska from 1972-1975 had different capture probabilities than whales marked in lower latitudes (see above).

We have shown that the pelagic migratory stock was concentrated along the highly productive Subarctic Frontal Zone south of the North Pacific Current during the summer months. We suggest that the Aleutians stock may have fed in the highly productive waters between the Alaska Stream and the North Pacific Current along the Aleutian Trench during summer months. We have shown that the pelagic migratory stock moves from wintering areas into areas of high productively progressively farther northwest as the season progresses from May, June, July and August (Figs. 11a-c). However, the whale that was feeding in the Aleutian Trench in May and in September does not follow the pattern of the pelagic migratory stock. The whale was feeding well north of the pelagic migratory stock in May and found to be feeding in the Aleutian Trench in September, which does not fit with the seasonal patterns of the pelagic migratory stock.

Sei whales have rarely been seen in the Aleutians since whaling moved south in the late 1960s. Survey effort presented in Figs. 15 and 16 show extensive effort in the Aleutians and across the Aleutian Trench with very few sightings reported (2 sightings on Fig. 15 and no sightings on Fig. 16).

Given the former abundance of sei whales in the Aleutians (Figs. 6b and 6c) and the near complete absence of sei whales at present (Figs. 15 and 16), it seems likely that there had been a stock of sei whales that spent much of the feeding season much farther north than the Subarctic Frontal Zone, feeding north of the North Pacific Current and into the Alaska Current in the Gulf of Alaska.

We propose that there had been an Aleutians/Gulf of Alaska stock with boundaries loosely based on Nasu's (Nasu 1966) proposed "sei whale grounds" (Nasu 1966; Fig. 9). As whaling depleted this stock, whalers moved south into pelagic areas. The Aleutians/Gulf of Alaska is a region of known and continued high productivity, so it is most likely that the continued absence of sei whales in this area is due to extreme depletion of the stock.

We also suggest that there may have been stock mixing in the Gulf of Alaska between this stock and the eastern North Pacific migratory stock (similar to blue whales in (Monnahan *et al.* 2014; Monnahan and Branch 2015)) based on seasonal overlap of Discovery mark recoveries in the Gulf of Alaska (Fig. 2).

Eastern North Pacific migratory stock

Gregr (Gregr 2000) analyzed whaling data from Canadian whaling stations and found that the seasonal pattern of sei whales in the Canadian whaling station catch data differed from the other baleen whale species landed there. He also suggested that sei whales were "intercepted as they migrated past Coal Harbour to feeding grounds elsewhere". He noted that northward migration peaked in July and found that there was "significant offshore movement" at that time. He suggested that the apparent reappearance of mature sei whales in the catch in September indicated a return migration to southern waters.

The Discovery mark recovery data support the coastal migratory theory proposed by Gregr (2000). In the eastern North Pacific, the long-distance movement of a whale marked near California in November 1962 to near Vancouver Island in August 1966 suggests a coastal migration along the California Current into the Alaska Current (Fig. 14). The movement of a whale marked near California in June 1965 and recovered in July 1969 well offshore the northern US west coast suggests an extensive summer feeding range of movements along the eastern edge of the North Pacific Current into the California Current. The seasonal movement of a whale marked offshore very early in the season, in April 1964 (near the Mendocino Fracture Zone) to near the border of Washington State off shore from Vancouver Island in August 1964, suggests a seasonal movement to feed in coastal areas during summer months within the California Current. The movement of a whale marked south of Kodiak Island in June 1960 to offshore Vancouver Island in July 1962 indicates the possibility of a large summer feeding range in the coastal eastern North Pacific that feeds within the Alaska, Subarctic and California Current systems. These movements are all restricted within the far eastern North Pacific. The only eastern North Pacific whale that was observed in the pelagic North Pacific was marked in April and recovered in August. Discovery mark data for the pelagic migratory stock show that those whales are much further south in the winter/spring (Figs. 2 and 14). No whales marked or recovered east of 140° W were ever found west of 156°W.

Based on analyses of seasonality and oceanographic data of sei whale catches at Canadian whaling stations as well as analyses of Discovery mark recovery data, we suggest that there had been an eastern North Pacific migratory stock of sei whales. No whales marked or recovered east of 140° W were ever found west of 156°W. Provisional stock boundaries should include the edges of the Alaska, Subarctic and California Current systems.

Discovery mark data also suggest that the eastern North Pacific migratory stock and the provisional Aleutians/Gulf of Alaska stock may mix in the Gulf of Alaska in a similar fashion shown in analyses of mixing of blue whale stocks in this area (see Monnahan *et al.* (2014) and Monnahan and Branch (2015)).

Southern North American coastal stock (coastal California)

Based on migratory timing and prevalence of baleen-wasting disease, it seems plausible that the sei whales which were caught along the coast of central California were distinct from those caught to the north off Vancouver Island. Sei whales rarely arrived in central California before late June, and did not become numerous until July (Rice 1977). This implies that the coastal migratory population may have migrated from its presumed winter grounds along a route too far offshore to be encountered by the California shore whalers.

Further strong support for the independence of the California coastal stock is based on both the differences in spring arrival times as well as the prevalence of an unusual baleen-wasting disease observed in a high proportion (7%) of sei whales taken at the California whaling stations. Rice also found the disease in 2 of 682 fin whales, but not in any of 234 humpback, 20 blue, or 316 gray whales taken off California.

The only other report of this disease anywhere in the North Pacific was by Soviet biologists who found some infected humpback, sei, fin and blue whales in the vicinity of the Aleutian Islands in 1961 and 1962; they reported that its occurrence was extremely localized, found in only a few aggregations of whales, and absent in nearby aggregations (Berzin *et al.* 1962). Strangely enough, the baleen-wasting disease has never been observed by Japanese (S. Ohsumi, Institute of Cetacean Research pers. comm.) or Canadian cetologists. Elsewhere in the world there is only one published reference, by Tomilin and Smyshlyaev (1968), who found several infected humpback, fin, sei and blue whales in Antarctic and Pacific waters during the 1961/62 and 1962/63 whaling seasons.

Based on migratory timing and prevalence of baleen-wasting disease not reported anywhere else in the eastern North Pacific, we suggest that the sei whales which were caught at California whaling stations were distinct from those caught to the north off Vancouver Island at Canadian whaling stations. Seasonality of catches suggest that the eastern North Pacific migratory stock may have migrated from its presumed winter grounds along a route too far offshore to be encountered by the California shore-based whalers. Boundaries for this stock are unclear.

Japanese coastal stock

Analyses of recovery data from the nearly 160 sei whales marked from 1949 through 1953 near the coast of Japan strongly suggest that there had been a coastal stock near Japan. Only 15 marks were recovered, none after 1961. Only one of these whales, a male marked in July 1953 and killed in July 1962, was recovered at some distance offshore (1,560 km), in the mixed-water region between the boundary of the Subarctic Current and the Kuroshio Extension (Fig. 9). No whales marked near Japan during this time period were killed in any other region of the North

Pacific even though these whales were available to be captured over a much longer time period than any other marked sei whales. From 1954 through 1975, 29,213 sei whales were caught by the Japanese pelagic whaling fleet all throughout the North Pacific (see Table 2, Figs. 6a-6c).

Furthermore, analysis of the movements of whales marked or recovered in September also suggests a coastal stock near Japan (Fig. 13). Based on the seasonality of the marking and recovery events (throughout the spring, summer and fall) and the absence of any recoveries of these marked whales in the areas of high catches in the Subarctic Frontal Zone, the data suggest that there had been a coastal stock of sei whales near Japan that did not migrate into other areas where sei whales were caught in large numbers. The Japanese coastal stock appears to have been hunted to near-extinction.

The *de facto* boundary set by Japanese regulations was 160° E, but it would be better to explore boundaries for this stock based on oceanographic systems, i.e., the boundaries of the Kuroshio to the east and Oyashio to the north. A boundary nearer to 150° E is more likely.

Summary of eastern North Pacific stocks

Recent surveys have encompassed the entire scope of North American coastal areas where sei whales had once been commonly hunted and have shown a dearth of sightings of sei whales in coastal areas of Alaska, British Columbia, Washington, and Oregon, as well as California and the U. S. mainland from 1980 through the present time. Even though some may have assumed that absence of sei whales in areas where they were formerly abundant could be due to the known vagaries of the species, the scope of the systematic survey effort from 1980 through the present time strongly suggests extreme depletions of stocks that had been hunted to extremely low levels, from an initial estimate of abundance of 42,000 in 1963 (Tillman 1977) to about 4,000 in 1975.

If our working hypothesis of multiple coastal stocks is correct, a logical conclusion is that these stocks have been hunted to near extinction in the eastern North Pacific and Aleutian Islands areas. Further evidence for separate stocks in the eastern and western North Pacific is provided by the prevalence of characteristic scars on the skin of the whales. Cookiecutter shark scars have been found on sei whales in the western and central North Pacific, but Rice never found evidence of fresh cookiecutter shark scars on the sei whales landed at the California whaling stations in the 1960s. Cookiecutter sharks are mainly inhabitants of warmer waters (Nakano and Tabuchi 1990; Campagno *et al.* 2005). In the western North Pacific they range north to southern Honshu, Japan. In the central North Pacific they range to the Hawaiian Islands, which places them in the known winter range of sei whales (Fig. 11a). In the eastern North Pacific, cookiecutter sharks have rarely been encountered much north of the equatorial belt, whereas sei whales rarely if ever go south of about 18º N during the winter (Rice 1977; 1979).

In the North Atlantic, there is circumstantial evidence for multiple stocks based on results from satellite telemetry studies of sei whales which show extensive movements throughout a number of feeding areas and also point to a discrete feeding area which may host a different stock, although genetics at this time are unknown (Prieto *et al.* 2014).

Mark-recapture abundance estimates and effects of heterogeneity of capture probabilities

We conducted two analyses to estimate abundance of sei whales. In one (presented in Appendix A), we used all marking events (pelagic and coastal). In our preferred analysis, we restricted the analysis to those whales marked in lower latitudes ("pelagically marked").

Using the full marking dataset, abundance estimates had ranged from a high of approximately 15,000 sei whales in 1972 to a low of approximately 7,000 sei whales in 1975 (see Appendix).

However, for our preferred analyses reported, we restricted the analysis to the 73 marks that were “pelagically marked” because we confirmed that recovery probabilities for coastally and pelagically marked whales were different. We suggest that our proposed “North Pacific pelagic stock” was the primary stock subject to whaling efforts between 1972 and 1975. Our preferred estimates of abundance for the North Pacific pelagic stock ranged from a high of approximately 11,000 whales in 1972 to a low of approximately 4,000 whales in 1975.

A key assumption of-mark-recovery models is that there is complete mixing between marked and unmarked animals between marking and recovery events such that all individuals in the population of interest have equal recovery probabilities. We sought to inviolate this assumption in two ways: 1) by limiting analysis to 1972 through 1975 we helped disaggregate marking and recovery events, and 2) by limiting analysis to the “North Pacific pelagic migratory stock” we limited heterogeneity in recovery probabilities owing to different marking locations. We believed the former to be important because prior to 1972 marking events often occurred in times and locations where whaling was also occurring, which ostensibly leads to positive covariance between marking and recovery events, and thus to negative bias in Lincoln-Petersen abundance estimators (see Conn (2007) and Appendix). The (unstratified) Lincoln-Petersen estimator is also not reliable when there are multiple stocks with different recovery probabilities, with the direction and magnitude of bias likely depending on how representative the sample of marked whales is of the population as a whole. This latter point is the primary reason we believe the restricted abundance estimate for the “North Pacific pelagic migratory stock” to be more reliable than that for the entire North Pacific.

Summary and conclusions

We explored the distribution, movements and population structure of sei whales in the North Pacific by analyzing 20th century whaling catch data as well as location data from recoveries of 106 of the 620 Discovery-type marks implanted in sei whales between 1949 and 1975.

Discovery mark recoveries show that sei whales migrate annually from low-latitude winter grounds in in the Subtropical Frontal Zone north to higher latitude summer grounds in the Subarctic Frontal Zone, an area of high productivity. These long-distance movements suggest a pelagic stock with nomadic movements on their summer grounds. None of the present data provide any support for separating the sei whale populations on the summer pelagic whaling grounds into more than a single management stock.

During the summer, many sei whales moved long distances across the higher-latitude pelagic whaling grounds. Long-distance movements up to 6,774 km have been documented, as well as time spans between marking and recovery of almost 11 years.

Tillman (1977) estimated that sei whale abundance had declined from approximately 42,000 whales in 1963 to approximately 8,600 whales in 1974. Our analyses suggest that the pelagic migratory stock, which had already been depleted by 1972, was likely reduced by a further 65% (95% CI 30-86%) from 1972 through 1975, to around 4,000 animals. Whaling mortality greatly exceeded what would have been sustainable levels for such a long-lived species with low reproductive rates. By the time catch regulations were instituted in 1975, sei whales had already become so severely depleted that it was difficult for the whalers to find enough sei whales to meet their catch quotas.

The data are also consistent with the hypotheses that there are, or were, separate stocks in other areas of the North Pacific. Analyses of the seasonality and distribution of the marking data provisionally suggest a depleted coastal stock near Japan and the possibility of several depleted stocks in the eastern North Pacific near the North American coast. The absence of long-distance recoveries of whales which had been marked near Japan in the early years of post-war whaling suggests that there had been a separate coastal stock near Japan which may be non-migratory. Analysis of marks and recoveries early and late in the whaling season, as well as extensive whale catches in what Nasu (1966) noted as "sei whale grounds" suggest a separate stock in the Aleutians that likely fed in the productive waters along the Aleutian Trench north of the North Pacific Current and extended as far east as into the Alaska Current in the Gulf of Alaska.

Discovery mark data as well as observed seasonal migratory schedules that differ from those of whales marked in other locations suggest that there had been an eastern North Pacific migratory stock as well as a separate California coastal stock. At the Canadian whaling stations, sei whales regularly arrived off the coast of Vancouver Island, Canada, in May and were found in highest numbers in July. At the California whaling stations, sei whales did not arrive until late June or July.

Further strong support for the independence of the California coastal stock is based on both the differences in arrival times as well as the prevalence of an unusual baleen-wasting disease that was not observed anywhere else in the eastern North Pacific, and observed only sporadically in the Aleutian Islands area.

Large-scale dedicated sighting cruises from 1980 through the present indicate that sei whales are now rarely seen in coastal waters where large numbers had been taken by whalers. This almost absolute absence of sei whales in coastal areas suggest that most sei whale stocks remain depleted almost 40 years after whaling was prohibited.

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Table 1. Reported land station catch of sei whales in the IWC catch database (December 2012 release). Catches reported prior to the enactment of the International Convention for the Regulation of Whaling in 1946 should be used with caution (see text).

Year	Canada	Japan	UK[2]	USA	USSR	Total
1916			4			4
1917			121			121
1918			130			130
1919			74	5		79
1920				1		1
1926				25		25
1928				1		1
1929		364				364
1934				2		2
1937				1		1
1946		544				544
1947		382		3		385
1948	2	538				540
1949	3	759			60	822
1950	24	299			51	374
1951	5	419			52	476
1952	22	666			188	876
1953	14	585			86	685
1954	134	646			126	906
1955	139	488			128	755
1956	37	782			171	990
1957	93	478		1	108	680
1958	39	823		2	336	1200
1959	185	1340		37	131	1693
1960		790		47	140	977
1961		782		51	52	885
1962	340	1063		22	79	1504
1963	154	855		97	16	1122
1964	612	873		13	35	1533
1965	604	466		22		1092
1966	354	311		60		725
1967	89	535		3		627
1968		806		14		820
1969		466		10		476
1970		484		4		488
1971		276		2		278
1972		214				214
1973		43				43

[2] These were taken at a land station in British Columbia, Canada operated by an English whaling company.

Year	Canada	Japan	UK[2]	USA	USSR	Total
1974		48				48
1975		30				30
Total	2850	17155	329	423	1759	22516

Table 2. Reported pelagic catch of sei whales in the IWC catch database (December 2012 release) and the corrected Soviet catch data per Ivashchenko *et al.* (2013). Catches reported prior to the enactment of the International Convention for the Regulation of Whaling in 1946 should be used with caution (see text).

Year	Japan	Norway	USA	USSR reported	USSR[3] corrected	Total
1925		26				26
1926		21				21
1927		42				42
1928		3				3
1935		6				6
1937			12		1	12
1949				21	21	21
1950				7	7	7
1951				16	16	16
1952	14			13	13	27
1953	98			26	26	124
1954	129			22	22	151
1955	21			28	28	49
1956	48			16	16	64
1957	166			36	36	202
1958	330			19	19	349
1959	32			93	93	125
1960	203			59	59	262
1961	4			54	54	58
1962	260			303	395	563
1963	945			514	583	1459
1964	1533			595	619	2128
1965	1398			695	706	2093
1966	2208			1545	829	3753
1967	3474			1994	986	5468
1968	3821			1105	310	4926
1969	3591			1091	408	4682
1970	3235			782	93	4017
1971	2420			299	33	2719
1972	2041			71	55	2112
1973	1710			103	103	1813
1974	1190			42	42	1232
1975	454			24	24	478
2001	1					1
2002	40					40
2003	50					50

[3] Ivashchenko, pers. comm.

Year	Japan	Norway	USA	USSR reported	USSR[3] corrected	Total
2004	100					100
2005	100					100
2006	101					101
2007	100					100
2008	100					100
2009	101					101
2010	100					100
2011	96					96
Total	30214	98	12	9573		39897

Table 3. Marking locations for sei whales marked by Japan

Marking location/Year	Sei* 1949	Sei* 1950	Sei* 1951	Sei* 1952	Sei* 1953	Sei* 1954	Sei 1955	Sei 1956	Sei 1957	Sei 1958	Sei 1959	Sei 1960	Sei 1961	Sei 1962	Sei 1963	Sei 1964	Sei 1965	Sei 1966	Sei 1967	Sei 1968	Sei 1969	Sei 1970	Sei 1971	Sei 1972	Sei 1973	Sei 1974	Sei 1975	Tot
II B: US and Canadian West Coast (120-140° W, 40-60° W)																20						2			5			27
II C: Southern California and northern Baja (120-140° W, 20-40° N)																5												5
III B: Gulf of Alaska (Yakutat to Alaska Peninsula) (140-160° W, 40-60° N)						2	2	2				10	7		10	5	4	7		8	9		2	1	5	1		75
IV A: Eastern Bering Sea (160-180° W, Aleutians to 60° N)								1									1	4										6
IV B: South of Aleutians (160°W-180, 40° N to Aleutians)						6		1	2		6		3	11	16	2	4	13	14	1		5	4	6		2	2	98
IV C (160-180° W, 20-40° N)																								1				1
V A: Western Bering Sea (160-180° W, Aleutians to 60° N)																		3										3
V B:South of Aleutians (160-180°E, 40° N to western Aleutians)								1	5	5								6	14	3	6	1	12	4				57
V C (160-180° E, 20-40° N)					3																			3	17	6		29
VI B:Sanriku-Hokkaido (140-160° E, 30° N to Kuril Islands)	*6*	*9*	*10*	*22*	*18*	*5*	*4*														19	13				6	6	*118*
VI C (140-160° E, 0-30° N)	**6**	**39**	**7**	**40**																				46				**92** 46
Total	12	48	17	62	21	13	6	5	7	5	6	10	10	11	26	32	9	33	28	12	34	21	18	61	27	15	8	557

Numbers in bold are likely Bryde's whales because they were marked during the summer in Bryde's whale summer areas. Numbers in italics could be either Bryde's or sei whales. All other numbers are presumed sei whales based on season and marking location. All whales marked after 1955 are likely to have been assigned the correct species Omura and Fujino (1954); S. Ohsumi, Institute of Cetacean Research, pers. comm.)

Table 4. Directed cetacean surveys conducted by the National Marine Mammal Laboratory from 1999-2012. A total of nine sei whales were observed. See text and Fig. 15.

Survey Nickname	Survey Name	Start Date	End Date	Survey Area	Data manager
99MF	Miller Freeman	07-Jul-99	03-Aug-99	Southeastern Bering Sea	Waite
00MF	Miller Freeman	10-Jun-00	02-Jul-00	Southeastern Bering Sea	Waite
01AM	DART	20-Jul-01	25-Aug-01	Gulf of Alaska (Kenai, Kodiak Island, south side of Alaska Peninsula) to eastern Aleutian Islands	Wade
02CP	DART	12-Jul-02	20-Aug-02	Gulf of Alaska (Kenai, Kodiak Island, south side of Alaska Peninsula) to eastern Aleutian Islands	Wade
02MF	Miller Freeman	16-Jun-02	28-Jul-02	Southeastern Bering Sea	Waite
03CP	DART	03-Jul-03	14-Aug-03	Gulf of Alaska (Kenai, Kodiak Island, south side of Alaska Peninsula) to eastern Aleutian Islands	Wade
03MF	Miller Freeman	27-Jun-03	15-Jul-03	Gulf of Alaska	Waite
04AE	ACE	21-Jul-04	27-Aug-04	Alaska Peninsula, eastern and central Aleutians and southeastern Bering Sea	Wade
04MF	Miller Freeman	04-Jun-04	04-Jul-04	Southeastern Bering Sea	Waite
05AE		31-May-05	11-Jul-05	Peninsula, Eastern and Central Aleutians and Southeastern Bering Sea	Wade

Survey Nickname	Survey Name	Start Date	End Date	Survey Area	Data manager
06OL		31-May-06	25-Jun-06	Aleutian Islands and Pribilof Islands	Wade
07OL		30-May-07	16-Jun-07	Unimak Pass and Pribilof Islands	Wade
08DY		01-Jun-08	30-Jul-08	Southeastern Bering Sea	Waite
07PR	PRIEST-ship	31-July-07	29-Aug_07	Southeastern Bering Sea	Rone
08PR	PRIEST-ship	2-Aug-08	14-Sep-08	Southeastern Bering Sea	Kennedy
08PR	PRIEST-aerial	20-Jul-08	31-Aug-08	Southeastern Bering Sea	Rone
09PR	PRIEST-ship	16-Jul-09	30-Aug-09	Southeastern Bering Sea	Kennedy
09PR	PRIEST-aerial	8-Jul-09	30-Aug-09	Southeastern Bering Sea	Rone
09OD	GOALS I	10-Apr-09	20-Apr-09	Central Gulf of Alaska	Rone
09AQ		21-Jun-09	14-Jul-09	Eastern, Central and Western Aleutian Islands, Pribilof Islands, and Southeastern Bering Sea	Wade
10PR	PRIEST-ship	30-Jul-10	23-Aug-10	Southeastern Bering Sea	Kennedy
11PR	PRIEST-ship	3-Sep-11	10-Sep-11	Southeastern Bering Sea	Kennedy
10CH	CHAOZ	24-Aug-10	20-Sep-10	Bering Sea, Chukchi Sea, Beaufort Sea	Rone
11CH	CHAOZ	12-Aug-11	11-Sep-11	Bering Sea, Chukchi Sea, Beaufort Sea	Rone
12CH	CHAOZ	8-Aug-12	3-Sep-12	Bering Sea, Chukchi Sea, Beaufort Sea	Rone

Survey Nickname	Survey Name	Start Date	End Date	Survey Area	Data manager
10AE		24-Jun-10	12-Jul-10	Eastern, central and western Aleutian Islands and southeastern Bering Sea	Wade
10DY		06-Jun-10	05-Aug-10	Southeastern Bering Sea	Waite
11CH	CHAOZ	12-Aug-11	11-Sep-11	Bering Sea, Chukchi Sea, Beaufort Sea	Rone
12CH	CHAOZ	8-Aug-12	3-Sept-12	Bering Sea, Chukchi Sea, Beaufort Sea	Rone
	BWASP	31-Aug-99	23-Oct-99	Beaufort Sea	Ferguson
	BWASP	1-Sep-00	17-Oct-00	Beaufort Sea	Ferguson
	BWASP	2-Sep-01	19-Oct-01	Beaufort Sea	Ferguson
	BWASP	22-Aug-02	7-Oct-02	Beaufort Sea	Ferguson
	BWASP	1-Sep-03	19-Oct-03	Beaufort Sea	Ferguson
	BWASP	1-Sep-04	18-Oct-04	Beaufort Sea	Ferguson
	BWASP	3-Sep-05	20-Oct-05	Beaufort Sea	Ferguson
	BWASP	2-Sep-06	16-Oct-06	Beaufort Sea	Ferguson
	BWASP	3-Sep-07	10-Oct-07	Beaufort Sea	Ferguson
	BWASP	5-Sept-08	18-Oct-08	Beaufort Sea	Ferguson
	BWASP	1-Sep-09	18-Oct-09	Beaufort Sea	Ferguson

Survey Nickname	Survey Name	Start Date	End Date	Survey Area	Data manager
	BWASP	1-Sep-10	15-Oct-10	Beaufort Sea	Ferguson
	COMIDA	16-June-08	7-Jul-08	Chukchi Sea	Ferguson
	COMIDA	3-Aug-08	26-Aug-08	Chukchi Sea	Ferguson
	COMIDA	21-Oct-08	10-Nov-08	Chukchi Sea	Ferguson
	COMIDA	24-Jun-09	29-Oct-09	Chukchi Sea	Ferguson
	COMIDA	3-Jul-10	25-Oct-10	Chukchi Sea	Ferguson
	ASAMM	17-Jun-11	24-Oct-11	Beaufort & Chukchi seas	Ferguson
	ASAMM	30-Jun_12	28-Oct-12	Beaufort & Chukchi seas	Ferguson

Table 5. Sei whale mark recovery data from 1972-1975 for Bayesian analysis. For the number of whales marked, the first number is the total number of animals marked, while the parenthetical entry is the number of marking events that occurred as part of research operations on pelagic wintering grounds. The latter were used to produce estimates of the pelagic stock reported in the body of this paper (see Appendix A for the alternative, single stock estimate based on all marks and recoveries during this time period).

		Recoveries			
Year marked	Number of whales marked	1972	1973	1974	1975
1972	61 (50)	9	5	4	1
1973	27 (17)		1	3	0
1974	15 (6)			2	0
1975	8 (0)				0
	Japanese Pelagic Catch	2,041	1,710	1,190	454

Table 6. Reported land station catch of sei whales in the eastern North Pacific by year and land station (IWC catch database, December 2012 release).

Year	Akutan	Coal Harbour	Fields Landing	Grays Harb BayCity	Kyoquot	Moss Landing	Naden Harbour	Port Hobron	Richmond, S_PabloPt	Rose Harbour	Sechart	Trinidad	Total
1916					4								4
1917					65					27	29		121
1918					101		14			15			130
1919				5	18		5			51			79
1920						1							1
1926												25	25
1928	1												1
1934								2					2
1937								1					1
1947			3										3
1948		2											2
1949		3											3
1950		24											24
1951		5											5
1952		22											22
1953		14											14
1954		134											134
1955		139											139
1956		37											37
1957		93							1				94
1958		39							2				41
1959		185							37				222
1960									47				47
1961									51				51
1962		340							22				362

Year	Akutan	Coal Harbour	Fields Landing	Grays Harb BayCity	Kyoquot	Moss Landing	Naden Harbour	Port Hobron	Richmond, S_PabloPt	Rose Harbour	Sechart	Trinidad	Total
1963		154							97				251
1964		612							13				625
1965		604							22				626
1966		354							60				414
1967		89							3				92
1968									14				14
1969									10				10
1970									4				4
1971									2				2
Total	1	2850	3	5	188	1	19	3	385	93	29	25	3602

Table 7. Annual estimates of abundance (*N*), instantaneous hunting mortality (*F*), and number of new recruits (*B*) for the pelagic stock of North Pacific sei whales, 1972-1975. Subscripts denote which model was used to estimate parameters (L-P = Lincoln-Petersen, SS = state-space). Annual recruitment estimates were only available for the state-space model. Table entries give posterior medians, together with posterior standard error (in parentheses).

	Year			
Parameter	1972	1973	1974	1975
N_{L-P}	9856 (3465)	12324 (6136)	5264 (2215)	7830 (32837)
N_{SS}	11348 (1704)	8198 (1691)	5718 (1860)	3967 (2008)
F_{L-P}	0.23 (0.08)	0.15 (0.07)	0.26 (0.19)	0.06(0.30)
F_{SS}	0.22 (0.04)	0.25 (0.07)	0.26 (0.13)	0.13 (0.16)
B	N/A	392 (374)	280 (311)	190 (267)

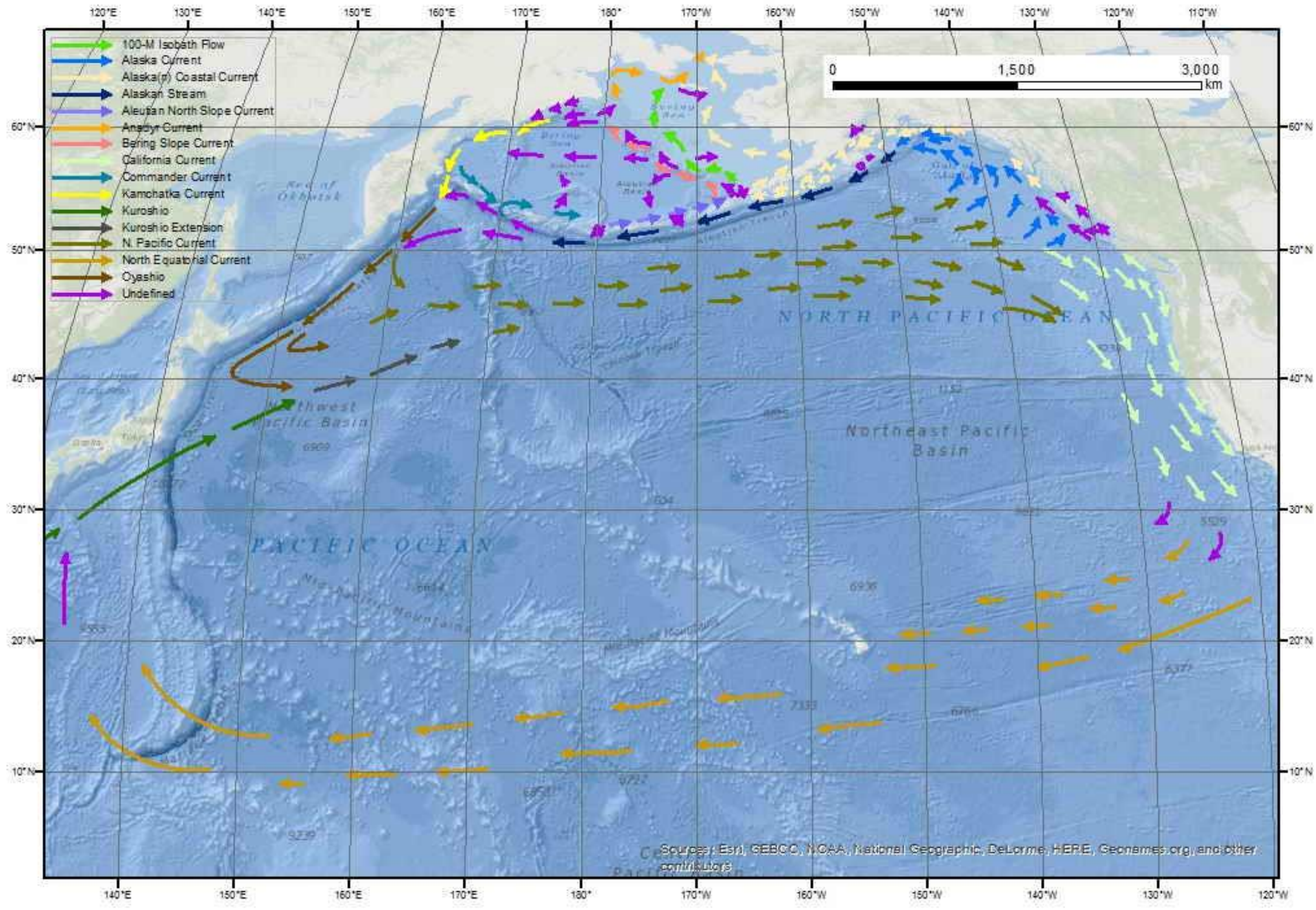

Fig. 1. Broad schematic of North Pacific ocean currents (P. Stabeno, pers. comm, digitized by J. Benson).

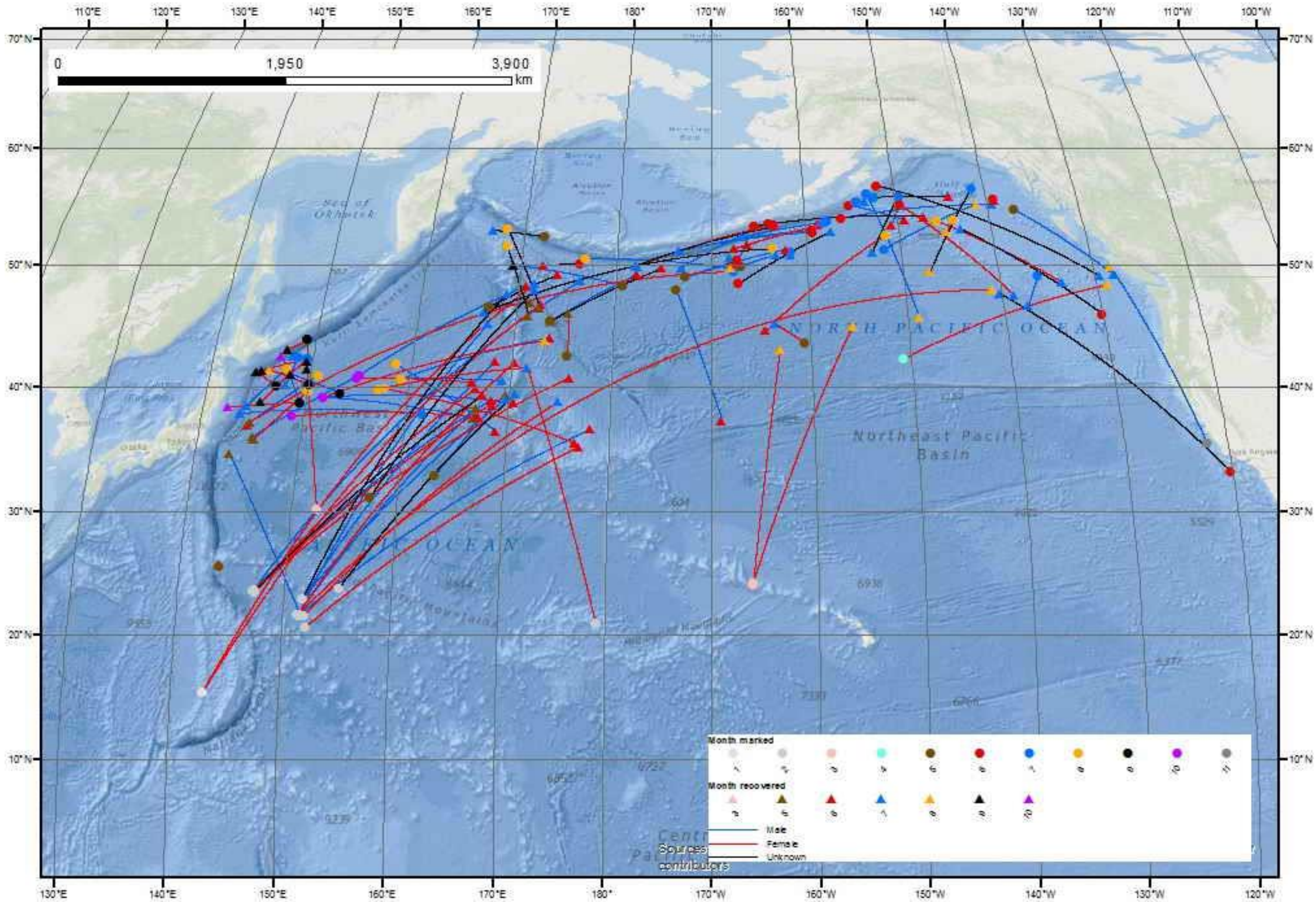

Fig. 2. Sei whale movements in the North Pacific based on Discovery mark recovery data of 106 marks (45 males, 41 females and 20 of unknown sex).

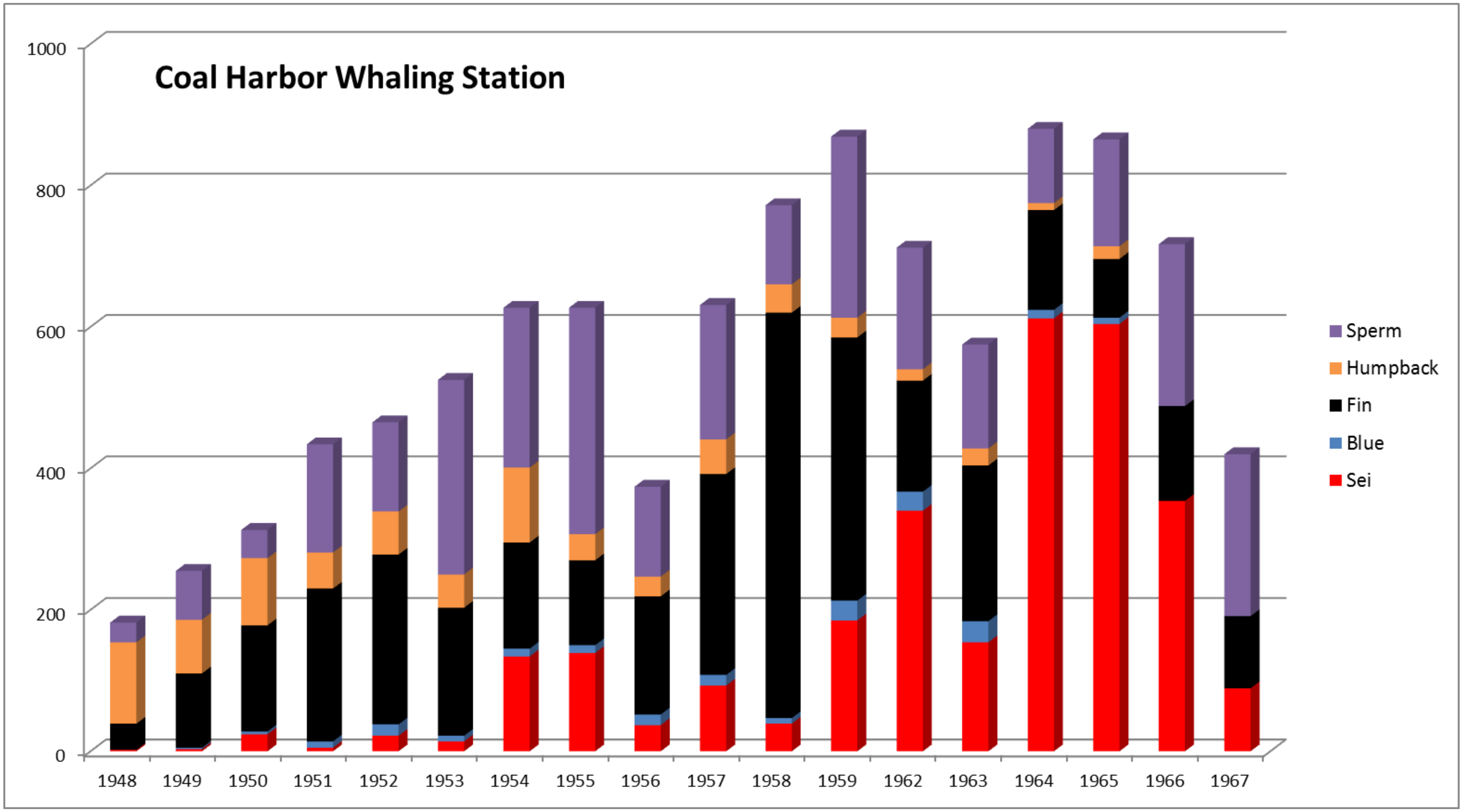

Fig. 3a. Post-WW II catch by species at the Coal Harbor land station off the Canadian Pacific coast.

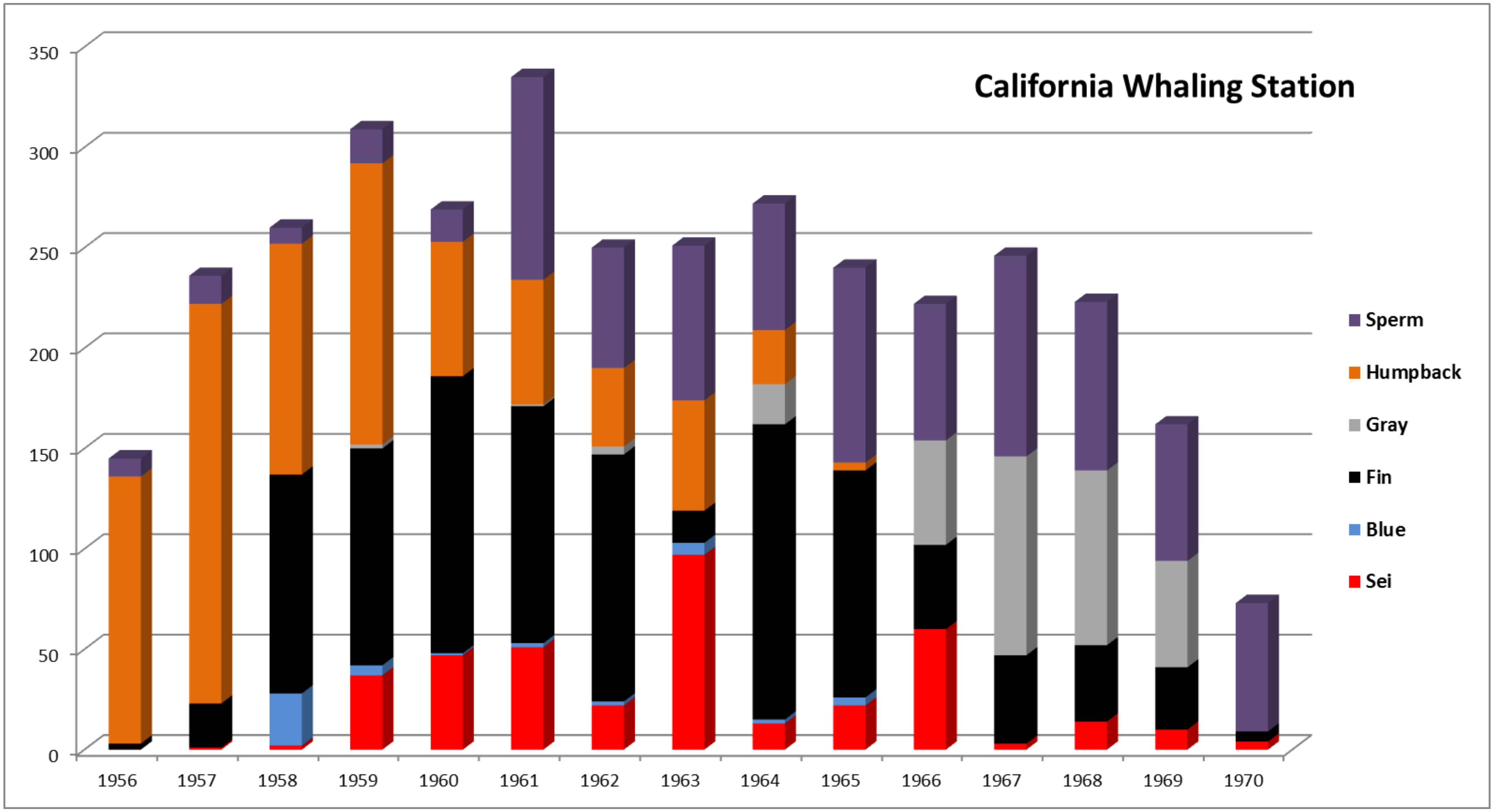

Fig. 3b. Post-WW-II catch by species at land stations in northern California.

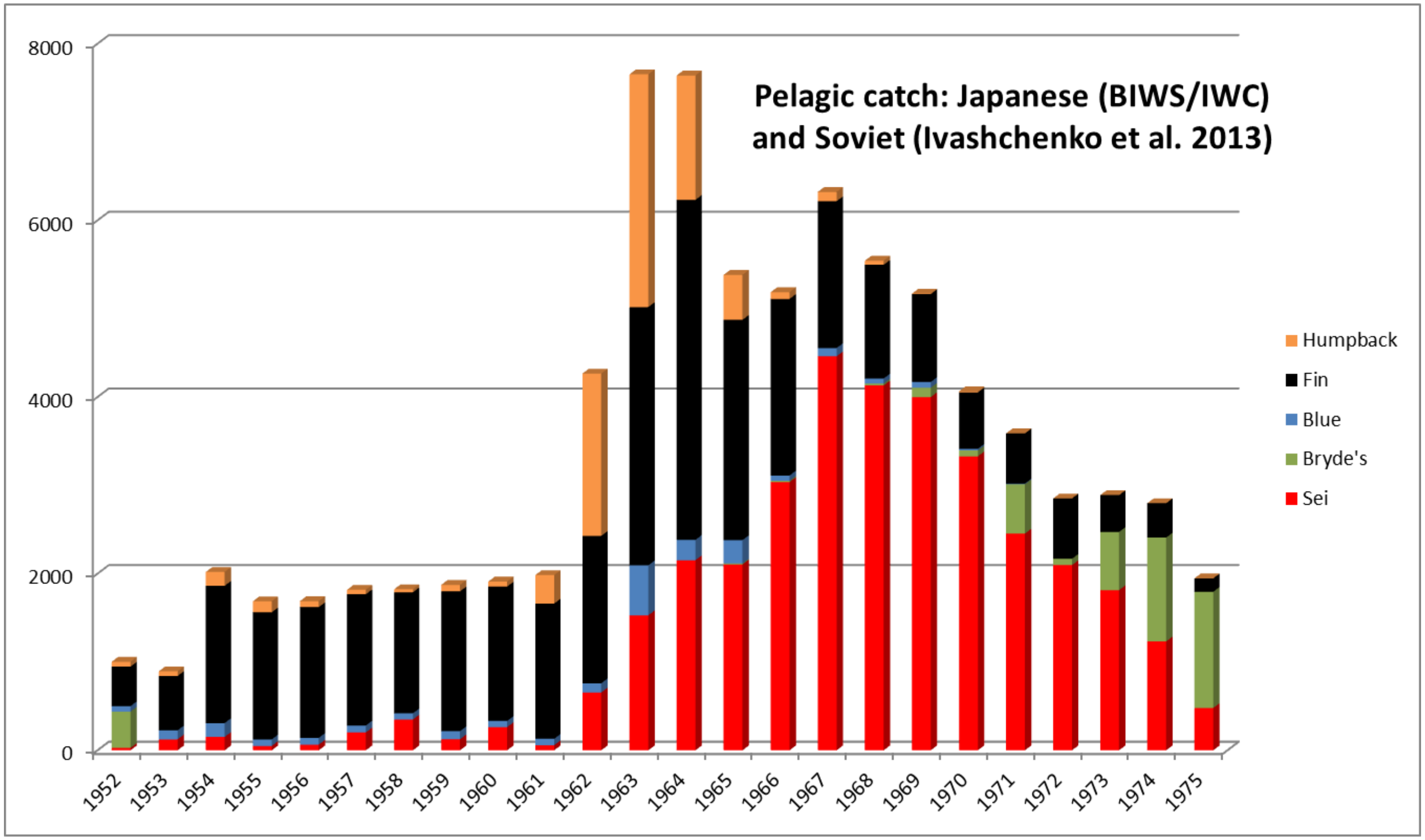

Fig. 4: In the North Pacific, there were no formal limits on the numbers of whales that could be killed until the 1971 season, well after the sei whale catches had peaked and long after the major species were already depleted. Includes the corrected Soviet data (Ivashchenko, *in litt.*) as well as the Japanese catch data as reported to the Bureau of International Whaling Statistics.

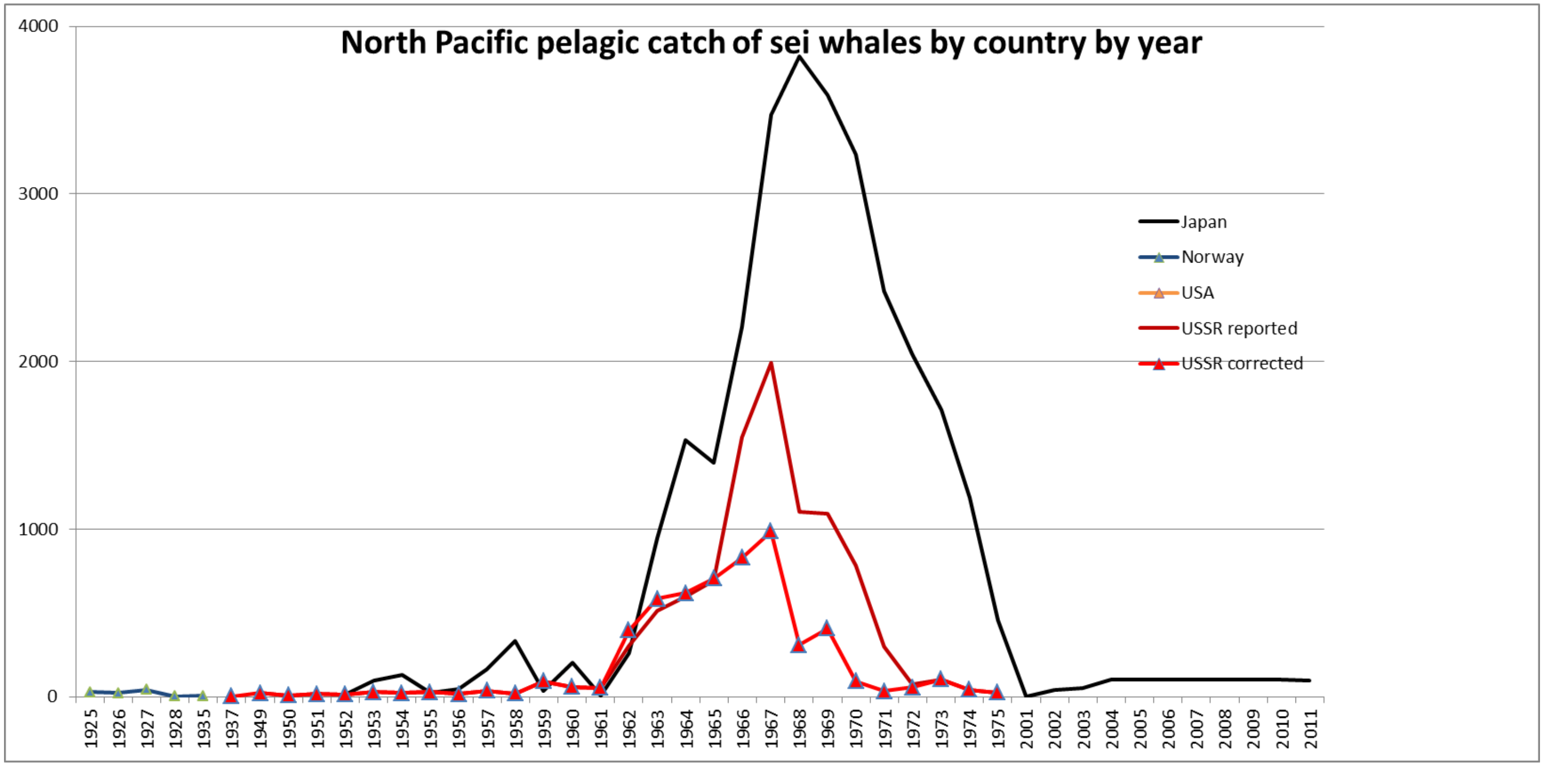

Fig. 5. North Pacific pelagic catch of sei whales by country by year. Corrected USSR numbers are from Ivashchenko (*in litt.*).

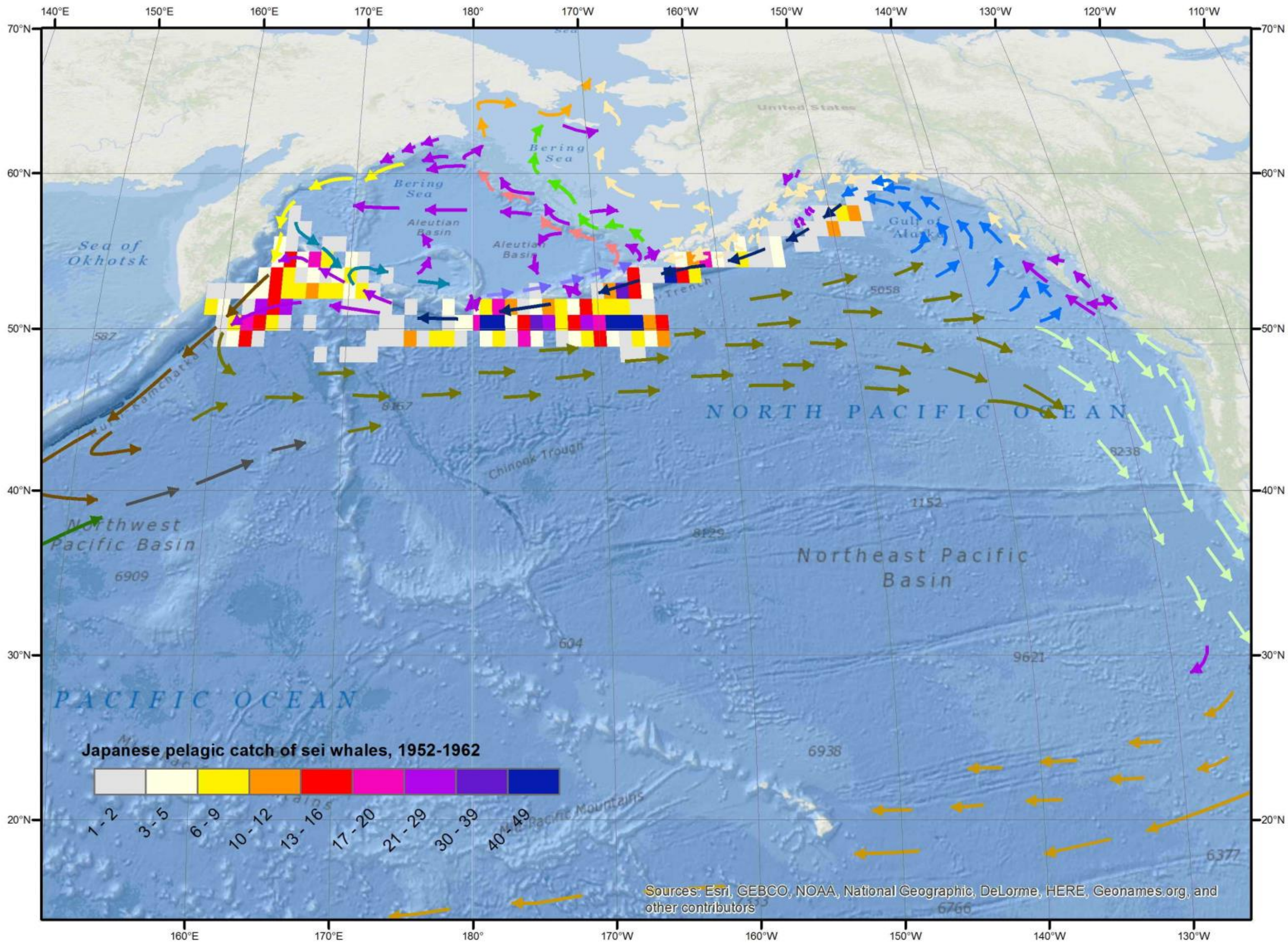

Fig. 6a. Japanese pelagic catch of sei whales from 1952 to 1962. Total catch = 1,305.

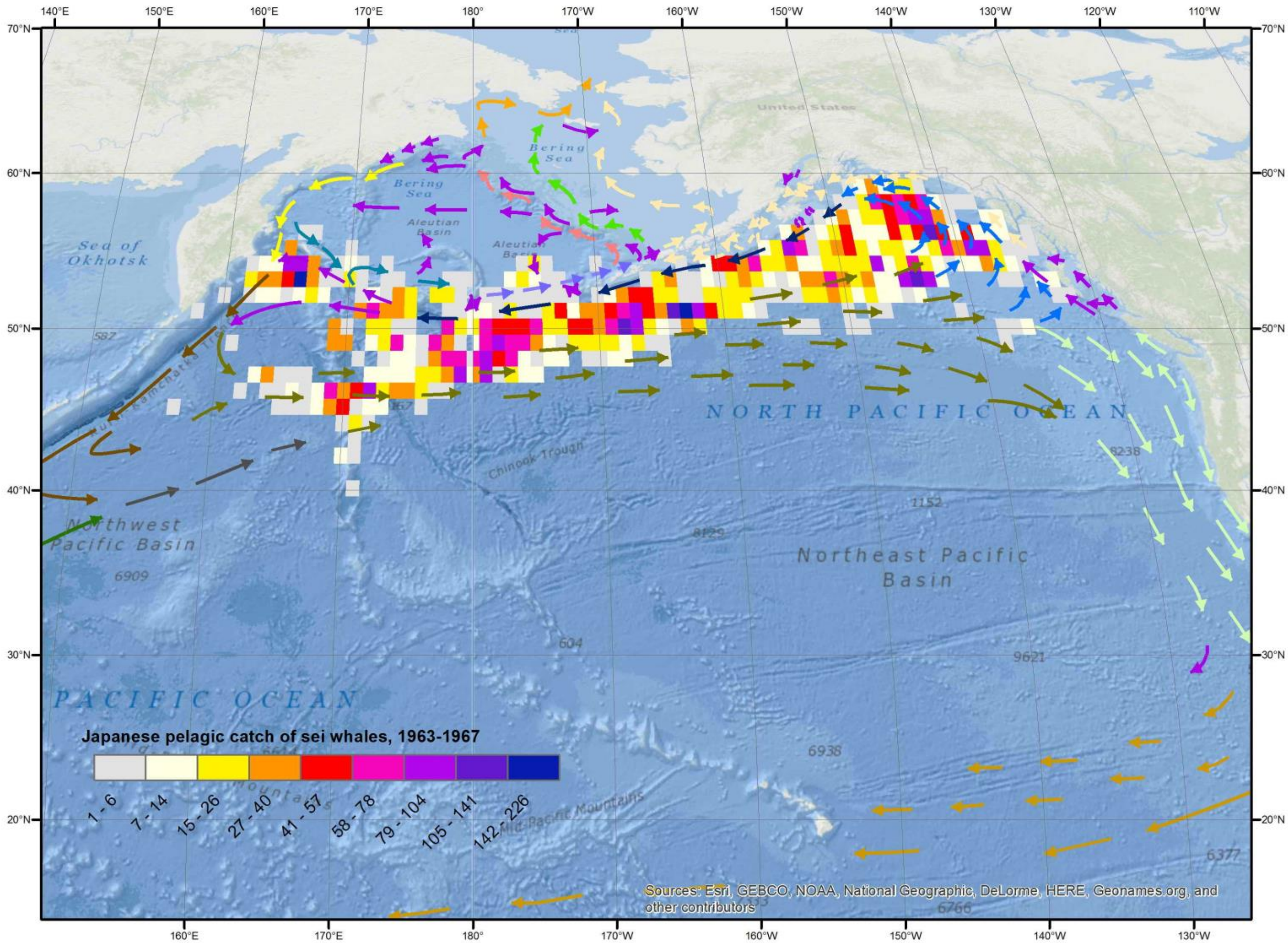

Fig. 6b. Japanese pelagic catch of sei whales from 1963 to 1967. Total catch = 9,558.

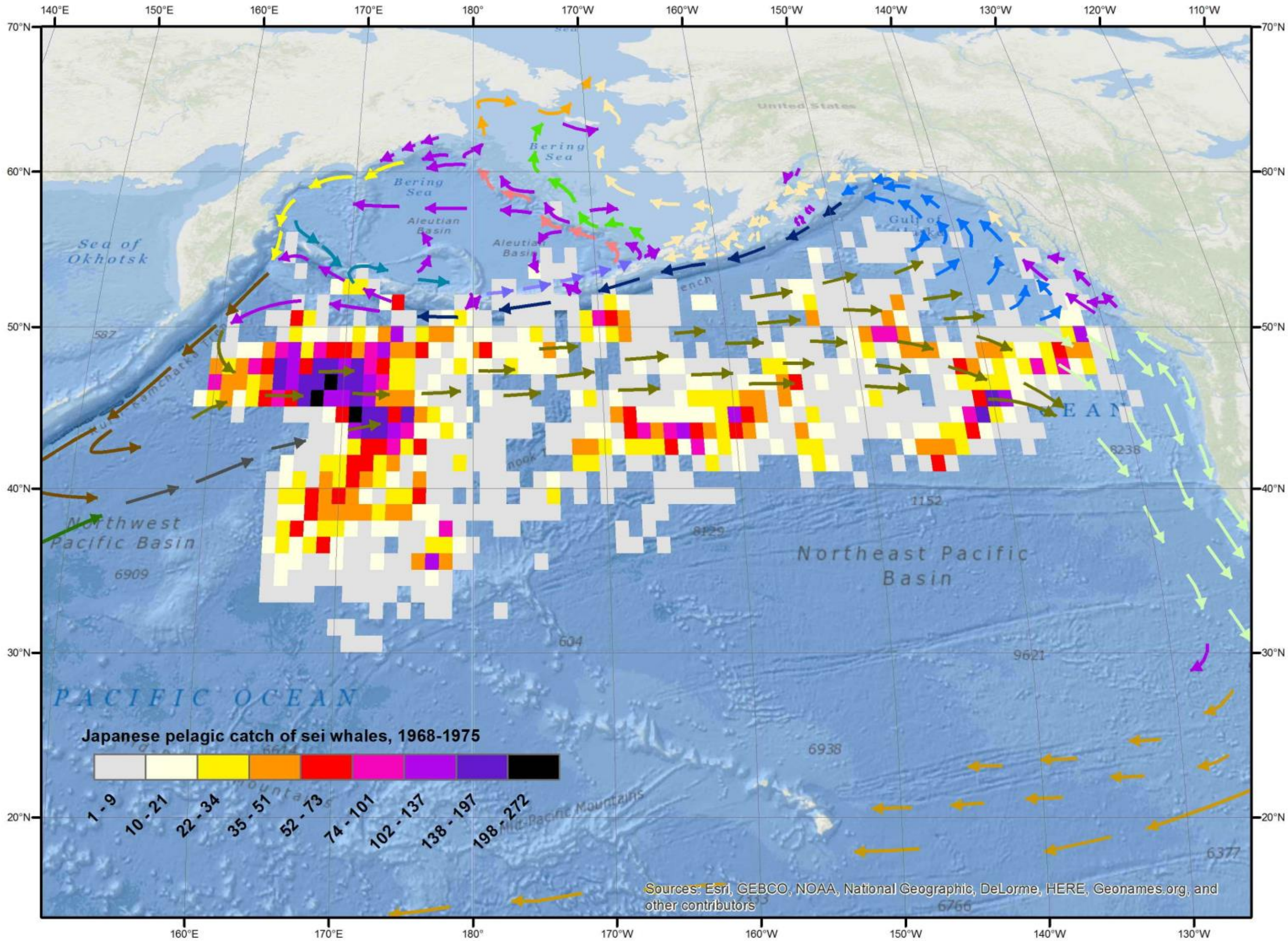

Fig. 6c. Japanese pelagic catch of sei whales from 1968 to 1975. Total catch = 18,462.

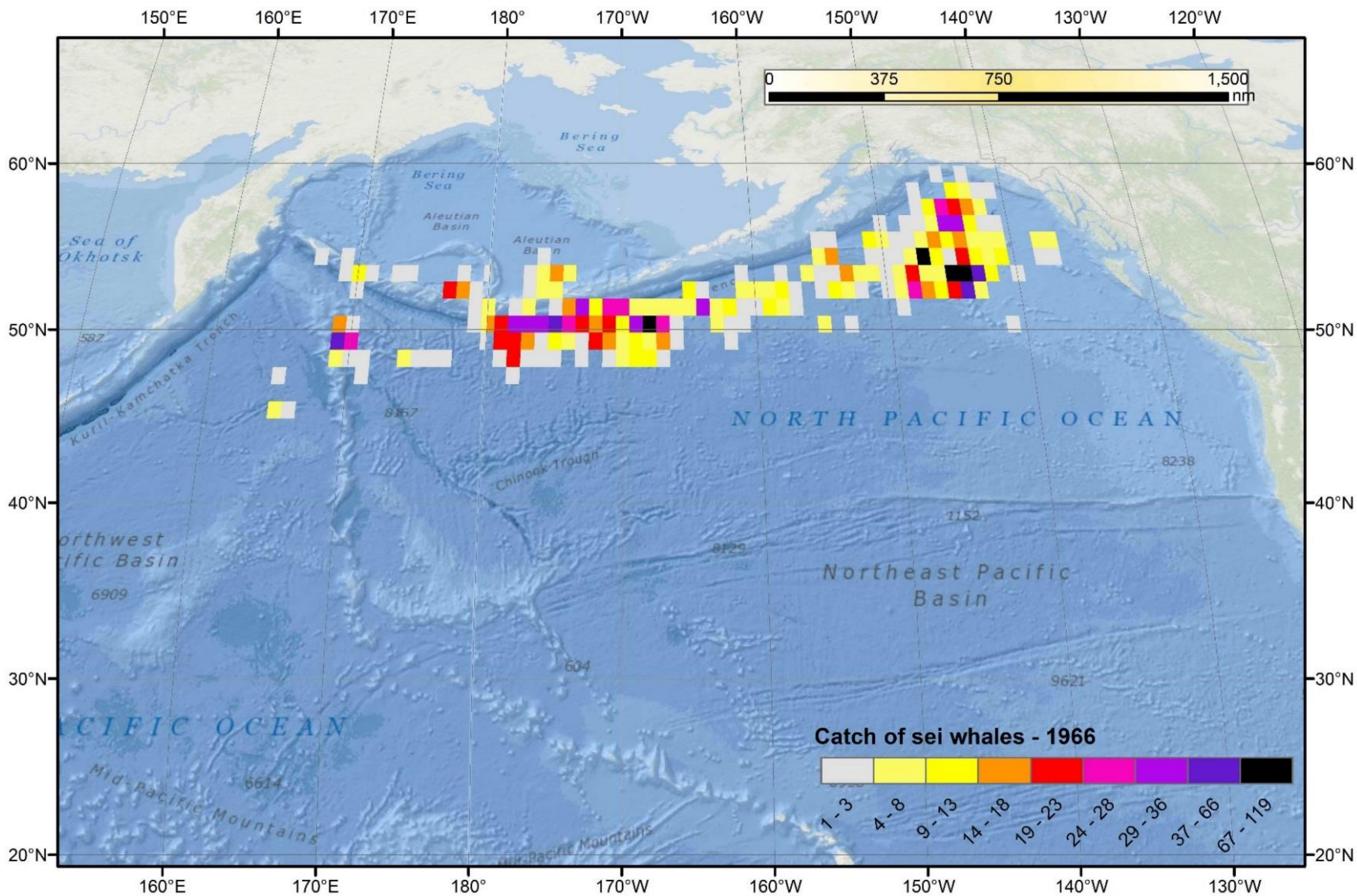

Fig. 7a. In 1966, whalers were still catching large numbers of other whale species. They were hunting in the same areas they had been whaling in the 3rd major era of whaling. Sei whales were caught all along the Aleutians and into the Gulf of Alaska, in and along the edges of the Alaska Stream. Catch of sei whales totaled 2,207.

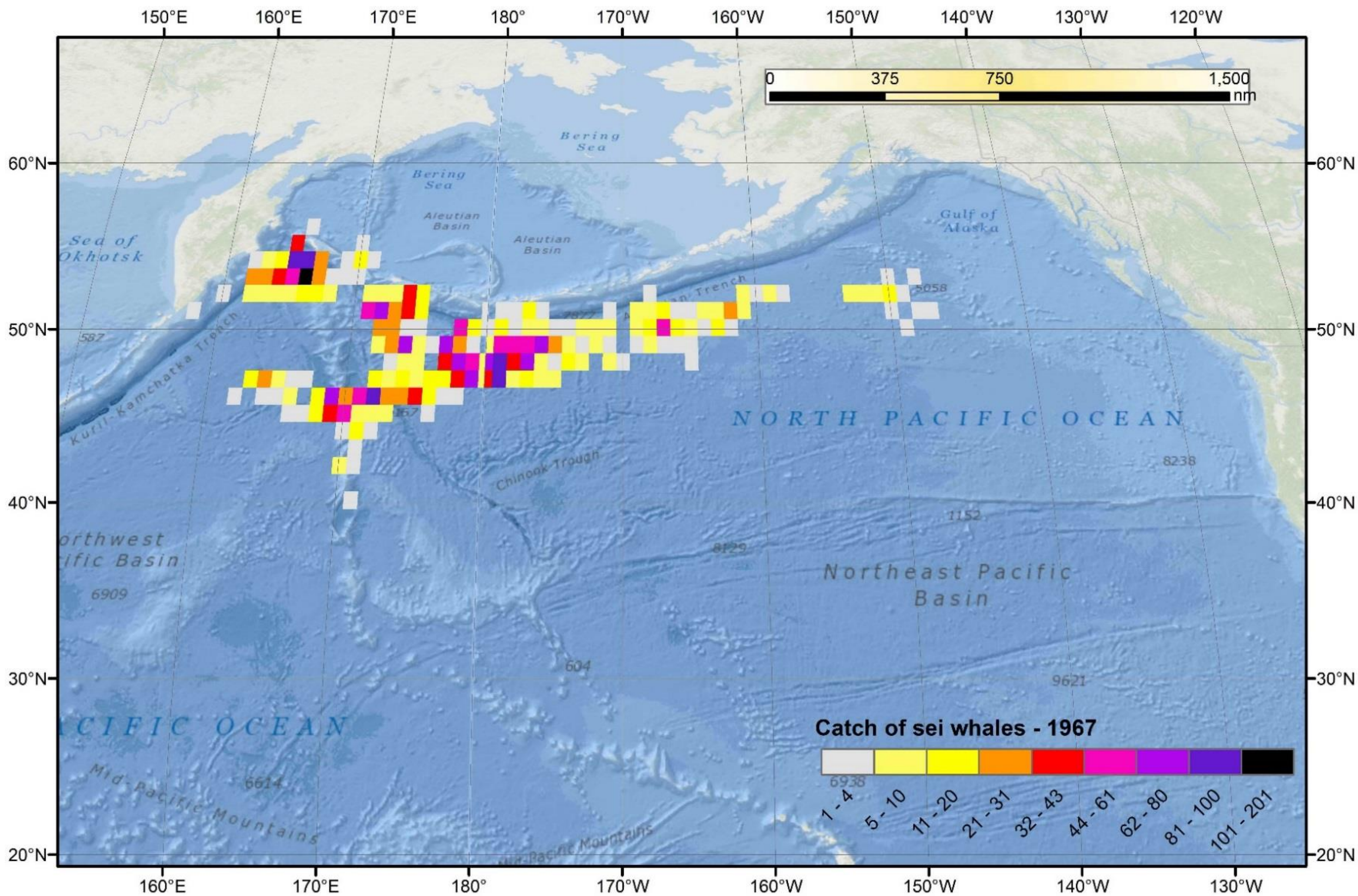

Fig. 7b. By 1967, sei whales were the dominant baleen whale being hunted. Whalers were exploring areas at the extremes of the Aleutians near Kamchatka, but also moving further south to try to find unexploited stocks of sei whales. Catch of sei whales totaled 3,473.

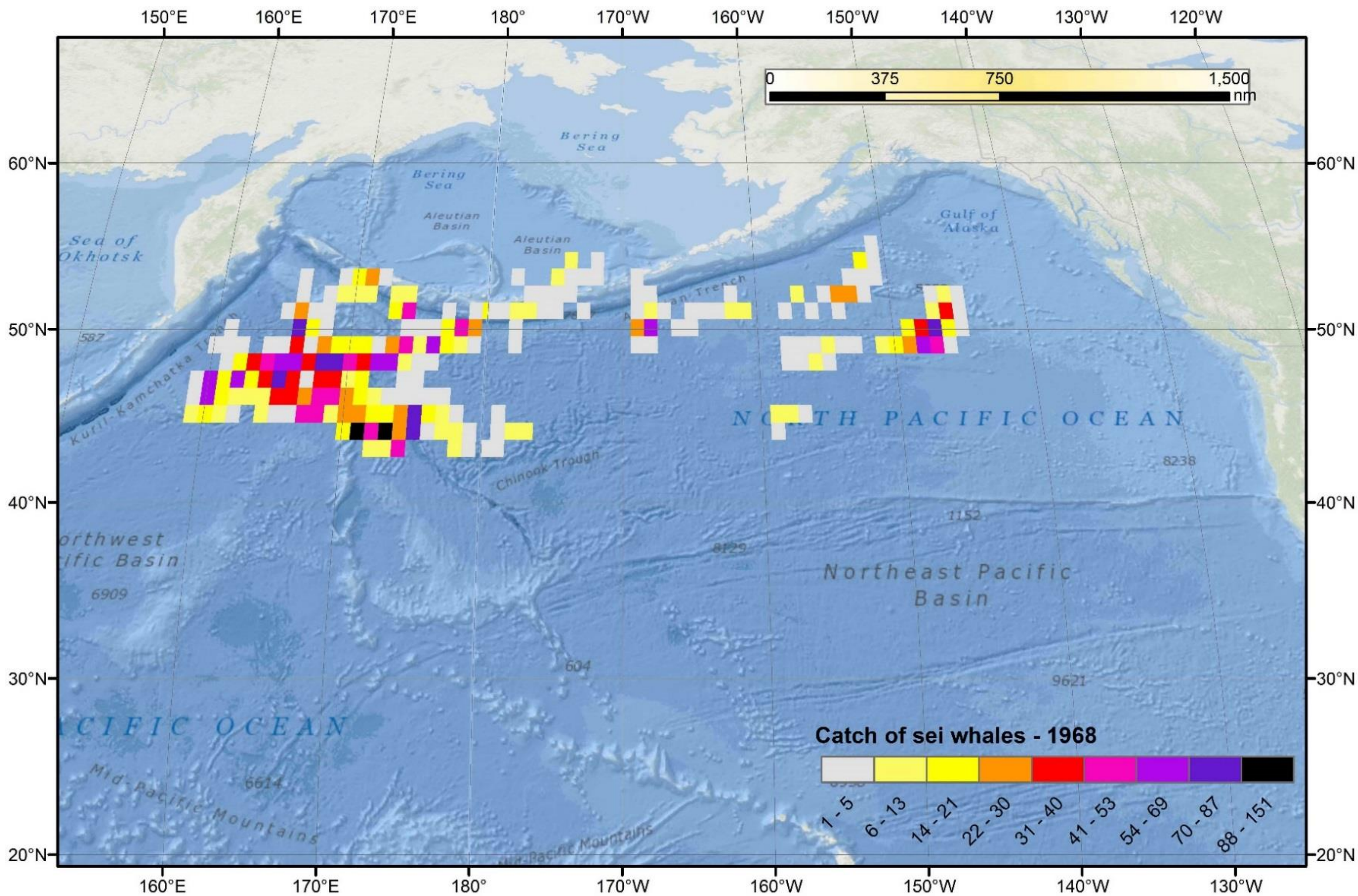

Fig. 7c. By 1968, hunting of blue and humpback whales had been banned. Pelagic fleets shifted their operations south and began to hunt large numbers of sperm and sei whales in the rich grounds along the Subarctic Frontal Zone (ca.40° N - 42° N). Catch of sei whales totaled 3,821.

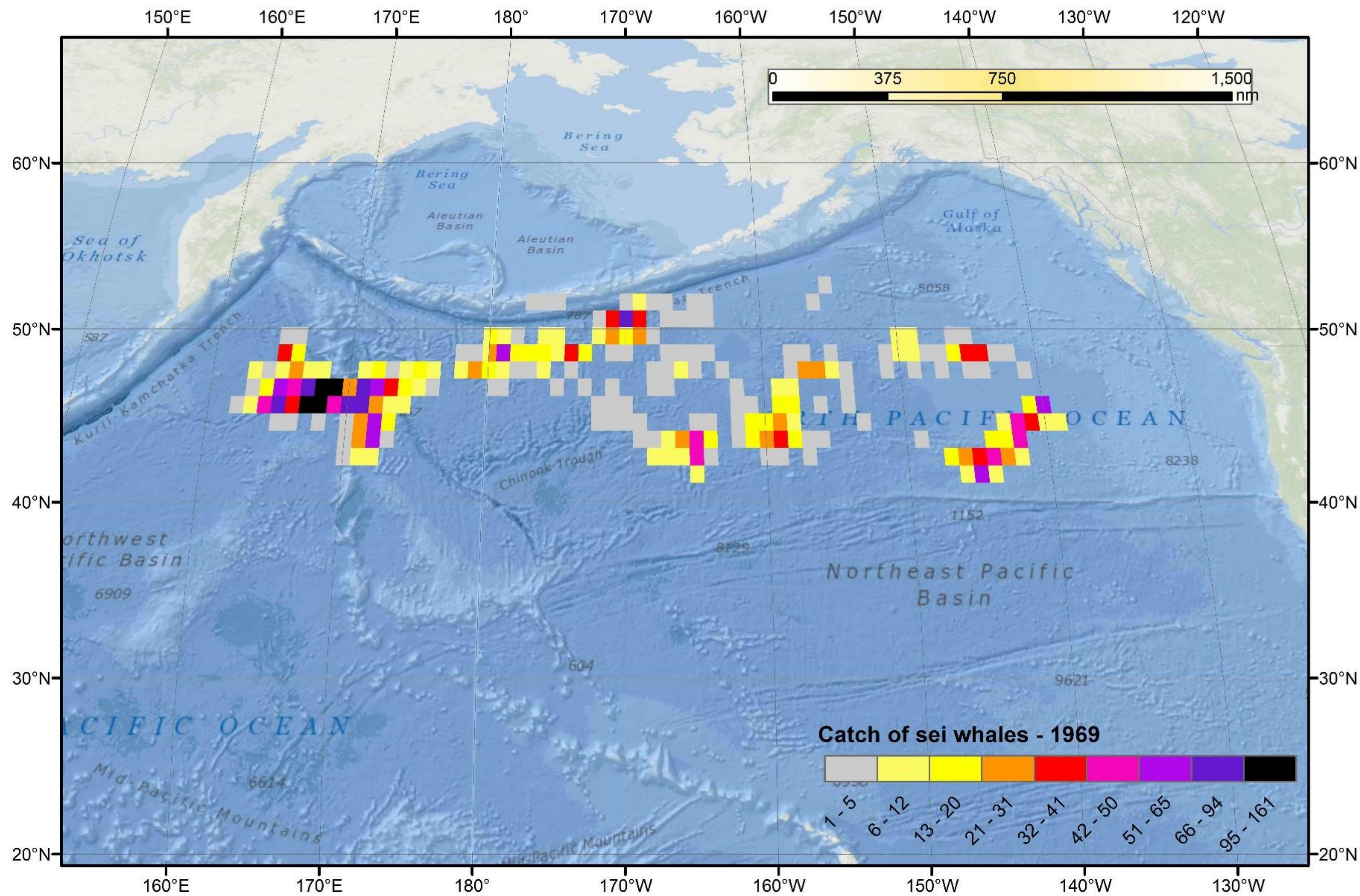

Fig. 7d. By 1969, whalers were taking sei whales all across the pelagic North Pacific along the Subarctic Frontal Zone. Catch of sei whales totaled 3,589.

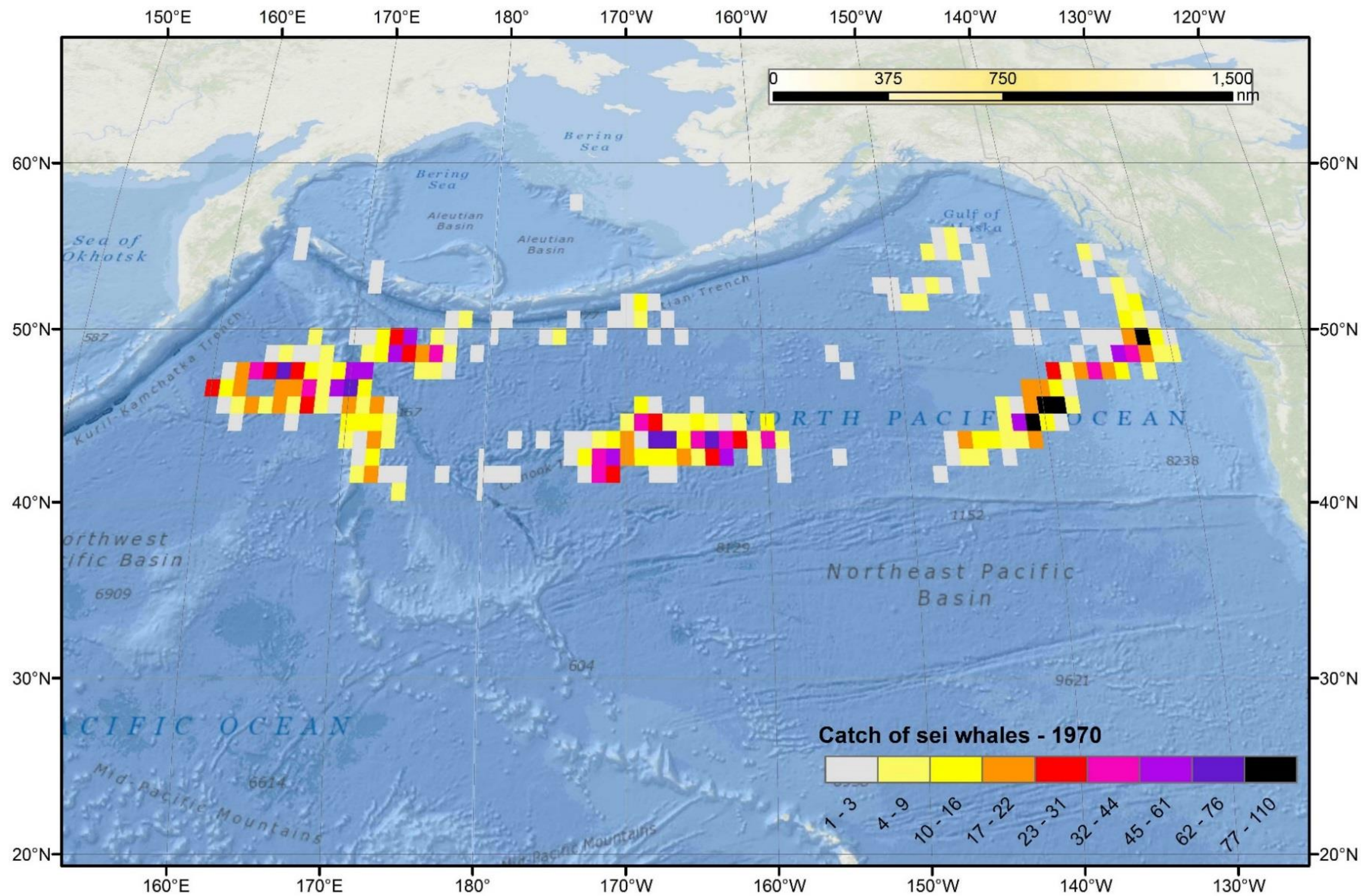

Fig. 7e. In 1970, whalers expanded to the eastern North Pacific near the Canadian coasts (areas near where the Canadian land station whalers had hunted with some success from 1962 to 1966 and also continued to work in the Subarctic Frontal Zone. Catch of sei whales totaled 3,253.

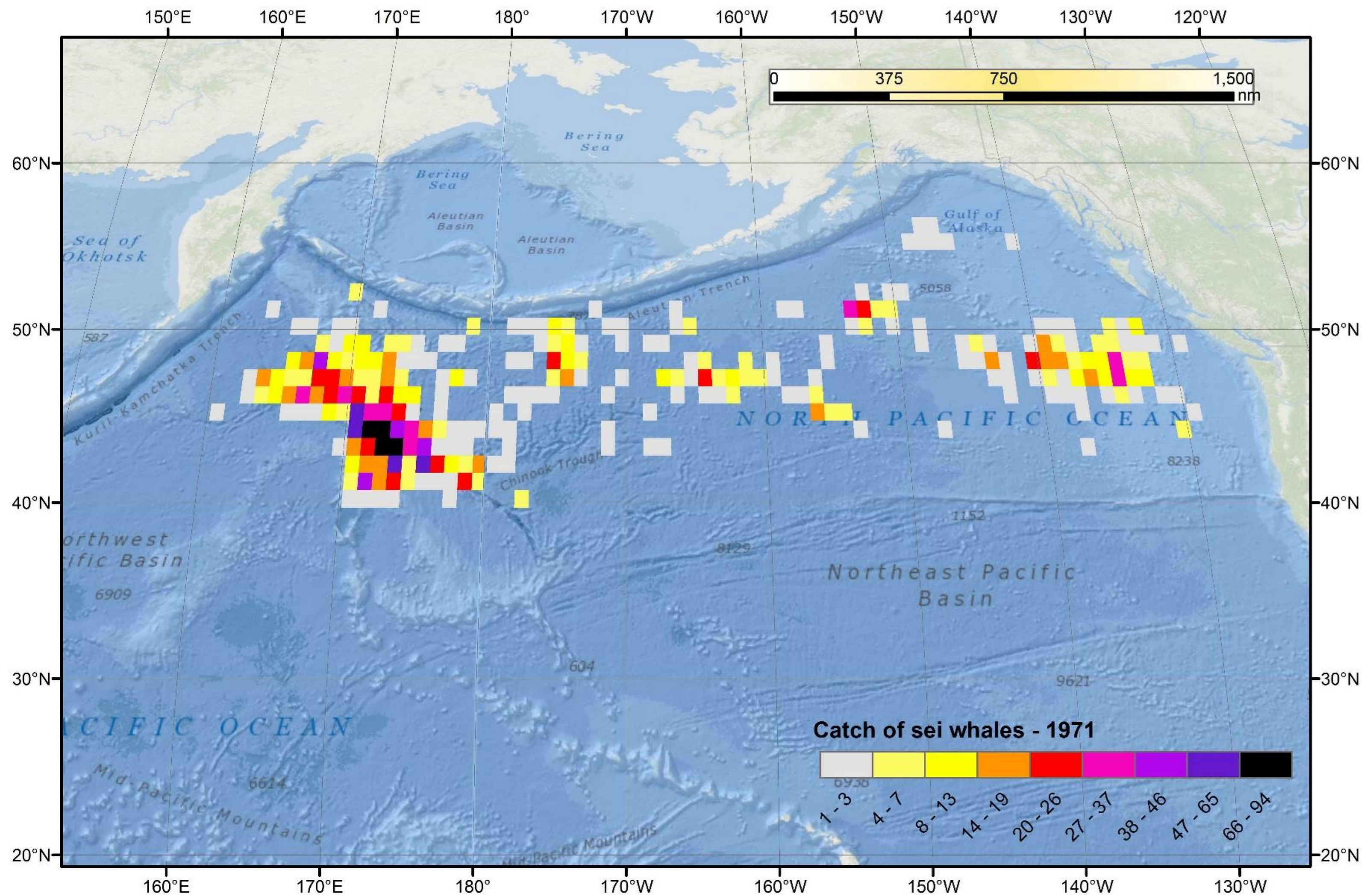

Fig. 7f. In 1971, whalers had moved even farther south. Catches were spread along the Subarctic Frontal Zone. Total pelagic catch of sei whales had dropped to 2,240.

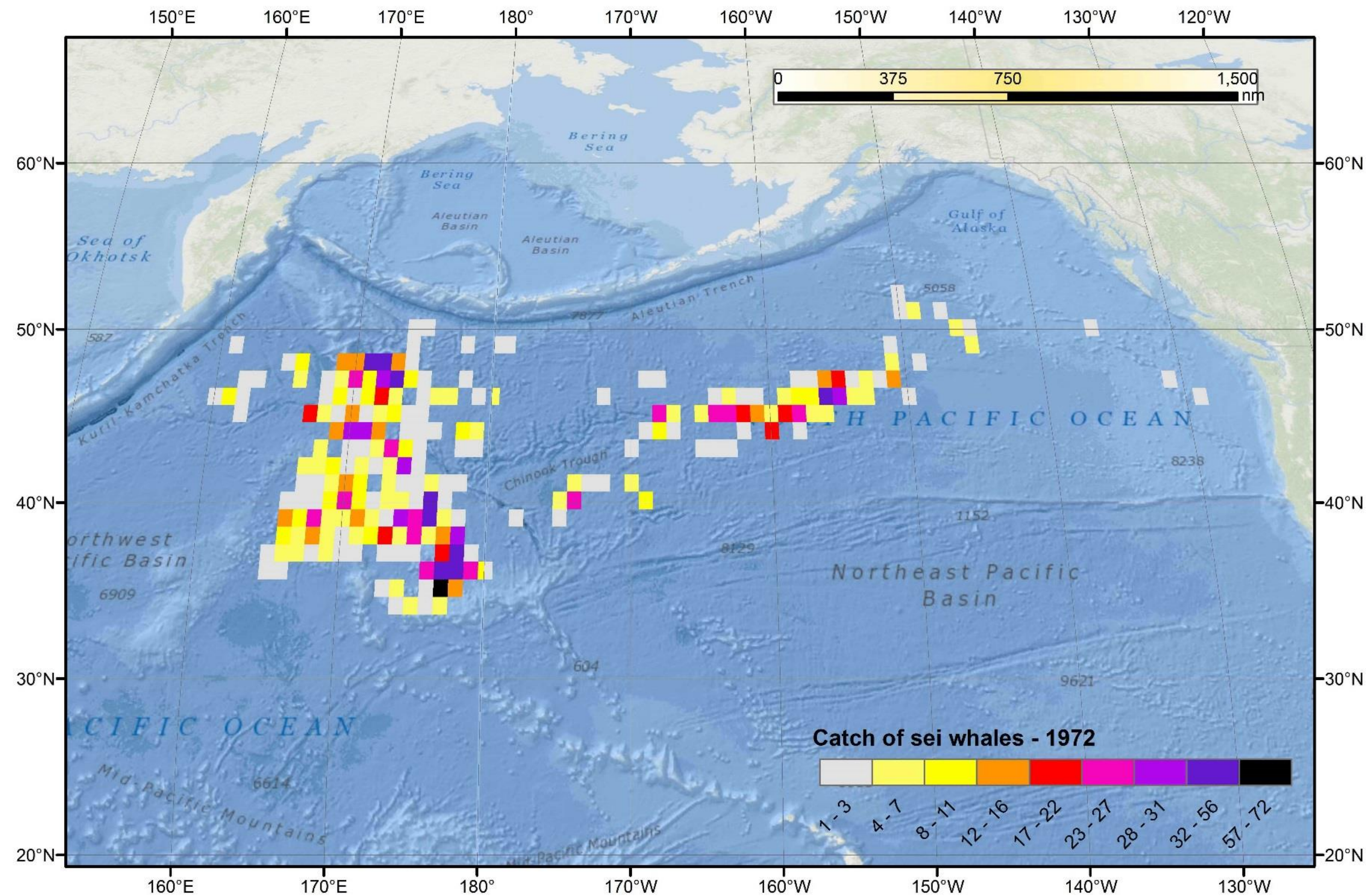

Fig. 7g. By 1972, sei whale catches in the North Pacific, the whalers had moved even further south to an area that encompassed both the Subarctic Frontal Zone and the Subtropical Frontal Zone. Catch of sei whales totaled 2,041.

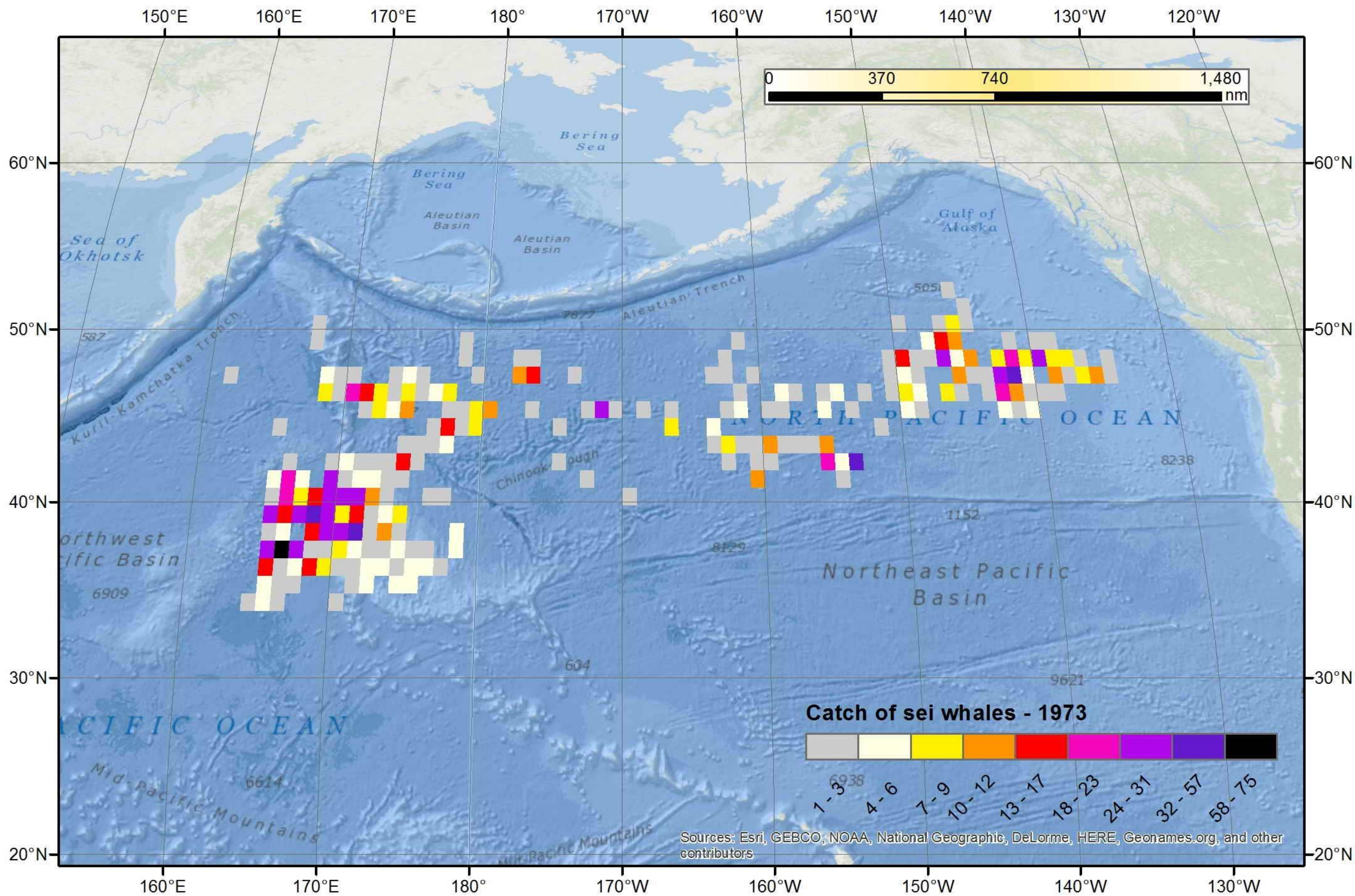

Fig. 7h. In 1973, whalers were hunting in roughly the same areas in the western North Pacific where they were hunting in 1972, but also expanded into the eastern North Pacific across the Subarctic Frontal Zone. Total catch of sei whales had dropped to 1,710.

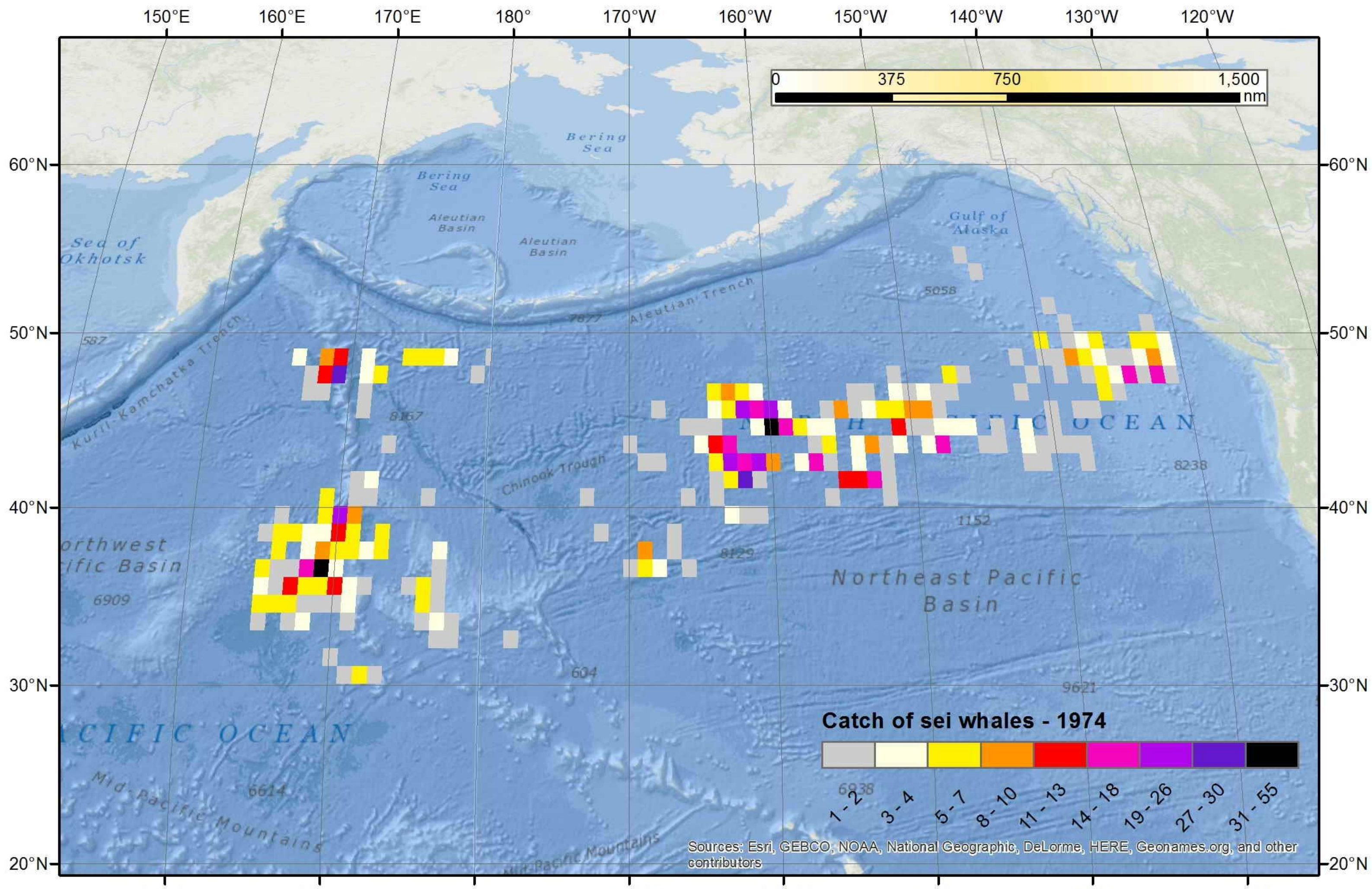

Fig. 7i. In 1974, whalers were hunting in similar areas as in 1973 but catches were much reduced, from over 1,710 whales in 1974 to fewer than 1,190 whales in 1974.

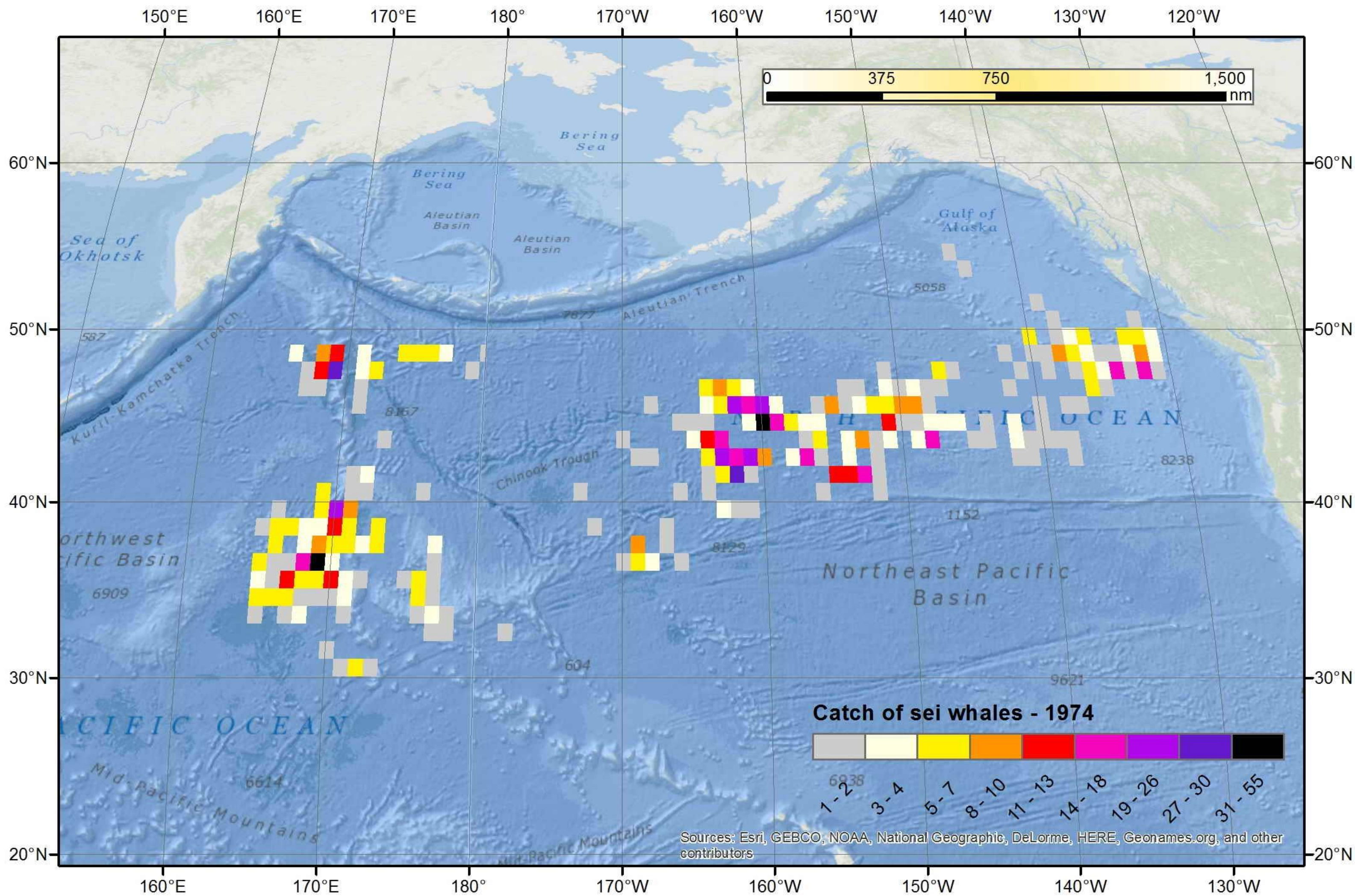

Fig. 7j. By 1975, the last year of commercial sei whale hunting, only 454 sei whales were caught. Whaling was scattered along the Subarctic Frontal Zone although a few sei whales were caught in the Gulf of Alaska and well offshore of the North American coast.

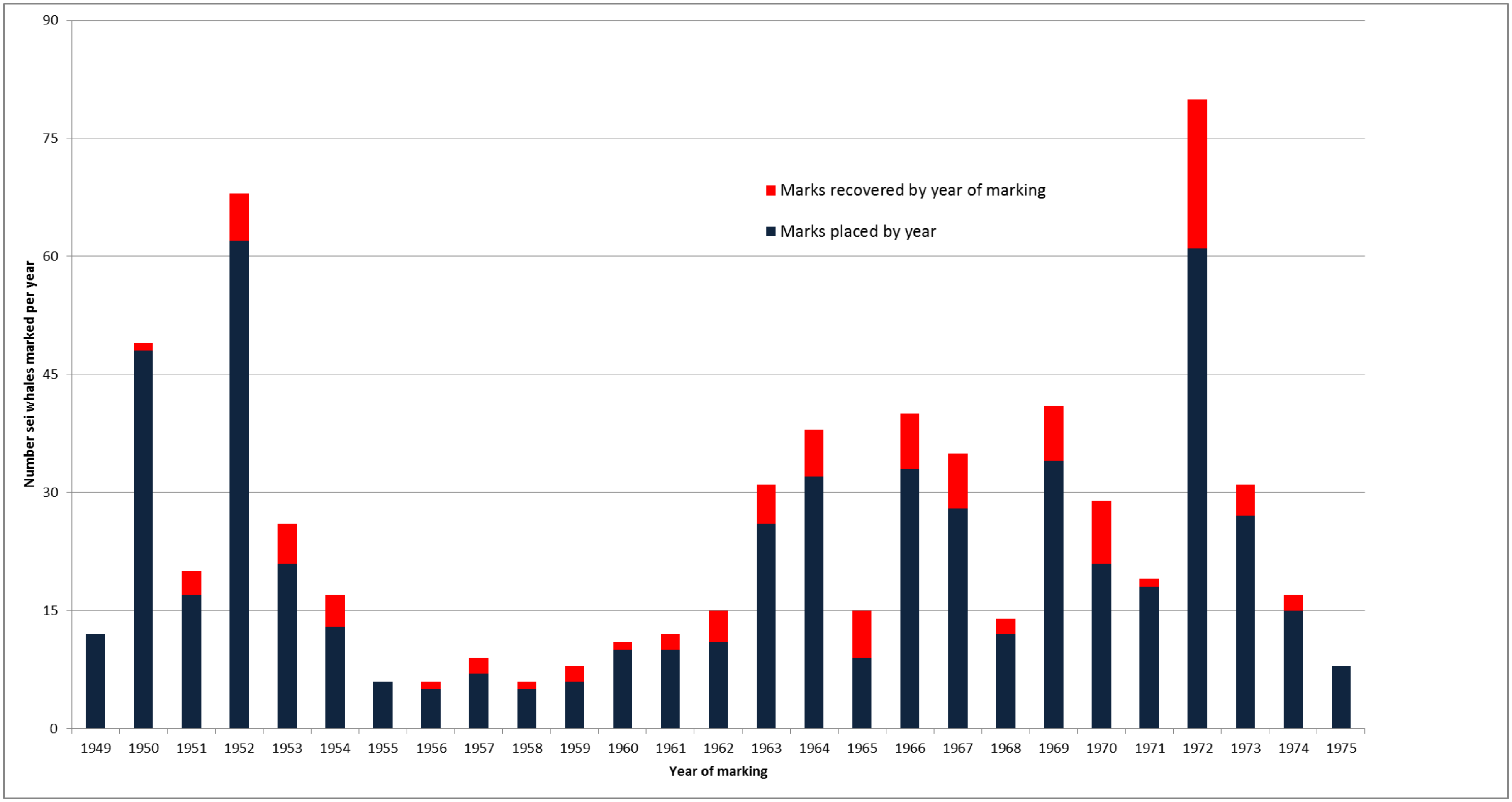

Fig. 8. Discovery marks placed and recovered by year of marking. Note the high number of recoveries of whales marked in 1972 (n = 19) in relation to number of marks deployed in 1972 (n = 61).

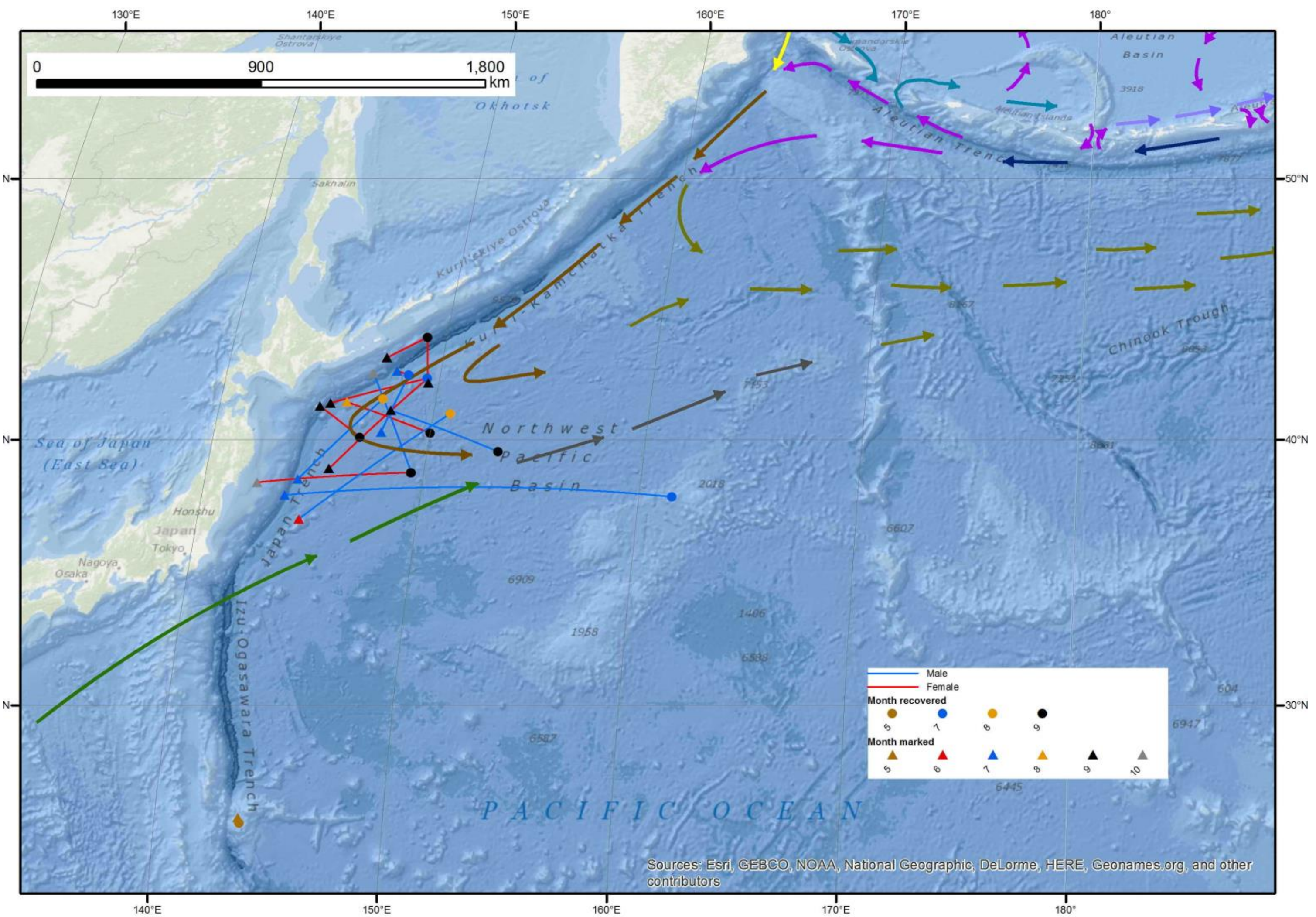

Fig. 9. Recoveries of marks placed between 1949 and 1953 (6 males and 9 females). There were no recoveries of any of these marks after 1961.

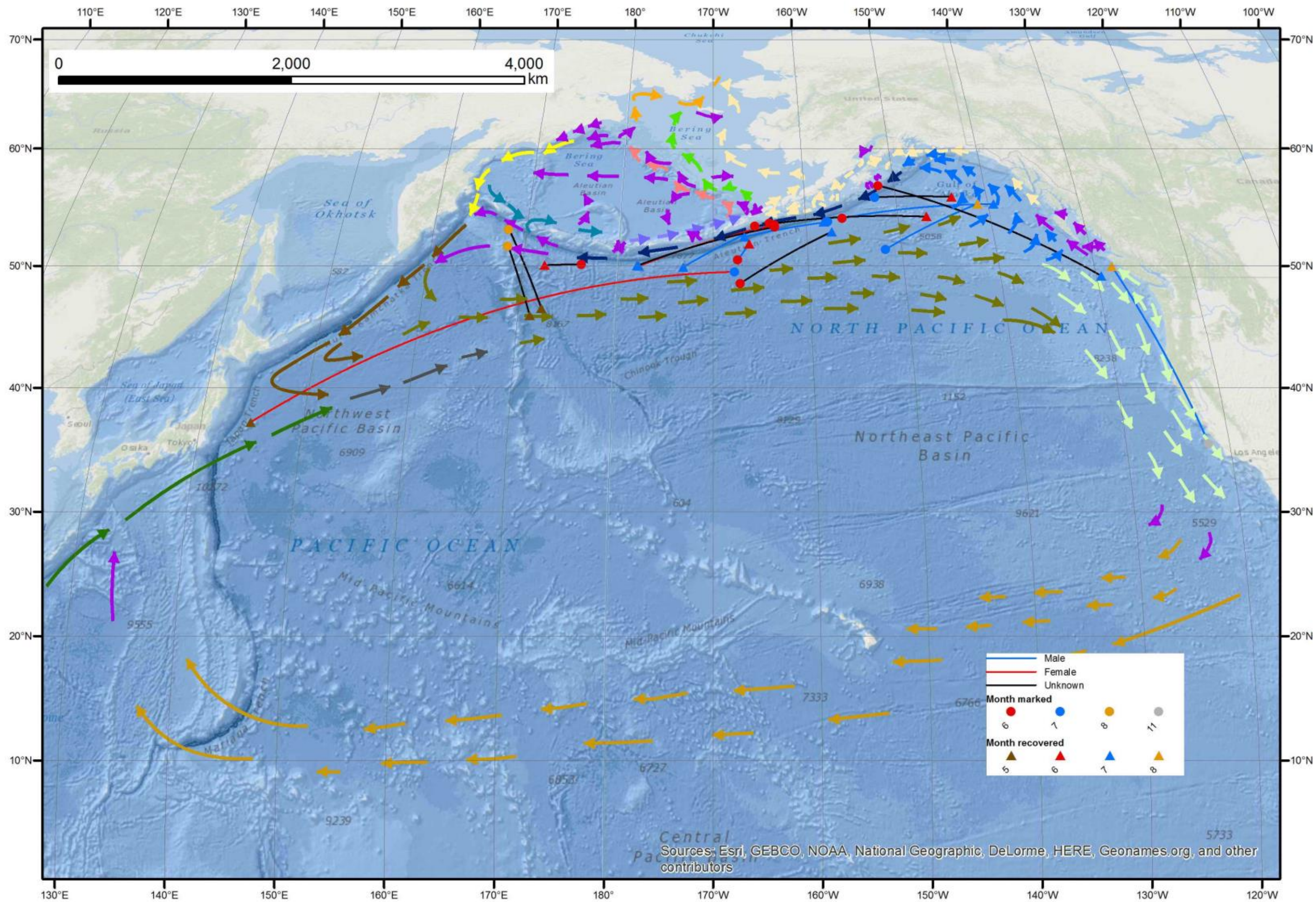

Fig. 10a. Recoveries of marks placed between 1954 and 1962 (6 males, 3 females and 8 of unknown sex). Fin whales were the preferred species during this time period.

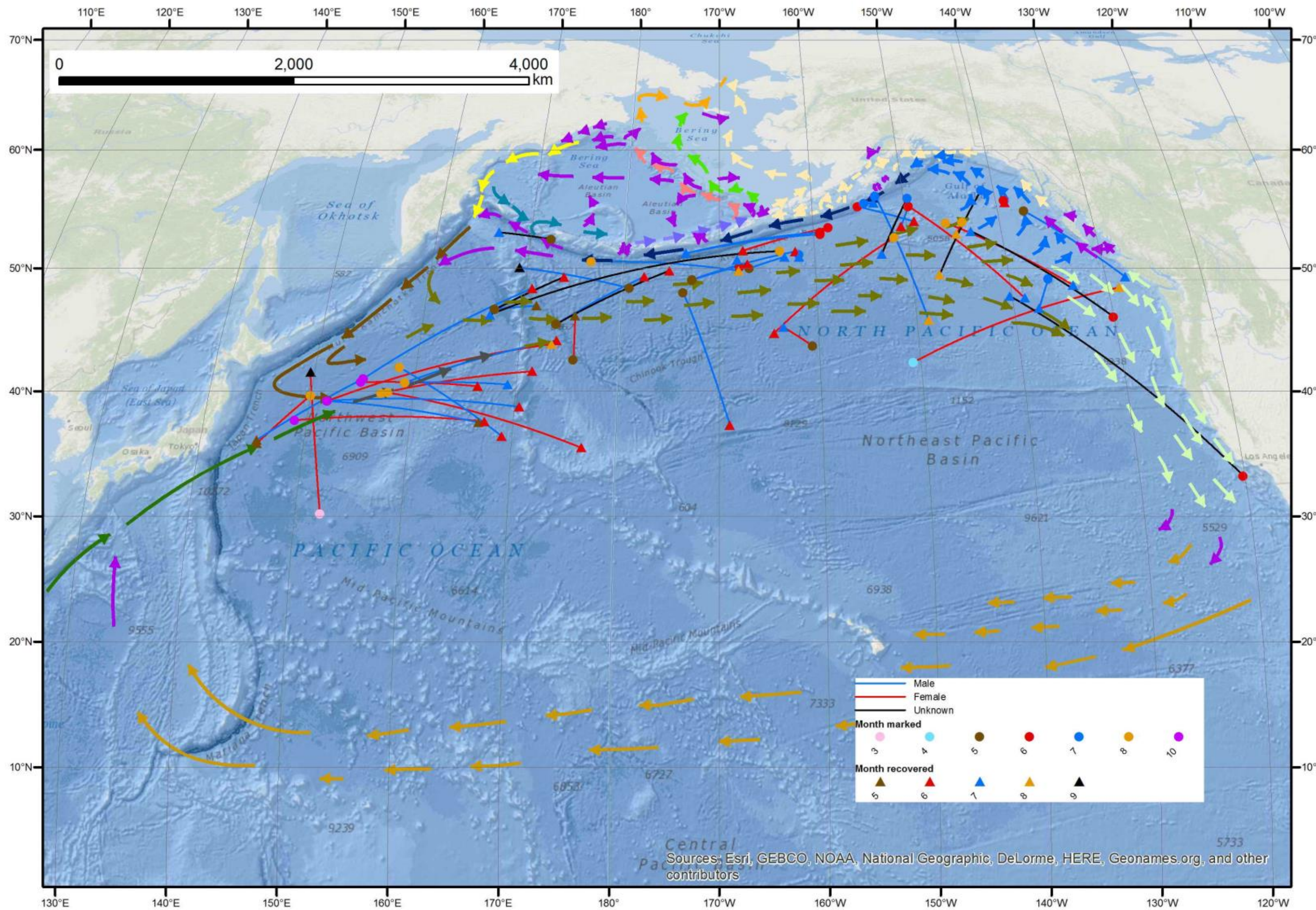

Fig. 10b. Recoveries marks placed between 1963 and 1971 (24 males, 17 females and 8 of unknown sex). Catches of sei whales increased during this time period.

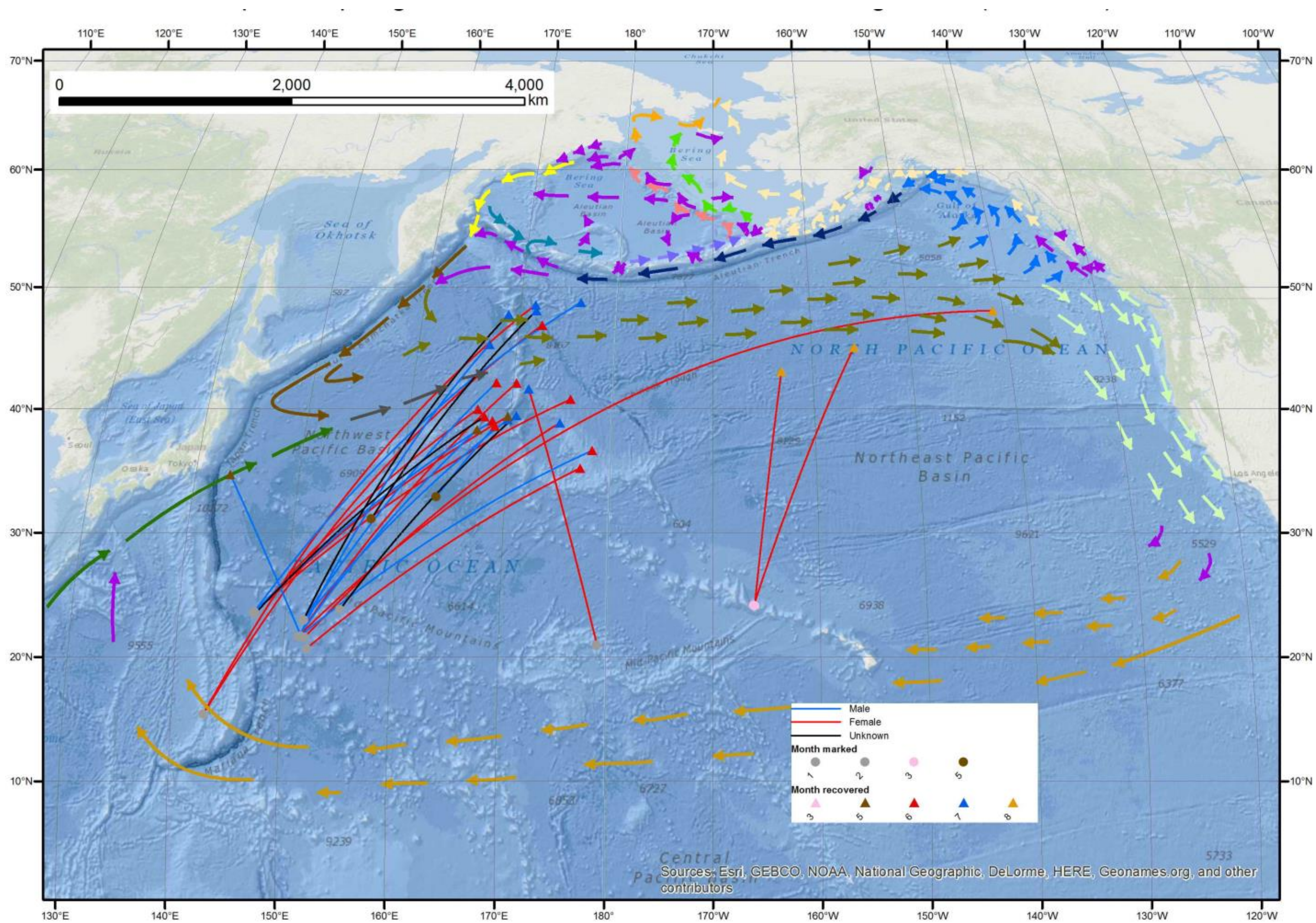

Fig. 11a. Recoveries of marks placed during or after 1972 (9 males, 12 females and 4 of unknown sex) in the last few years of whaling, when sei whales were the preferred species of baleen whales and Japanese pelagic whalers continued to search for new sei whale grounds.

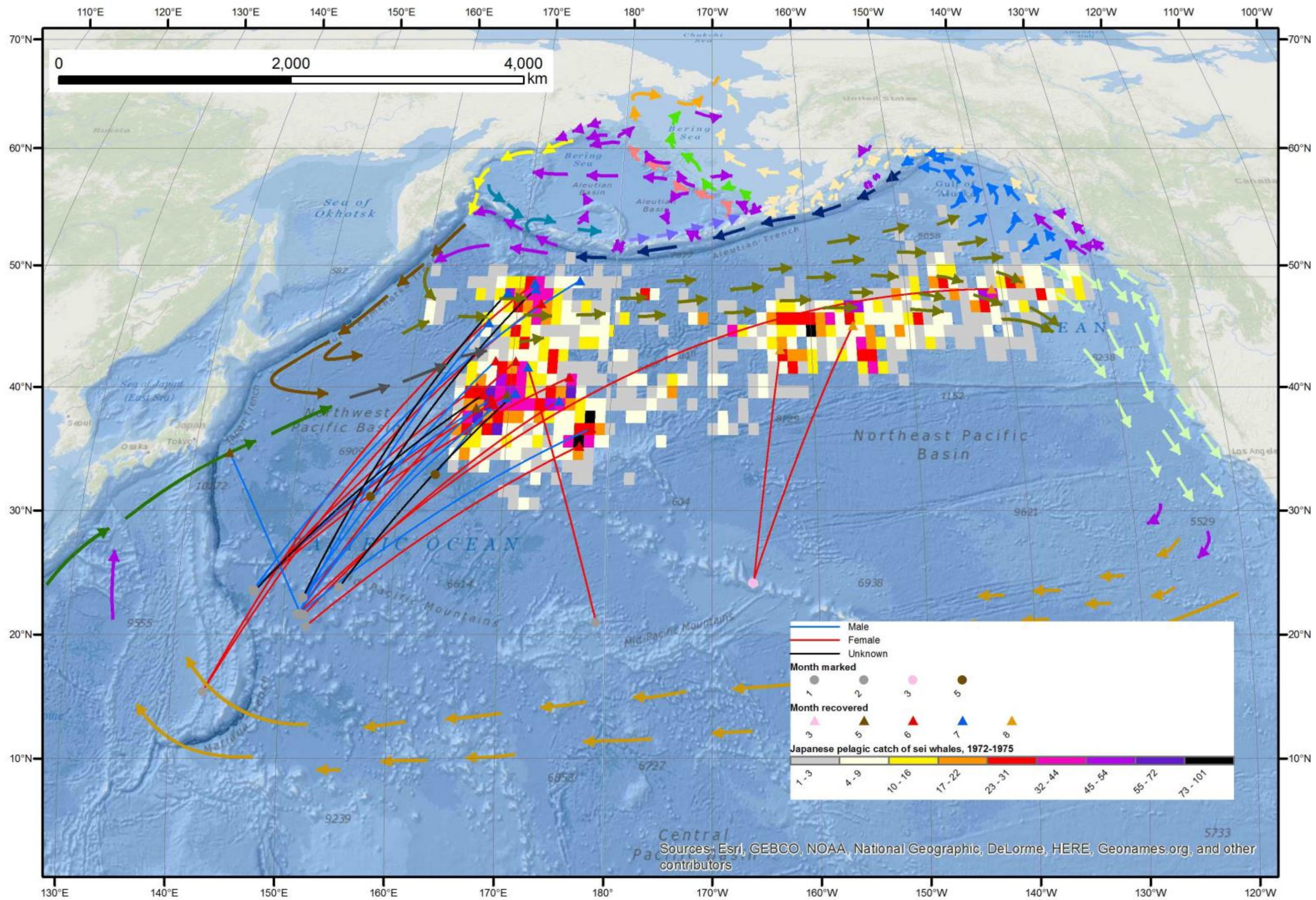

Fig. 11b. Recoveries of marks placed during or after 1972 in relation to Japanese pelagic catches (n = 5,395) of sei whales from 1972 through 1975.

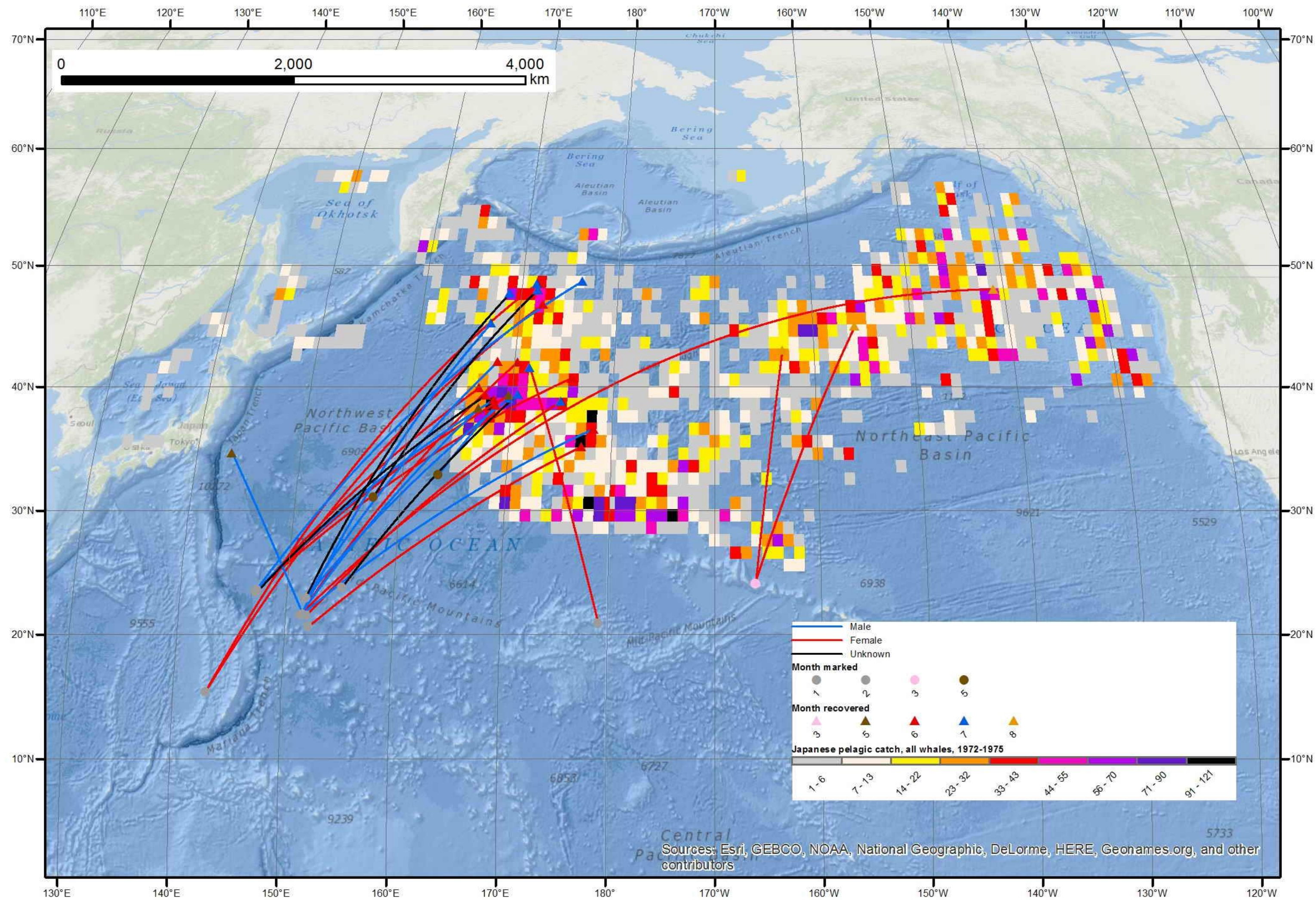

Fig. 11c. Recoveries of marks placed during or after 1972 in relation to Japanese pelagic catches of all whales (n = 14,889) from 1972 through 1975.

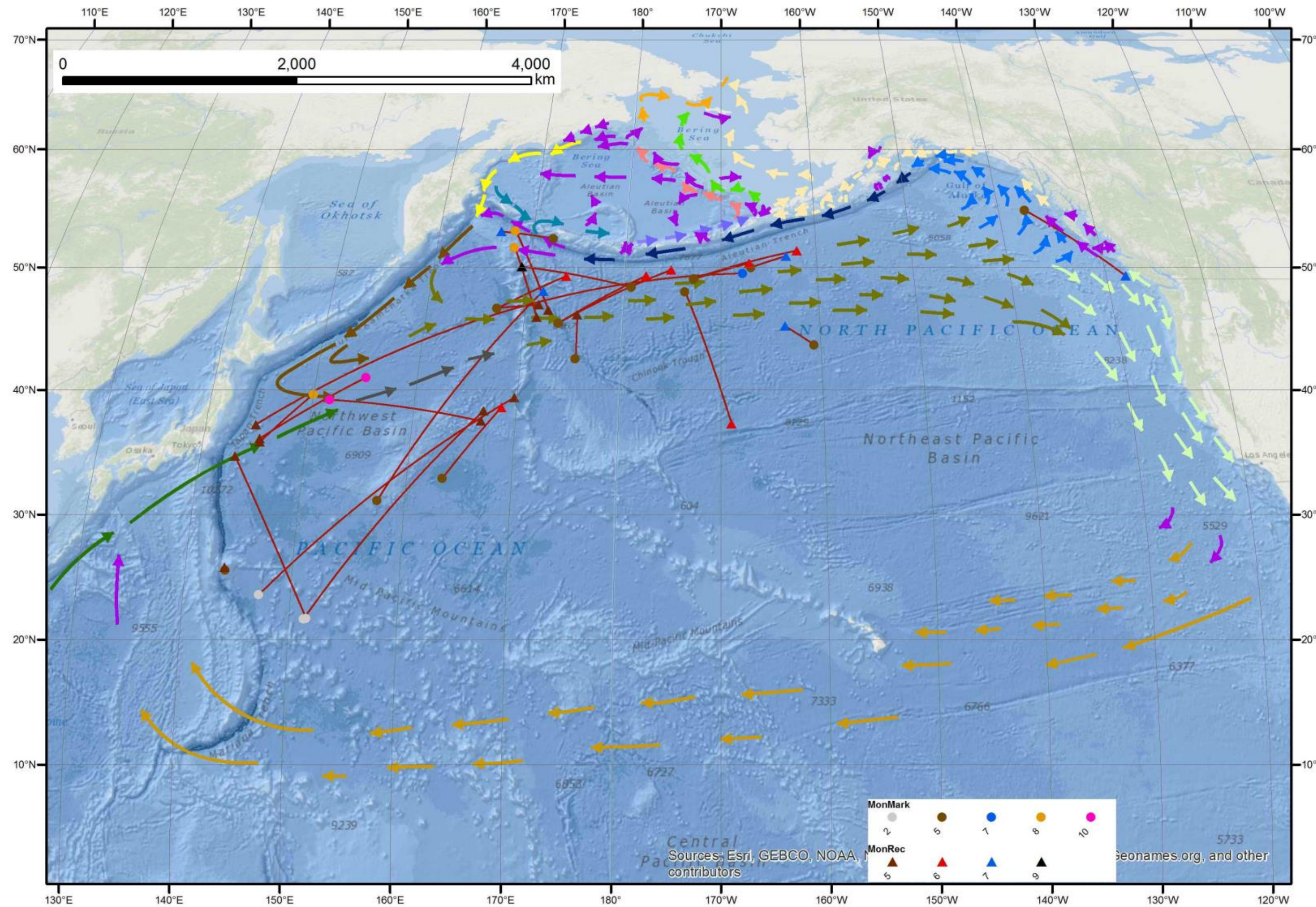

Fig. 12. Movements of whales marked or recovered in May (n = 25)

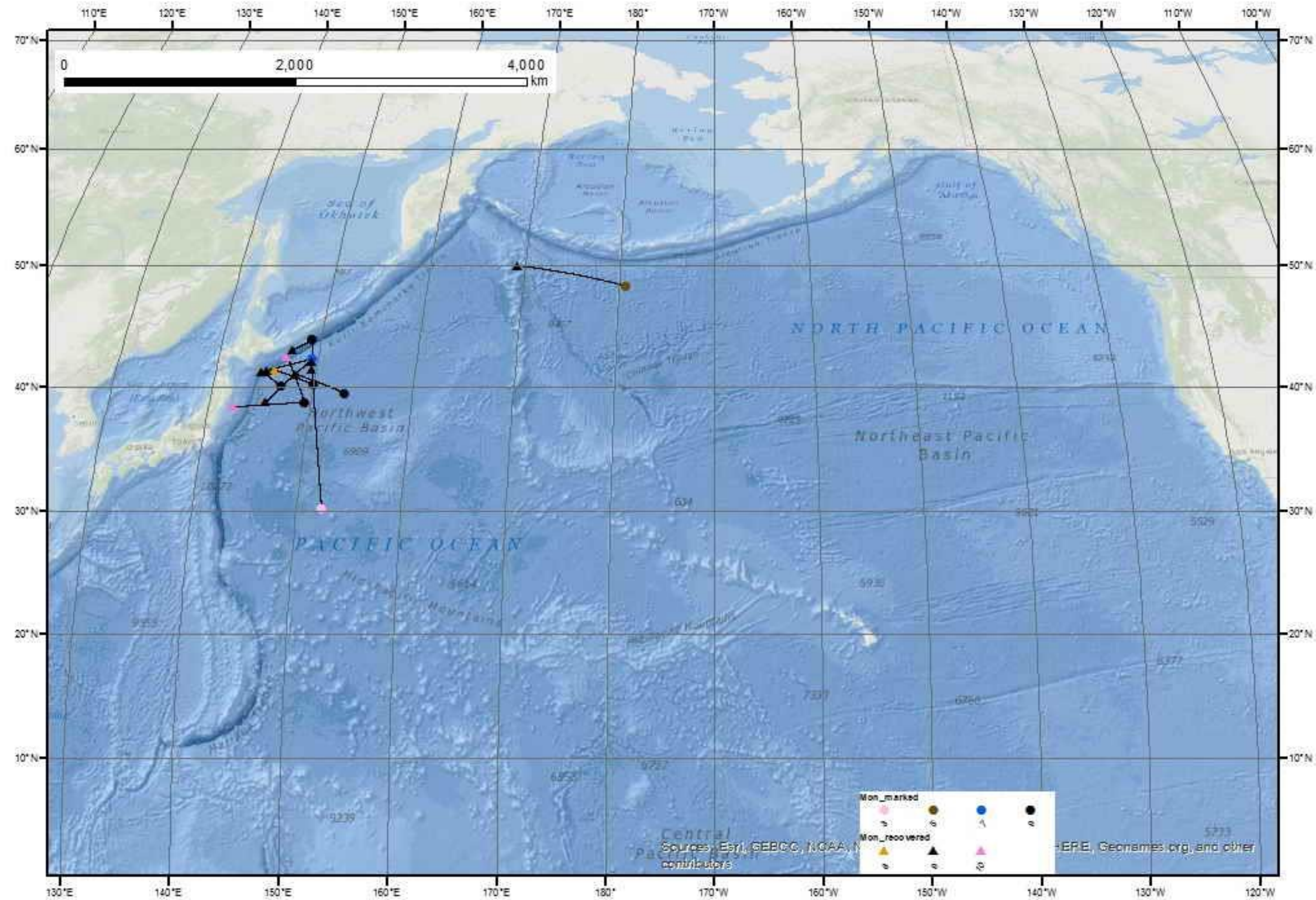

Fig. 13. Movements of whales marked or recovered in September (n = 11).

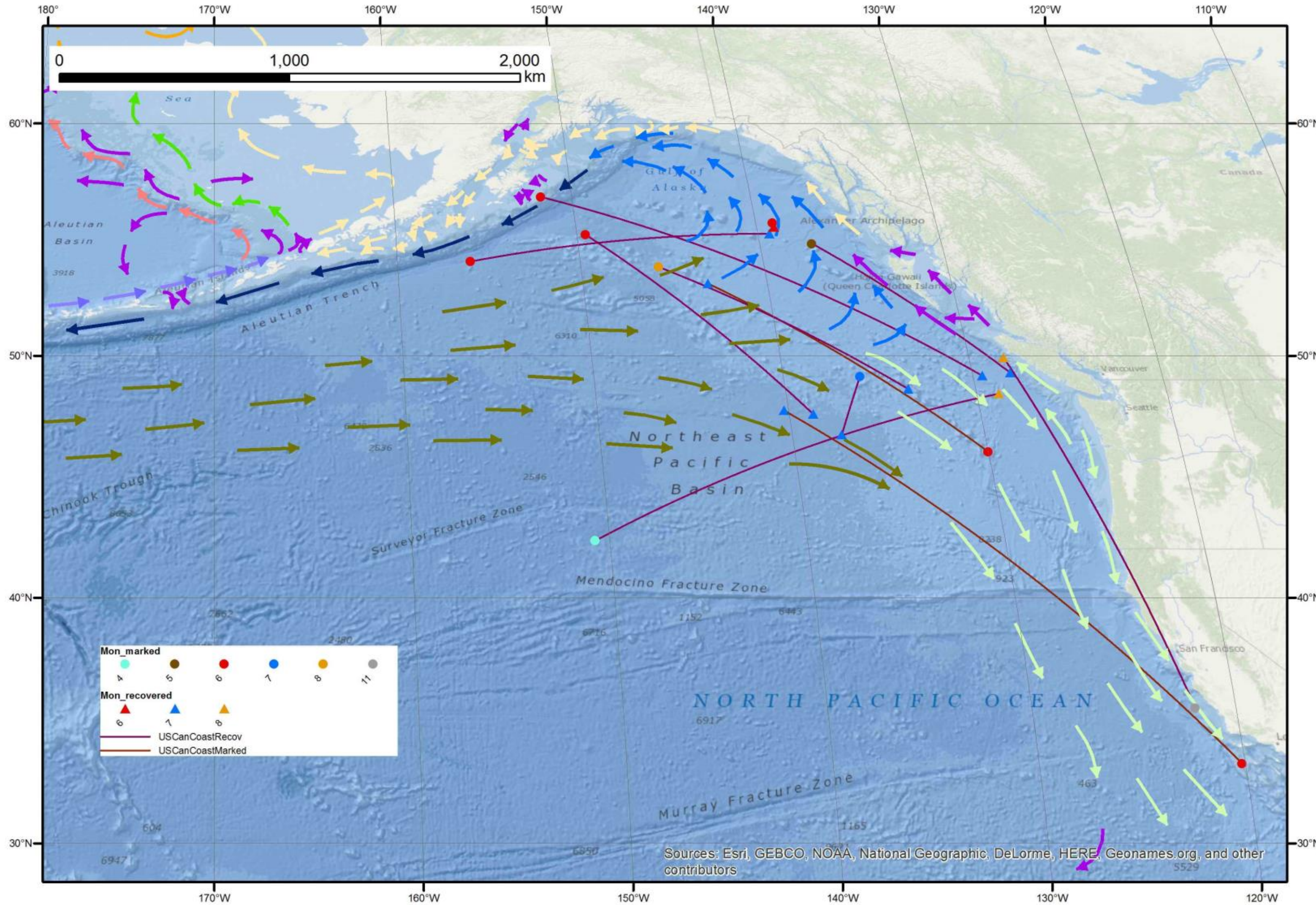

Fig. 14. Recoveries of marks placed or recovered east of 140° W (n = 11).

Figure 1. Study area boundary (thinner outer line) and planned cruise tracks (thick zig-zag line) for the 1994 Aleutian Island Marine Mammal Survey.

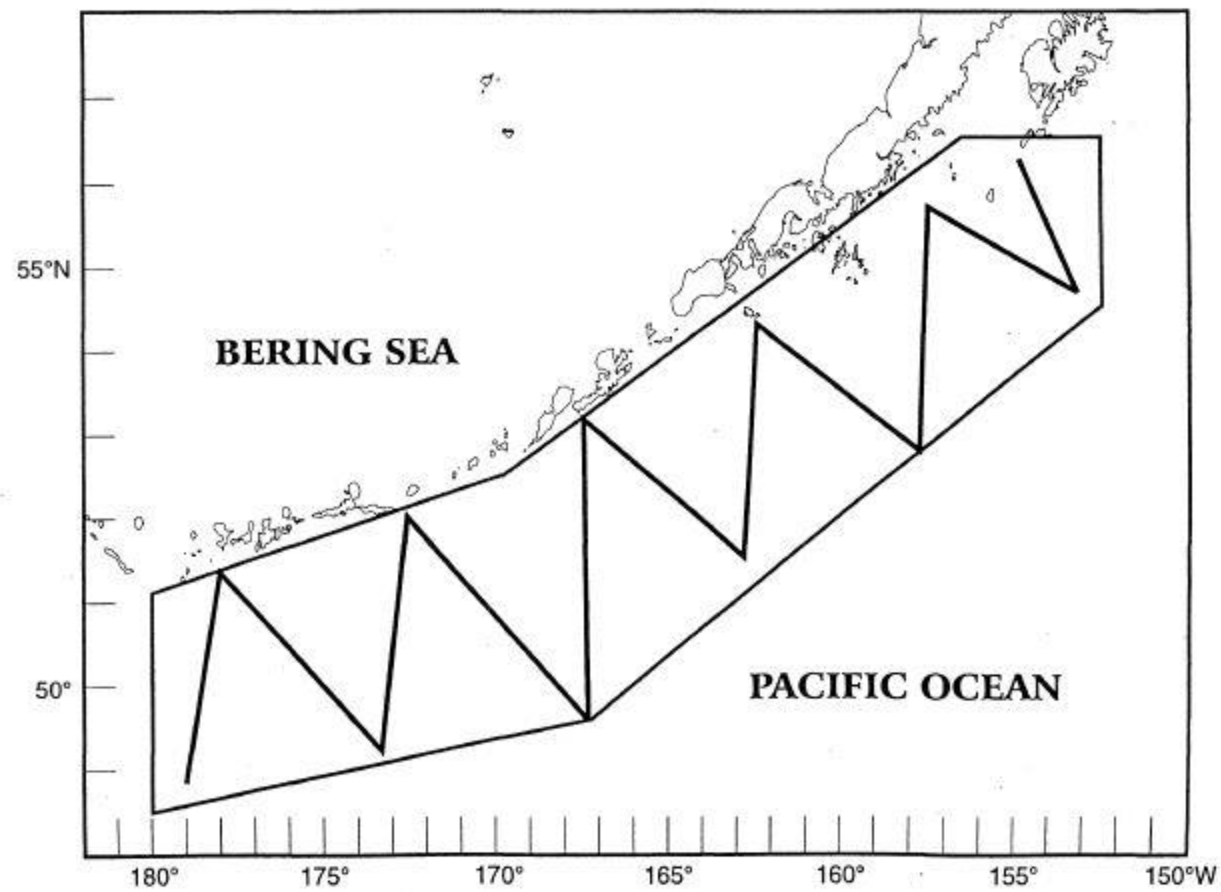

Fig. 15. Survey tracklines for the 1994 survey in the Aleutian Island/Aleutian Trench area (see text).

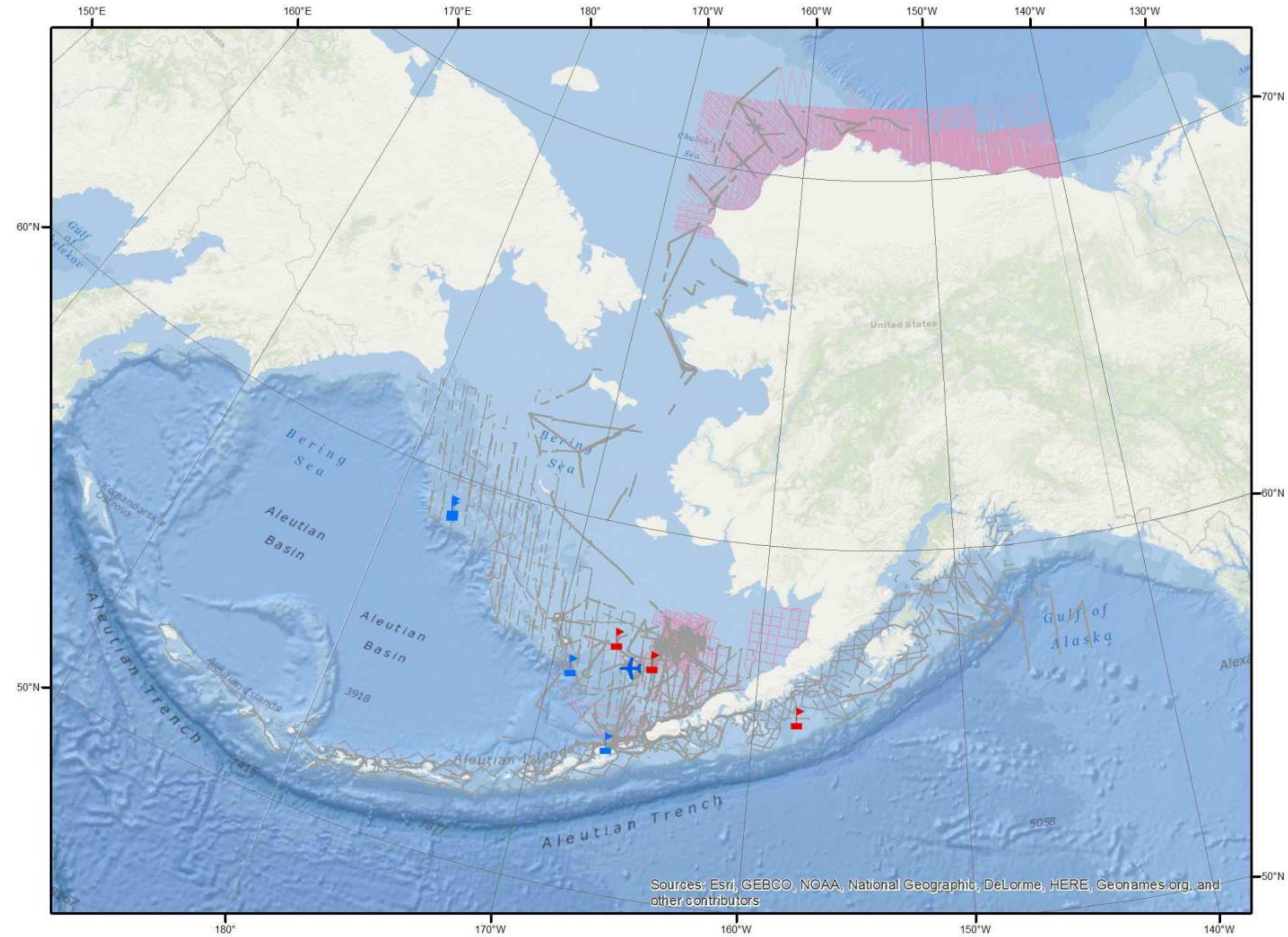

Fig. 16. Systematic shipboard surveys (gray lines) and aerial surveys (pink lines) conducted by researchers at the National Marine Mammal Laboratory from 1999 to 2012. A total of 3 sei whale groups were observed in June (red symbol) and 6 sei whale groups were observed in July (blue symbol).

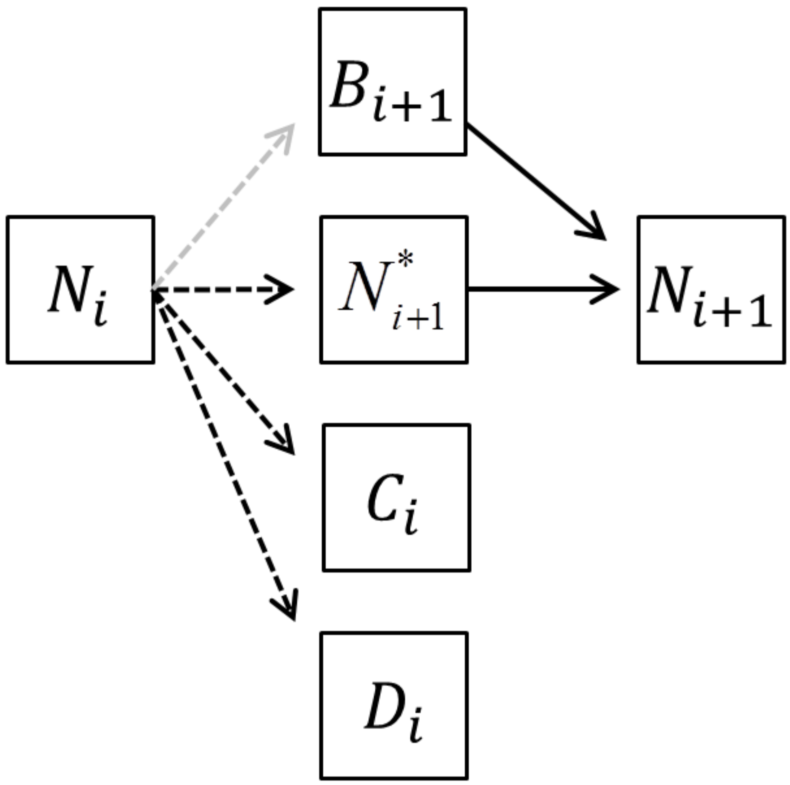

Fig. 17. A depiction of the state space process used to model annual changes in sei whale abundance, with dotted lines denoting probabilistic transitions and solid lines denoting deterministic transitions. Abundance in year *i* contributes to the number of new recruits to the population in year *i*+1 (B_{i+1}) through a Poisson birth process. The number of whales that are alive at the beginning of year *i* that survive to the next year (N^*_{i+1}), are harvested in year *i* (C_i), or die of "natural" causes (D_i; note this includes unreported catch), are modeled with a multinomial distribution. Finally, the number of whales alive at the beginning of year i+1 is given simply as $N_{i+1} = B_{i+1} + N^*_{i+1}$.

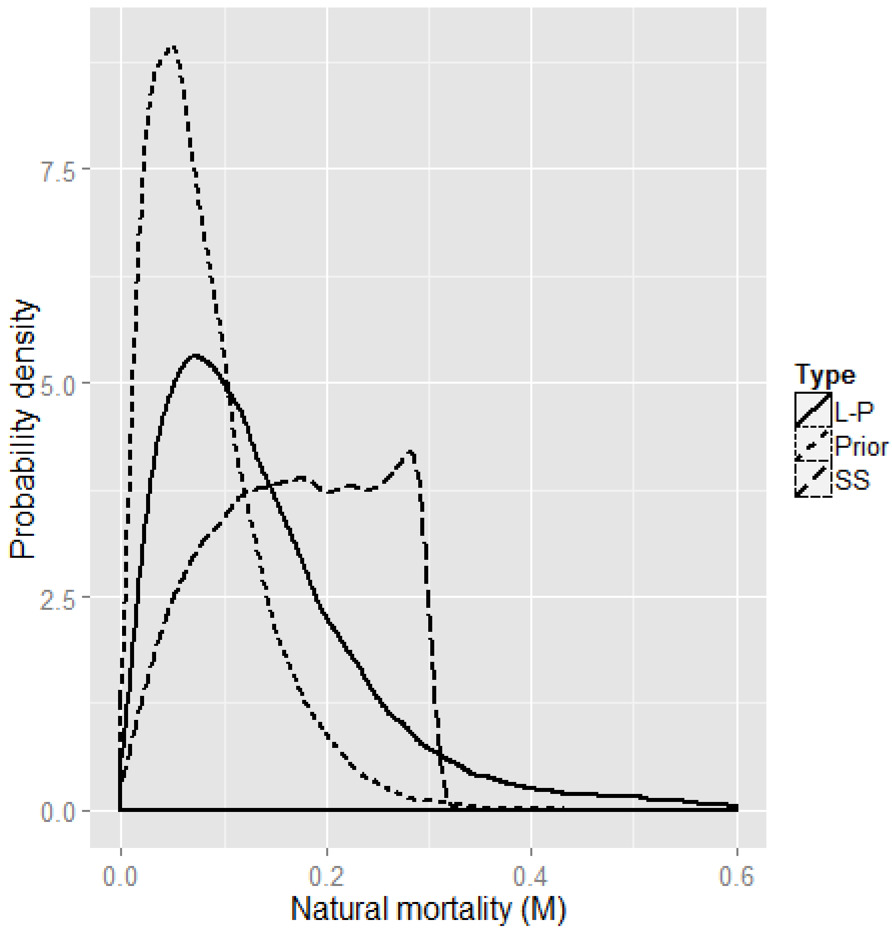

Fig. 18. Prior and marginal posterior densities for the instantaneous rate of natural mortality (*M*) for the pelagic stock of North Pacific sei whales, 1972-1975. The Lincoln-Petersen (L-P) only uses mark-recovery data to estimate mortality rates, while the state-space model (SS) uses both mark-recovery and fishery catch information during the estimation process. The estimated *M* includes both natural mortality and fisheries mortality from unreported sources (e.g., Soviet fisheries). State space estimates were constrained to have $M < 0.3$ to improve estimation.

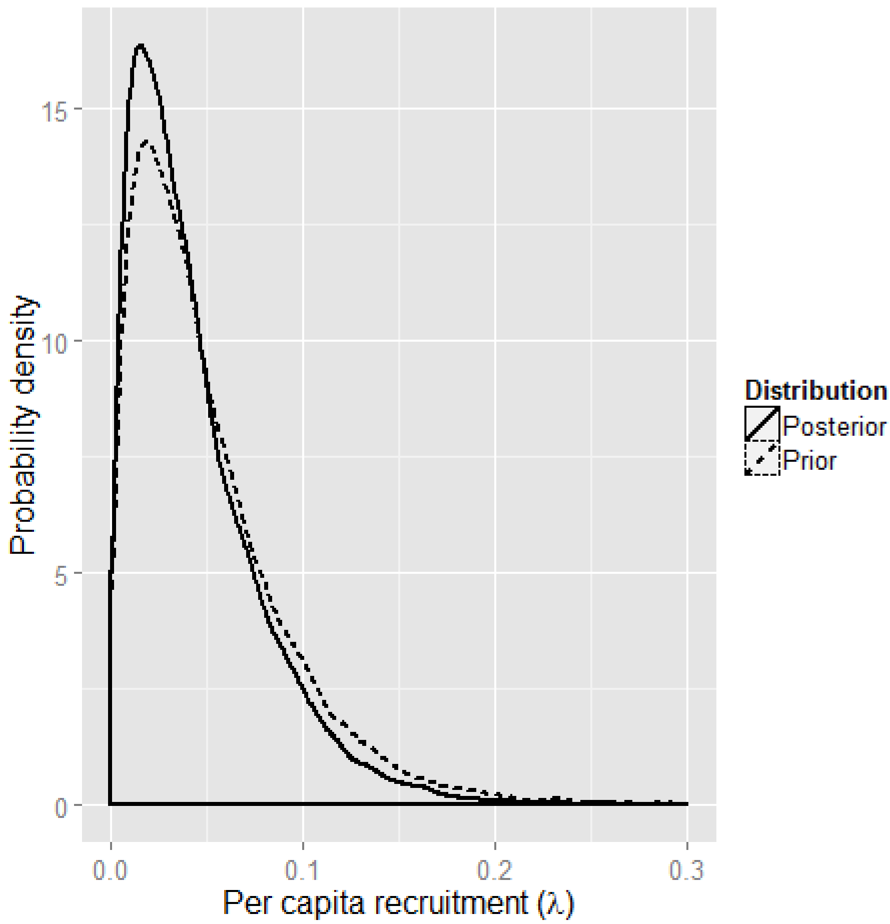

Fig. 19.. Prior and marginal posterior densities for per capita recruitment (λ) for the pelagic stock of North Pacific sei whales, 1972-1975, as obtained from a state-space model (SS) fit to mark-recovery and fishery catch data sets. That the two distributions are virtually identical suggests there is no information in the data to help estimate per capita recruitment.

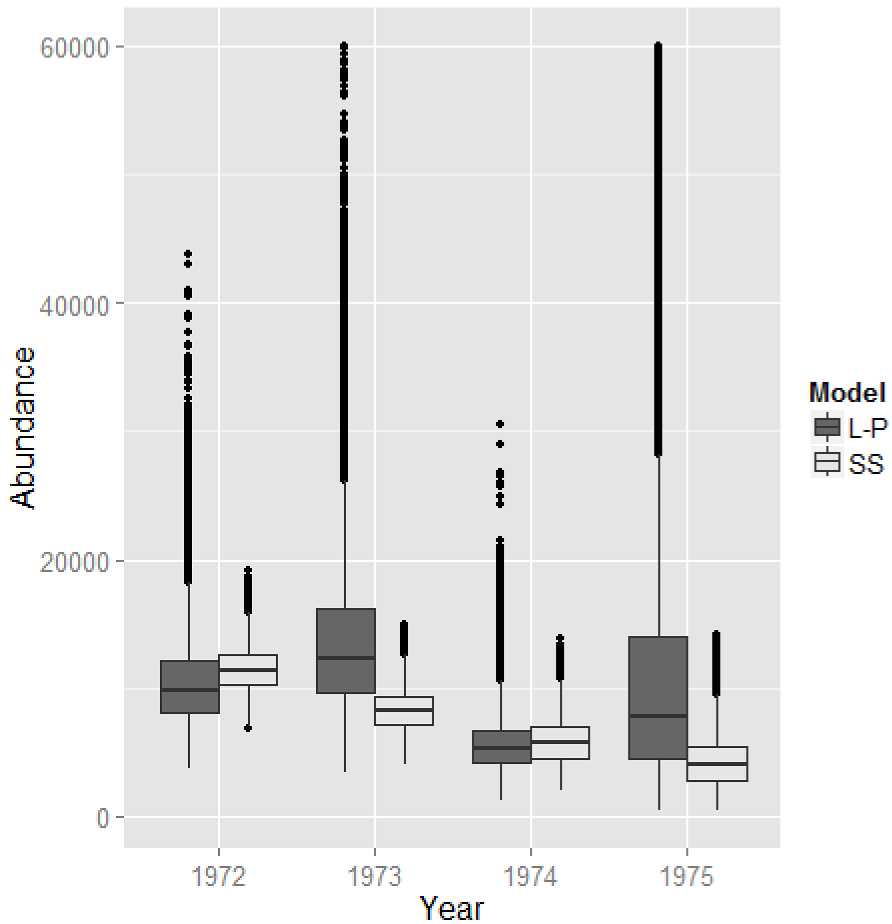

Fig. 20. Boxplots summarizing marginal posterior densities for the abundance of the pelagic stock of North Pacific sei whales, 1972-1975. The lower and upper limits of each box correspond to first and third quartiles, while whiskers extend to the lowest and highest posterior samples within 1.5 interquartile range units from the box. Outliers outside of this range are denoted with points (note that outliers were truncated at 60,000 for clarity of presentation). Horizontal lines within boxes denote posterior medians.

Appendix

Data, assumptions, and procedures used in Bayesian mark-recovery modeling of historical sei whale mark-recovery data, including alternative, full stock estimates

We fit two conceptually different models to historical sei whale marking and recovery (whaling) records. The first uses a modified Lincoln-Petersen estimator, while the second incorporates prior distributions for recruitment and survival processes within a state-space modeling framework. We now describe the data and models used, and provide details on the assumptions that needed to be made for each analysis.

Mark-recovery data

Our formulation for mark-recovery data largely follows estimation procedures for band recoveries of waterfowl described by Brownie *et al.* (1985). However, initial band recovery models were written in terms of annual survival and exploitation rate, whereas we find it easier to work with models parameterized in terms of continuous rates of hunting and natural mortality. As such, we used a parameterization of the Brownie model developed for use with fish populations (e.g., Hoenig *et al.* (1998a)). Specifically, let R_i be the number of releases of marks at the beginning of each year *i*, and m_{ij} be the number of those marks recovered in year *j*. We then write a likelihood function for mark-recovery data as

$$L_{m-r} = \prod_i \text{Multinomial}(\boldsymbol{m}_i; R_i, \boldsymbol{\pi}_i),$$

where $\boldsymbol{m}_i$ is the vector of mark returns corresponding to releases in year *i*, with an additional entry corresponding to the number of whales from release cohort *i* whose marks were never returned. Multinomial cell probabilities associated with release cohort *i* are given by $\boldsymbol{\pi}_i$, and are written as follows:

$$\pi_{ij} = \begin{cases} F_j/Z_j[1-\exp(-Z_j)] & i = j \\ F_j/Z_j[1-\exp(-Z_j)]\prod_{k=i}^{j-1}\exp(-Z_k) & i < j \\ 1-\sum_{j=i}^{T}\pi_{ij} & j = T+1 \end{cases}$$

Here, F_j gives the instantaneous rate of hunting mortality in year *j*, Z_j gives the total mortality rate in year *j*, and *T* gives the total number of years for which marks are collected. In fisheries applications, the total mortality rate, Z_j, is often written as $Z_j = F_j + M$, where natural mortality rate (*M*) is assumed constant over time.

Mark-recovery models make a number of assumptions about the target population (Brownie *et al.* 1985), and several of these are worth addressing with respect to the sei whale marking and recovery program conducted in the mid-1970s. First, our mark-recovery model assumes that marked animals completely mix with unmarked animals, such that marked and unmarked animals have the same hunting mortality and natural mortality rates. Essentially, we want the marked cohort to be "representative" of the entire population of sei whales in the North Pacific with respect to natural mortality and exploitation. Due to data sparseness, it was not possible to test this assumption definitively (e.g., with models permitting incomplete mixing of animals; see Hoenig *et al.* (1998b)). However, it seemed clear that pelagically marked whales had very different recovery probabilities than coastally marked whales (see section entitled *Post hoc likelihood ratio test for stock composition* in main text). In particular, it appeared that whales marked pelagically on wintering grounds were highly exploited, but whales marked in coastal areas were not subject to whaling during this time period. As such, our primary mode of inference (reported in the main text) was to estimate abundance for the pelagic stock only, limiting analysis to whales marked pelagically in winter only and assuming that all harvested animals came from this stock. However, at the end of this appendix, we also report estimates from an analysis of all marking records (assuming that all marked whales were members of a single stock and were all exposed to similar levels of whaling effort). This latter assumption is probably a poor one, but results are still presented for completeness.

It is worth noting that marking and recovery events for pelagically marked sei whales were temporally and spatially disassociated (Fig. 10a in the main text), and that recovery events for marked whales had a similar spatial distribution to those of all whales killed (compare Figs 9b and 10a in the main text). These observations suggest that the level of mixing was likely sufficient for us to treat marked whales as representative of the pelagic stock as a whole.

Unless auxiliary information on reporting rates are available, mark-recovery models also require that all marks, if found, are reported. However, this assumption only needs to be met if one wishes to separate natural and hunting mortality (see Pollock *et al.* (1995)). In the case of the sei whale, the mark reporting rate was likely extremely high for the Japanese whalers, who were responsible for the majority of the catches of sei whales. There is also evidence that the mark reporting rate for Soviet whaling was very low (Ivashchenko, AFSC, pers. comm.). Even in a paper published in 1975, Ohsumi and Masaki (1975) noted a very low “recovery efficiency” of 3.6% for sei whale marks reported by the Soviets. As such, estimates of natural mortality from our mark-recovery models will include some additional hunting mortality from non-reporting sources. Similarly, estimates of hunting mortality will be negatively biased in that they do not account for whaling operations that do not report marks. However, it is important to note that violation of the complete reporting assumption does not bias abundance estimation (see subsequent sections), provided that total sei whale catches are reported at the same frequency as marks from marked whales. The latter is likely a reasonable assumption, as the Soviet catch was not included in these analyses.

A final assumption particular to our hunting and natural mortality parameterization has to do with the timing of mortality events within the year. Strictly speaking, our formulation assumes constant hunting and natural mortality hazard rates (sensu Cox and Oakes (1984)), whereas during this time period, sei whales were hunted from May to August. However, a number of authors have investigated timing of capture and recovery events in a variety of scenarios (e.g., Hoenig *et al.* (1998a), and O'brien *et al.* (2005)) and have noted little consequence on resulting estimates.

Lincoln-Petersen abundance estimation

A simple approach to generating abundance estimates ($\widehat{N}_i$) from catch records and estimates of exploitation is to simply divide the total harvest in a given year *i* (C_i) by an estimate of the exploitation rate in year *i* ($\hat{u}_i$):

$$\widehat{N}_i = C_i/\hat{u}_i.$$

For instance, Diefenbach *et al.* (2004) used this approach to estimate black bear population size in Pennsylvania. For our mark-recovery model, exploitation rate is defined as

$$\hat{u}_i = \hat{F}_i/\hat{Z}_i[1 - \exp(-\hat{Z}_i)].$$

For details on how we generated a posterior predictive distribution for $\widehat{N}_i$, see the later section *Prior distributions and Bayesian computation*.

State-space abundance estimation

Although the Lincoln-Petersen procedure produces unbiased abundance estimates when relevant mark-recovery model assumptions are met, there is no guarantee that consecutive estimates will be biologically coherent. For instance, sampling error can easily result in abundance estimates that increase substantially from one year to the next, despite biological constraints limiting recruitment (Conn *et al.* 2008). These constraints are considerable for a long-lived species such as sei whales. An alternative is to consider a latent, state-space model for abundance, where changes in abundance from one year to the next are an explicit function of survival and recruitment processes.

We implemented such a model by embedding a population dynamics (Fig. 15 in the main text) into the estimation procedure. In particular, we model the number of whales exhibiting different survival outcomes (i.e., survived, dead in harvest, dead of "natural" causes) at the end of a year according to a multinomial distribution. Specifically, letting the bracket notation $[A|B]$ denote the conditional probability distribution of A given B, we set

$$[N_{i+1}^{*}, C_i, D_i | N_i, F_i, M] = \text{Multinomial}(N_i; \{\exp(-Z_i), u_i, 1 - u_i - \exp(-Z_i)\})$$

Following Conn *et al.* (2008), we modeled the number of new recruits in the population at the beginning of year i+1 (B_{i+1}) using the Poisson formulation

$$[B_{i+1}|N_i, \lambda] = \text{Poisson}(\lambda N_i),$$

where λ denotes a per capita recruitment parameter, here assumed to be time invariant. A complete data likelihood (sensu Dempster *et al.* (1977)) for abundance can then be specified hierarchically:

$$L_N = \prod_{i=2}^{T-1} \{[B_{i+1}|N_i, \lambda][N_{i+1}^*, C_i, D_i|N_i, F_i, M]\}.$$

Simultaneous inference using both mark-recovery and total whale harvest data can then be performed using the product likelihood $L_{comb} = L_{m-r} L_N$. Technically, multiplying the likelihoods together in this fashion requires that data be independent, which is not the case for the sei whale data as marked whales are included in the mark-recovery dataset as well as the total catch data. However, Conn (2007) showed that dependence between the two datasets is only really problematic when marked animals make up a large proportion of the total catch, which is not the case here.

Prior distributions and Bayesian computation

The state space likelihood includes a large number of latent parameters (i.e. N_1, B_i, N_i^*), which makes conventional analysis via maximum likelihood prohibitive. In addition, the sparseness of data available would likely make separately identifying all model parameters difficult or impossible. An alternative, which also allowed us to constrain life history to plausible parameter spaces, was to specify prior distributions for model parameters and to conduct a Bayesian analysis (e.g., see Gelman *et al.* (2004)). In particular, we needed to set prior distributions for the following set of parameters: $\{N_1, F_i, \lambda, M\}$. We used the scale prior (i.e., $N_1 \propto 1/N_1$) for initial abundance, as suggested by Link (2013). For F_i, we used a flat, improper prior on positive values of F_i (i.e., $F_i \propto 1$ for $F_i > 0$ and zero otherwise), suggesting no prior knowledge about likely ranges of hunting mortality. For natural mortality and per capita recruitment rate, we used life history information to impose informative priors.

Masaki (1976) reported that the annual instantaneous natural mortality rate for North Pacific sei whales was 0.054 for males and 0.06 for females. Horwood (1987) reviewed a variety of mortality rate estimates for sei whales and concluded that those by Masaki (1976) were the most comprehensive and had reasonable sample sizes. Horwood (1987) assumed that "several hundred animals contributed to each of Masaki's estimates". However, the natural mortality rate estimated in the present study also includes mortality due to unreported Soviet Discovery mark recoveries.

We thus set the prior distribution for $\widehat{M}$ to be Gamma(2,25)- which has an expected value of 0.08 but puts substantial mass on likely values (Fig. 16 in the main text). For analysis of the pelagic stock (the analysis reported in the main text), initial runs showed instability with the value of $\widehat{M}$ wandering off to implausibly high levels within Markov chain Monte Carlo (MCMC) simulations. For the pelagic analysis, we thus imposed the additional constraint that $\widehat{M} < 0.3$.

For per capita recruitment, we used an assumed sex ratio of 0.5, an average interbreeding interval of 2.5 years, an average number of calves produced (1.0), and survival up to the age at first breeding (here assumed to be 8 years) to help define a likely range of values for λ. Substituting in different values of Z into the equation

$$E(\lambda) = 0.2 \exp(-8Z)$$

provides an equilibrium solution to the expected per capita recruitment (i.e. assuming total survival was Z for all female age classes in all preceding years). As such, it is just an approximation; female survival likely varies by age and exhibited marked declines leading up to the years of these surveys.

Nevertheless, plugging in different values of Z proves illuminating in defining expected levels of annual recruitment: substituting in $Z = 0.065$ produces $E(\lambda) = 0.12$; substituting in $Z = 0.2$ (combining natural mortality with a relatively high level of hunting mortality) produces $E(\lambda) = 0.04$; substituting in $Z = 0.4$ (an extremely high mortality rate) results in $E(\lambda) = 0.01$. Evidently a prior distribution for λ should encompass all these values; we selected a Gamma (1.5,30) distribution for as a prior on λ (Fig. 17 in the main text).

The likelihood L_{comb}, together with our prior distribution specifications, provide the necessary structure to perform Bayesian inference. We constructed an MCMC sampler that used Metropolis-within-Gibbs updates (Gelman *et al.* 2004) to generate samples from the joint posterior distribution of model parameters. This approach works by cyclically sampling each parameter from its so-called full conditional distribution. Candidate proposals were generated as uniform deviates centered on the prior MCMC iteration's parameter value, with a standard deviation chosen to yield acceptance rates between 0.3 and 0.4 as suggested by Gelman *et al.* (2004). We ran separate analyses to generate Lincoln-Petersen and state-space estimates of abundance; for the Lincoln-Petersen approach, we computed a posterior predictive distribution for abundance by calculating $\widehat{N}_i = C_i/\hat{u}_i$ at each iteration of the Markov chain. Preliminary runs and diagnostic plots indicated good mixing for the mark-recovery model used to generate Lincoln-Petersen estimates; for this model, we conducted inference using two Markov chains which were each run for 55,000 iterations, with the first 5,000 iterations discarded as a burn-in. After inspecting each chain to help ensure convergence to a stationary distribution, values from the two chains were combined to produce a total sample of 100,000 from the joint posterior. In contrast to the basic mark-recovery model, our MCMC sampler for the state-space model exhibited poor mixing; in this case, we ran each of two Markov chains for 10.1 million iterations, discarding the first 100,000 iterations as a burn-in. Recording only one out of every 1,000 parameter values to help save disk space, and combining samples from the two chains resulted in a sample of 20,000 from the joint posterior.

All analysis was conducted in the R programming environment (R Development Core Team 2013). Script files to implement our custom-built MCMC sampler are available as an online supplement.

Assumptions required

Our state-space estimation approach made a number of assumptions that are worth addressing here. First, we had to develop informative priors for natural mortality and per-capita recruitment. Although natural mortality was informed by the data (as evidenced by shifts to the right in the posterior distribution; Fig. 17 in the main text), per capita recruitment was entirely driven by the prior (Fig. 18 in the main text). In some modelling scenarios, this is not a desired outcome because it imbues results with subjectivity. However, in our case, we had reasonable auxiliary data on reproductive life history to help formulate a reasonable prior. We would argue that it is preferable to include such information in the estimation process to help constrain population dynamics to reasonable values.

Second, our population dynamics model was quite simple, with single mortality and recruitment rates applied regardless of age or sex class. In reality, survival and recruitment are likely a function of the age and sex composition of the population. However, we had no real information to help estimate such relationships. We view our solution as a pragmatic one developed in the same spirit as biomass dynamic models commonly used in data-poor fisheries (see e.g., Quinn and Deriso (1999)).

Finally, our analysis required the assumption that hunting and natural mortality parameters were the same for marked whales as for unmarked whales. For the pelagic stock, we note that the marking and hunting locations were separated both spatially and temporally, which should help break up dependence between marking and recovery events. However, this does not guarantee independence. If marked whales are more likely to be recovered than unmarked animals, our estimates of abundance could be biased low. However, the decreasing trend in abundance estimates is likely robust to violations of this assumption.

Single stock estimates

Here, we provide estimates of population size and demographic parameters for the case where all marking data are analyzed. That is, we assume that (i) all marked sei whales are part of the same stock and that (ii) all sei whales are exposed to the same level of whaling effort. These validity of these assumption seems questionable given the available data on stock structure, but estimates may still be reasonable if the distribution of marks among pelagic and coastal stocks is reflective of the abundance of animals in each stock (an admittedly untestable condition). Nevertheless, these estimates are presented for completeness and for possible comparison with previous work (e.g., Masaki 1976).

Table A.1. Annual estimates of abundance (*N*), instantaneous hunting mortality (*F*), and number of new recruits (*B*) for North Pacific sei whales, 1972-1975 from a single stock analysis (all marking data analyzed). Subscripts denote which model was used to estimate parameters (L-P = Lincoln-Petersen, SS = state-space). Annual recruitment estimates were only available for the state-space model. Table entries give posterior medians, together with posterior standard error (in parentheses).

	Year			
Parameter	1972	1973	1974	1975
N_{L-P}	12267 (4443)	17974 (8656)	8953 (3396)	17628 (56777)
N_{SS}	15297 (2494)	11696 (2396)	9032 (2792)	7132 (3135)
F_{L-P}	0.18 (0.06)	0.10 (0.04)	0.14 (0.05)	0.03 (0.02)
F_{SS}	0.16 (0.03)	0.17 (0.05)	0.15 (0.09)	0.07 (0.11)
B	N/A	594 (535)	447 (468)	331 (428)

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