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# Estimates of abundance and migratory destination for North Pacific humpback whales in both summer feeding areas and winter mating and calving areas

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**ABSTRACT**

The first comprehensive photo-identification study of humpback whales throughout the North Pacific occurred in 2004-2006 during the SPLASH project (Structure of Populations, Levels of Abundance and Status of Humpbacks). Total abundance for the entire North Pacific was estimated by Barlow et al. (2011) to be 21,808 (CV=0.04).  Here we estimate abundance within all sampled winter and summer areas in the North Pacific, as well as estimate migration rates between these areas. Based on genetic analyses (Baker et al. 2013) and an examination of migratory destinations, winter areas were defined to be (1) Asia (including Ogasawara, Okinawa, and the Philippines), (2) Hawaii, (3) Mexico, and (4) Central America, and summer areas were defined to be (1) Kamchatka, Russia, (2) the Aleutian Islands and Bering Sea (including the Commander Islands and Gulf of Anadry in Russia), (3) the Gulf of Alaska, (4) Southeastern Alaska and northern British Columbia, (5) southern British Columbia and Washington, and (6) California and Oregon.  Photo-identification data were collected for three years (2004-06) in winter areas and for two years (2005-06) in summer areas. A multi-strata mark recapture model was fit to the photo-identification data using a six-month time-step, with the four winter areas and the six summer areas defined to be the sample strata.  The strongest migratory connection was between the Kamchatka feeding area (N=1,111, CV=0.37) and the Asia breeding area (N=1,059, CV=0.08).  The feeding areas in Alaska, as well as northern British Columbia, support the majority of the North Pacific population, including the Aleutian Islands and Bering Sea (N=2,427, CV=0.20), the Gulf of Alaska (2,089, CV=0.09), and Southeastern Alaska and northern British Columbia (N=6,137, CV=0.07).  Those feeding areas all have a strong migratory link (Psi (probability of movement from one strata to another) > 0.86) to Hawaii (N=11,398, CV=0.04), with the link between Southeastern Alaska/northern British Columbia and Hawaii (psi=0.94, CV=0.17) particularly high.  In return, nearly all Hawaiian whales migrate to Alaska and northern British Columbia. The migratory destination of whales that winter in Mexico (N=3,264, CV=0.06) is the most diverse, with whales going to all feeding areas except Kamchatka, with the highest proportion going to California and Oregon (Psi=0.74, CV=0.06). Nearly all Central American whales (N=411, CV=0.30) migrate to California and Oregon to feed (Psi=0.92, CV=0.06), but the California/Oregon feeding area (N=3,734, CV=0.11) represents primarily whales that migrate to Mexico (Psi=0.90, CV=0.16), with the remainder migrating to Central America (Psi=0.10, CV=0.45).

**INTRODUCTION**

Humpback whales (*Megaptera novaeangliae*) occur throughout the North Pacific Ocean, migrating from winter breeding and calving areas, such as Mexico and Hawaii, to summer feeding areas, such as California and Alaska.  Whaling for humpback whales in the North Pacific has existed for centuries, and at various times has occurred throughout much of the range of the species in the North Pacific (Reeves and Smith 2006).  Catch records exist for some coastal whaling areas on the main islands of Japan dating back to the mid-1600s, with >2,600 whales known to be taken between 1650 and 1900, primarily using nets (Omura 1986).  More

modern coastal whaling operations operated in the first half of the 20th century, with large catches in Japan (>2,800, including Okinawa and Ogaswara), Alaska and northern British Columbia (>7,500 whales), southern British Columbia and Washington (>3,900), California (>2,100, including catches in the 19th century), and Baja, Mexico (>2,200) (Ivashchenko et al. 2015). Post World War II, pelagic factory ship whaling by Japan and the Soviet Union killed humpback whales primarily in Alaska (>7,500) but also in Asia, Russia, and along the west coast of North America. The total number of humpback whales killed by whaling in the 20th century in the North Pacific is estimated to be ~29,000 (Ivashchenko et al. 2013, 2015). The International Whaling Commission set the quota for humpback whales to zero in 1966 because their populations were thought to be severely depleted (Gambell 1976; Johnson and Wolman 1984), but it is now known that illegal whaling by the Soviet Union, which started in  continued until 1972 (Ivashchenko et al. 2011, 2013). More than three decades later, the abundance of humpback whales throughout the North Pacific is of great interest to begin to determine whether they have recovered from whaling.

One of the primary methods for estimating the abundance of whale populations is by mark-recapture methods applied to either photo (Katona et al. 1979) or genetic (Palsboll et al. 1997) identification data. Photo-identification studies of North Pacific humpback whales have been conducted in a variety of locations, and in some areas for over several decades.  The first comprehensive photo-identification study of humpback whales throughout the North Pacific occurred in 2004-2006 during the SPLASH project (Structure of Populations, Levels of Abundance and Status of Humpbacks).  The SPLASH project consisted of over 50 research groups and more than 400 researchers working in 10 countries collecting both photo-identification data and genetic samples, with three winter seasons (2004, 2005, and 2006) and two summer area seasons (2004 and 2005).

Results from SPLASH include studies on genetic population structure (Baker et al. 2013), Persistent Organic Pollutants (Elfes et al. 2010) and stable isotopes (Wittenveen et al. 2009).  Additionally, Barlow et al. (2011) analyzed SPLASH photo-identification data and estimated abundance for the entire North Pacific as 21,808 (CV=0.04), and conducted simulations for bias correction, resulting in a final bias-corrected estimate that is slightly lower (21,063). From that work they concluded that the overall humpback whale population in the North Pacific has continued to increase from it's post-whaling level.

Regional estimates of abundance in both winter breeding and calving areas (hereafter termed "winter areas") and summer feeding areas (hereafter termed "summer areas") are of interest for a number of reasons.  The winter areas represent the breeding populations, and there are at least four main winter areas with large concentrations of humpback whales – Central America, Mexico, Hawaii, and Asia (Baker et al. 2013). Breeding populations are the fundamental demographic units whose recovery from depletion by whaling should be monitored. Population stocks of North Pacific humpback whales under the US Marine Mammal

Protection Act (MMPA) are defined by breeding areas (e.g., Caretta et al. 2015), and therefore abundance in the winter area represents abundance of the stock. Moreover, proposed designation of Distinct Population Segments under the US Endangered Species Act (ESA) are also based on winter areas (80 FR 22303, and see Bettridge et al. 2015 for further background), so abundance of these units is relevant to potential changes in listing status under the ESA.

The abundance in summer areas is also of importance as they represent the fundamental ecological units of North Pacific humpback whales, where aggregations of whales are tied to the abundance of their prey. Most summer areas in the North Pacific represent mixtures of whales from more than one breeding population, so most summer areas do not correspond one-to-one with single breeding populations (Baker et al. 2013). Despite this, summer areas show strong genetic differentiation across the North Pacific, primarily due to a strong matrilineal fidelity to single feeding areas, with relatively little interchange between regions detected from photo-identification studies (Baker et al. 2013, Calambokidis et al. 2001). Therefore, these regions will also function as demographically independent units, and the population dynamics of these regions will be closely tied to the ecology and abundance of prey in these areas, whereas the population dynamics of many of the breeding populations will be tied to the ecology of several regions. Additionally, many of the current threats facing humpback whales, such as fisheries bycatch, occur in summer areas (e.g., SE Alaska, Allen and Angliss 2015), so it is important to evaluate the effect of human impacts relative to local abundance in these summer areas.

Regional estimates of abundance for humpback whales have been made for many of the winter areas including Mexico, Hawaii, and Asia, but abundance has not been estimated previously for Central America. Prior to SPLASH, summer feeding-area abundance estimates have been made for some areas where photo-identification studies have taken place for many years, including California, Southeastern Alaska, the Shumagin Islands, Alaska, and the southeastern Bering Sea shelf. However, comprehensive estimates are lacking for many of these regions, and some areas, such as Russia, have never been previously surveyed for abundance.

Here we conduct a comprehensive analysis estimating abundance for all winter and summer areas from the SPLASH photo-identification data. We use an integrated spatial multi-strata mark-recapture model to simultaneously estimate abundance for all winter and summer areas sampled during the SPLASH project. We contrast these with comparable estimates using standard closed mark-recapture models using just winter area data (3 samples) or just summer area data (2 samples). These represent the first estimates of abundance for Central America and Russia. These also represent the first estimates of abundance for Asia that include the Philippines, the first estimate for the Bering Sea region that includes the Aleutian Islands, and the first comprehensive estimate for the entire Gulf of Alaska. For some other areas, the greater spatial coverage and larger sample sizes (e.g., Southeastern Alaska and Northern British Columbia) make these the best estimates of abundance that have

been calculated to date. Furthermore, abundance has never been estimated simultaneously across the winter or summer areas using identical methods. The multi-strata model also provides estimates of movement parameters that provide the first quantitative analysis of the migratory destinations of each winter or summer area. The movement parameters, in combination with winter area abundance estimates, are also used to provide the first estimates of the proportion of whales from each breeding population that are found in each summer area.

**METHODS**

The SPLASH project was designed to sample as much of the known winter and summer areas of humpback whales in the North Pacific that was practical. Here we describe the field protocols, the regional stratification scheme used for abundance estimation, and the mark-recapture statistical modeling approach.

*Field Protocols*

Photographs were taken of the ventral side of humpback whale flukes using digital SLR cameras. Most photographs were taken from 6-8 m boats making day trips from shore. Small boat sampling locations included Ogasawara, Okinawa, and the Philippines in the western Pacific, the Hawaiian Islands, the Revillagigedo Archipelago, Baja California, and mainland Mexico, Guatemala, El Salvador, Nicaragua, and Costa Rica in Central America, the US West Coast (from many different ports), British Columbia (mostly west of Vancouver Island and the mainland coast), and Alaska (Southeastern Alaska, Prince William Sound, Kenai Peninsula, Kodiak Island, Barren Islands, Shumagin Islands, and Unalaska Island). A variety of larger vessels were used to sample more remote and offshore locations, often together with small boats launched from those ships. Sampling effort was allocated based on *a priori* appraisal of the relative number of humpback whales in each sampling area, as well as the availability of researchers and resources. More details, including a map of ship effort, are available in Barlow et al. (2011).

Sampling protocols were established for all participants, and fluke photographic protocols were designed to avoid heterogeneity in the likelihood of sampling different individuals or demographic classes and thereby to avoid biases in mark-recapture abundance estimates. Most importantly, to avoid under sampling whales that raise their flukes out of the water less often, participants were directed to stay with a group until identification photographs had been obtained from all animals in the group, or until a minimum of three dive series or 30 min had passed, whichever occurred first. For multiple groups of whales encountered in close proximity, participants were instructed to photograph whales while moving consistently through the area, in order to obtain as large and representative a sample of all animals as possible. Sampling protocols also specified a set of data to be collected by all SPLASH participants, including information on search effort and each humpback whale that was encountered. Further details are available in Barlow et al. (2011).

A best fluke photograph from each encounter was selected by the data collection group or a regional coordinator, and, the best photograph from each encounter was compared with all others within that season and region, even if the best photograph was of low quality. These regional catalogues, including the identified best photograph of each whale within the region, were submitted each season to the overall SPLASH coordinator for between-region and between-season matching. The SPLASH data coordinator rated each fluke photograph for pigmentation pattern (5 ranked categories from all white to all black) and photographic quality (ranked 1-5 on each of five features: proportion visible, vertical angle, lateral angle, focus/sharpness, and exposure). To ensure consistency, photographs were rated by the same person throughout this study.  Photographic matching was conducted by a team of six people experienced in matching humpback whale photographs.  Several protocols were developed to expedite matching, including restricting the number of color categories a fluke was compared against.

To minimize matching errors (i.e., *sensu* Friday et al. 2008), photographs with a score of four or five in any of the five measures of photographic quality (e.g., eliminating flukes with less than 50% visible) and photographs with a score of three in four (or more) measures of quality were not used in the analysis. Suspected matches were verified by a second matcher. The error rate for undiscovered matches was calculated by two methods, and was estimated to be ~8.6% (Barlow et al. 2011), similar to the match error rate found in a previous study using similar quality scoring criteria as employed here (Calambokidis et al. 1997).

*Regional strata*
During the SPLASH project, sample locations were categorized into pre-determined spatial areas, based primarily on a combination of discrete sampling areas and areas with a hiatus (or nearly so) in distribution between them. Many of those areas were on a finer-scale of resolution than needed here, so samples were aggregated across some of those areas into broader spatial areas, based on known interconnections between areas and on the genetic analysis results from samples collected during SPLASH (Baker et al. 2013). A description of the areas is provided here.

In the winter humpback whales migrate to mate and give birth in near-tropical breeding grounds of the eastern, central, and western North Pacific. Based on genetic differences in both mitochondrial and nuclear DNA, Baker et al. (2013) concluded there were likely five breeding populations of humpback whales in the North Pacific: Central America, Mexico, Hawaii, Asia (Okinawa/Phillipines), and a second West Pacific breeding population whose exact location is unknown (and was therefore un-sampled). The following is an explanation and description of those winter areas.

<u>Central America</u>
The waters from southern Mexico south along the Central America coast are used as a wintering area for humpback whales thought to be almost exclusively from feeding areas off California (Steiger et al. 1991, Calambokidis et al. 2000, Rasmussen

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et al. 2001). SPLASH photo-ID surveys were conducted in Guatemala, El Salvador, Nicaragua, and Costa Rica, with the greatest number of identifications coming from Costa Rica. Although whales from Central America overlap in summer in California with whales from Mexico, Baker et al. (2013) found strong genetic differences between Central America and Mexico, so Central America was used as a sampling stratum for the analysis here. It should also be noted that these whales likely migrate through Mexican waters on their way to feeding areas in California.

Mexico
There are three main winter aggregations in the Mexican Pacific: the southern end of the Baja California Peninsula (Baja); the Bahia Banderas area including the Islas Tres Marias and Isla Isabel along the mainland Mexico (Mainland); and the offshore Revillagigedo Archipelago (Urban and Aguayo, 1987). Field effort was conducted between January and April. In Baja California, the fieldwork covered the area from La Paz to Cabo Falso in the southern part of the Baja California Peninsula. In mainland Mexico field effort was conducted primarily around Bahia de Banderas with some surveys around the Isla Tres Marias. In the Revillagigedos, field work was conducted in January-March primarily around Isla Soccoro, with a smaller amount of effort at Isla Clarion.

Before the SPLASH project, from available photo-identification matches it was thought that both the Baja and Mainland aggregations have as their main migratory destination the coasts of California-Oregon-Washington and British Columbia feeding grounds. However, there are matches with all the other studied feeding areas. Also, there were few known matches between the offshore Revillagigedo Islands area and any of the well-studied feeding areas, so no main migratory destination for this group had been identified (Urban et al. 2000). Given the apparent different main migratory destinations between the Revillagigedo Islands and the coastal areas, the lack of substantial interchange documented between the Revillagigedo and the mainland (Urban et al., 1999) and genetic analyses (Medrano et al., 1995), it has been proposed that the Revillagigedo Islands represents a second subpopulation in the Mexican Pacific. However, Baker et al. (2013) found only low levels of genetic differentiation between mainland Mexico and the Revillagigedo Island, and a moderate amount of interchange was also seen between the two areas (Calambokidis et al. 2008).  Baker et al. (2013) recommended treating all of Mexico as a single breeding population. Furthermore, they noted that the Baja area appears to be primarily a migratory corridor with whales from both mainland Mexico and the Revillagigedo Islands passing through. Therefore, data from all 3 areas were pooled into a single Mexico stratum for analysis here.

Hawaii
A large number of humpback whales use the waters surrounding the Hawaiian Islands each winter, thought to be approximately half of the humpback whales in the North Pacific at the time of a survey in 1993 (Calambokidis et al., 1997). While peak densities are consistently found in the four Island region and Penguin Bank, aerial surveys have shown increasing densities off the Big Island, and in the Kauai and

Niihau region (Mobley et al., 1999, 2001).  Several studies confirm extensive movement of individuals between the islands (Cerchio, 1998).  In Hawaii, field work was conducted from December through April in the main islands of Hawaii, with survey effort around Kaua'i, Oahu, Penguin Bank, Molokai, Maui and the Island of Hawaii. Considerable interchange was documented between all of these subareas during the SPLASH project (Calambokidis et al. 2008). Samples from all areas were therefore combined into a single Hawaii stratum.

Asia
Three areas were surveyed in Asia, including Ogasawara (Bonin Islands), Okinawa (Ryukyu), and the Philippines. Sampling was conducted in the following areas: 1) Ogasawara including Chichi-jima, Haha-jima, and Muko-jima 2) Okinawa including the Okinawa mainland and Zamami Islands, and 3) in the Philippines, only the area around the Babuyan Islands (Acebes et al. 2007). There has been documented interchange of individuals between the three areas, particularly between Ogasawara and Okinawa (Darling and Mori 1993, Barlow et al. 2011). However, the amount of interchange seen during the SPLASH study was not high (Calambokidis et a. 2008), and significant genetic differences were found between Ogasawara and Okinawa (Baker et al. 2013). This suggested that a component of the western breeding grounds was missing or inadequately sampled. One possibility is that whales from an unknown and un-sampled breeding area further south migrate through Ogasawara, and mix there with whales from Okinawa and the Philippines. As noted above, Baker et al. (2013) concluded there were two breeding populations in the western North Pacific, one in Okinawa and the Philippines, and one in an unknown location, but likely migrating through Ogasawara. However, given that the other breeding area, if it exists, was un-sampled, and that both areas migrated through Ogasawara, we pooled all three areas into an Asia stratum.

It was not immediately clear how to define all summer areas for abundance calculations. As noted above, sampling areas were aggregated into broader regions for analysis based primarily on known interconnections between areas and on the genetic analysis results from samples collected during SPLASH (Baker et al. 2013). One consideration for the multi-strata analysis is that the number of parameters to estimate increases rapidly with the number of strata used. The SPLASH dataset is large, but it would still not be sufficient to estimate a model where the summer areas were defined on too small of a scale, so it was important to aggregate across the largest units that made sense.

California and Oregon
The coastal waters off California are used by a distinct feeding aggregation of humpback whales that has been fairly well studied since the late 1980s. Humpback whales also occur along the coasts of Oregon and Washington. There is thought to be a relatively high rate of interchange of whales among regions from southern California to Washington and very little interchange with areas farther north (Calambokidis et al., 1996). Humpback whales in this region primarily use waters on the continental shelf and near the shelf break within 50 nm of the coast. Even

though there is interchange between California and Washington, the density of whales is relatively low north of California along the outer coasts of Oregon and Washington, with few whales seen in Oregon, and a gap in sightings of humpbacks occurs between central Oregon and central Washington (Calambokidis et al. 2008). To the north, a higher density area is only found in northern Washington and southern British Columbia (Northern Washington/Southern British Columbia), referring to the shallow offshore banks off the northwestern point of Washington (Cape Flattery) and southwest of Vancouver Island (Barlow et al. 2011). Baker et al. (2013) found strong genetic differentiation between California/Oregon (California/Oregon) and Northern Washington/Southern British Columbia in both mitochondrial and nuclear DNA. Given this and the near-hiatus in distribution between the areas, we therefore estimated abundance separately for the California/Oregon and Northern Washington/Southern British Columbia areas.

Northern Washington and Southern British Columbia
The aggregation of whales on the shallow banks off southwestern Vancouver Island is clearly contiguous with areas in northern Washington, so this represents a single aggregation of humpback whales. Aggregations of humpback whales are also known from areas farther north such as eastern Queen Charlotte Sound, and off the east and north shores of Haida Gwaii (the Queen Charlotte Islands). During the SPLASH project, humpback whales were seen to be at a relatively low density along the western-side of Vancouver Island, with a higher density area off the northern tip of the island. In inland waters, there is a near-hiatus in distribution of humpback whales in the area (i.e., Strait of Georgia) between Washington and areas north of Johnston Strait in British Columbia (Calambokidis et a. 2008).  Baker et al. (2013) also found strong genetic differentiation between Northern Washington/Southern British Columbia samples from northern British Columbia in both mitochondrial and nuclear DNA, so Northern Washington/Southern British Columbia was kept separate from Northern British Columbia.

Southeastern Alaska and Northern British Columbia
Given the international boundary, SPLASH sampling was conducted by different groups in British Columbia and Southeastern Alaska. Southeastern Alaska extends from Dixon Entrance to Yakutat Bay. Since 1979, a few areas have been well studied in the northern part of Southeastern Alaska; these include Glacier Bay, Frederick Sound and Sitka Sound. There are reports of high humpback whale concentrations offshore in the eastern Gulf of Alaska along the continental shelf from Dixon Entrance to the Fairweather Grounds.  There are also high humpback whale concentrations in southern Southeastern Alaska, including Snow Passage and western Prince of Wales Island.  The high density of humpback whales in southern Southeastern Alaska is contiguous with the high density areas in northern British Columbia south of Dixon Entrance, including eastern Queen Charlotte Sound, and off the east and north shores of Haida Gwaii.  Additionally, Baker et al. (2013) did not find significant genetic differences between Southeastern Alaska and northern British Columbia. Therefore, these two sampling areas were combined into one grouping for abundance estimation.

A small amount of interchange was documented between the northern Gulf of Alaska and Southeastern Alaska. However, a number of the documented movements were of offshore whales in the northern Gulf of Alaska which then moved into Southeastern Alaska, suggesting this was their migration path. Baker et al. (2013) found strong genetic differences between the northern Gulf of Alaska and both Southeast Alaska and Northern British Columbia, so the Gulf of Alaska was handled separately.

Gulf of Alaska
Humpback whales occur throughout the central and western Gulf of Alaska from Prince William Sound to the Shumagin Islands. Seasonal concentrations are found in coastal waters of Prince William Sound, Barren Islands, Kodiak Archipelago, Shumagin Islands and south of the Alaska Peninsula. Large numbers of humpbacks have also been reported in waters over the continental shelf, extending up to 100 nm offshore in the western Gulf of Alaska. Sampling during SPLASH covered all of those areas, including the offshore waters. However, extensive coverage of offshore waters both in the Gulf and in the Aleutians Islands only occurred in 2004 because in 2005 the NOAA RV *Oscar Dyson*, which was scheduled to cover those areas, experienced a mechanical breakdown that prevented the survey from accomplishing much offshore effort west of Kodiak Island in that year. There is a moderate amount of exchange between areas in the northern Gulf, including Kodiak, Barren Islands, and the Kenai Peninsula and Prince William Sound. Humpback whales occur at a lower density between Kodiak Island and the Shumagin Islands, suggesting a minor break in distribution (Zerbini et al. 2006). However, some interchange has been documented between these areas (Wittenveen et al. 2004, Calambokidis et al. 2008). Baker et al. (2013) found significant differences between the W Gulf of Alaska and the N Gulf of Alaska using $F_{ST}$ values for mtDNA, but did not find differences using $Phi_{ST}$ values for mtDNA, and did not find differences in nuclear DNA. Therefore, all areas in the central and western Gulf of Alaska were pooled into a single Gulf of Alaska stratum.

Aleutian Islands and Bering Sea
Humpback whales have been observed throughout much of the shelf waters of the Bering Sea, but densities of humpbacks appear relatively low in the northern shelf area, with relatively few sightings north of St. Lawrence Island (Moore et al. 2000, 2002, Friday et al. 2012).  Humpback whales are consistently concentrated in coastal waters north of Unimak Pass (Friday et al. 2012). In the Aleutian Islands, there are high densities of humpback whales in the eastern Aleutians, but the densities decline in the western Aleutian Islands (Zerbini et al. 2008).

Interchange was seen during the SPLASH project between the eastern Aleutians and the Bering Sea, and there were no genetic differences between the areas (Baker et al. 2011). Given the close proximity of the two areas, it is sensible to group the eastern Aleutian Islands and Bering Sea.  There was no interchange between the eastern Aleutians/Bering Sea and the western Gulf of Alaska, even though sample

sizes were relatively high in both areas. The western Gulf of Alaska had significant genetic differences from the Bering Sea, but not the Eastern Aleutian Islands, though this may be due to the relatively small sample size in the eastern Aleutians (n=37). Given the lack of interchange seen, the Aleutian Islands and Bering Sea were designated a separate stratum from the Gulf of Alaska.

To the west, humpback whales in Kamchatka, Russia, have a strong connection with the Asian breeding areas, and represent a separate stratum from the eastern Aleutian Islands/Bering Sea, where whales are primarily connected to the Hawaii and Mexico winter areas. Three other sampling areas with a relatively small number of identifications are intermediate to Kamchatka and the eastern Aleutian Islands/Bering Sea, and needed to be assigned to one or the other stratum. All three areas were added to the eastern Aleutians/Bering Sea stratum based on similarity in winter destination. First, the western Aleutian Islands had 11 identifications in 2004 and none in 2005 (due to no effort), with one match to Okinawa and 2 matches to Hawaii. Second, the Commander Islands, Russia, had 11 identifications in 2004 and 7 in 2005, with one match to Ogasawara, one match to Hawaii, and one match to the Revillegedos Islands; additional data from years other than the SPLASH project also document matches to the Philippines (Silberg et al. 2013). Third, the Gulf of Anadry (including the eastern coast of the Chukotka Peninsula) had no identifications in 2004 (due to no effort) and 25 in 2005, with one match to Okinawa and 3 matches to Hawaii.

<u>Kamchatka, Russia</u>
Kamchatka was the only region where the majority of the whales had an Asian area as their winter destination. There were 25 identifications in 2004 and 38 in 2005, with 9 matches between years, for a total of 54 unique identifications. Of those 54, there were 5 matches to the Philippines, 14 matches to Okinawa, and 7 matches to Ogasawara.

*Model description*
Mark-recapture analyses were conducted using the programs MARK (White and Burnham 1999) and RMark (Laake 2013).

<u>Summer-summer estimates of abundance</u>
There were only two summer sampling seasons, so the only mark-recapture model that could be used to estimate abundance using only summer data was a simple two-sample Chapman-Peterson modification of the Lincoln-Peterson estimator (Seber 1982).

<u>Winter-winter estimates of abundance</u>
With three sampling seasons, it was possible to use model selection to compare alternative closed mark-recapture models. The models compared were all variations of three-sample Chapman-Peterson estimators, with models specifying constant, time-varying, stratum-specific, or time-varying and stratum-specific capture

probability.  Considerable heterogeneity in capture probability is thought to exist in humpback whale winter areas (Barlow et al. 2011), so an alternative estimate was calculated using a Chao estimator (Mth) with time varying capture probability and individual heterogeneity in capture probability (Chao et al. 1992).  Simulation studies have demonstrated this estimator is most reliable (less biased) when there is a reasonable amount of heterogeneity in the population (Schwarz and Seber 1999).  The Chao estimate was calculated using the program CAPTURE, as implemented in program MARK.

Multi-strata mark-recapture model
Multi-strata mark-recapture models are used for situations where samples can be grouped according to an a priori stratification, and where individuals can move between the strata during each time step.  These models are often used to create spatially-explicit models, where each stratum is a different location, and individuals have the potential to move between each location. These are open mark-recapture models, so there are parameters for survival and capture probability in each stratum, and parameters for movement between each stratum.  Note that the multi-strata model used for preliminary abundance estimates in Calambokidis et al. (2008), from Hilborn (1990), is essentially identical in its basic form, but uses a slightly different likelihood function.

The SPLASH data represent a unique application of the multi-strata model where the migration between winter and summer areas is explicitly modeled over 5 seasons, with four time steps of one-half of a year, representing a total of 2 years (winter 2004 to winter 2006). Therefore, the individuals are moving between two separate sets of strata (winter and summer) each time step.

Three capture probability models were specified, where (1) capture probability was constant across strata and time, (2) capture probability was different in each stratum but was constant across time, and (3) capture probability was different in each strata and also varied across time. There was no data collection in winter areas during the summer season, and vice versa, so the capture probabilities were fixed at 0.0 for locations in the off-season (e.g., capture probabilities for the four winter areas were fixed at 0.0 for both the summer 2004 and summer 2005 seasons).

Given the short time period of the study (2 years), estimates of survival were not a primary objective and would be unlikely to be precise. Therefore, survival was assumed to be constant across time and spatial areas. Note that the parameter represents 6-month survival, not annual survival, because the time steps of the model are 6 months. Preliminary analyses resulted in un-realistically low estimates of survival (S=0.896, which translates to an annual survival of ~0.8). Therefore, survival was fixed to a realistic value from the literature.  Zerbini et al. (2010) reviewed humpback whale life history, and summarized the most reliable values. For the North Pacific estimates of non-calf survival for the largest areas (Hawaii and Alaska) ranged from 0.931 to 0.963 from Mizroch et al. (2004).  Whales can first be identified in the SPLASH study as ~6 month old calves during their first summer.

The only estimates of annual survival of 6 month old calves is 0.85 for the Gulf of Maine (Barlow and Clapham 1997). Taking an annual non-calf survival of 0.95 combined with a calf survival rate of 0.85 results in an average annual survival rate from age 6 months of ~0.94. Therefore, the survival parameter was fixed at 0.9695 to equate to an annual survival rate of 0.94.

In a multi-strata model, the number of movement parameters increases greatly with the number of strata. For example, with only 2 strata there are 4 parameters – the probability of moving from stratum 1 to stratum 2, the probability of staying in stratum 1 ("moving" from stratum 1 to stratum 1), the probability of moving from stratum 2 to stratum 1, and the probability of staying in stratum 2. However, only 2 parameters are estimated; the movement parameters for a given stratum have to sum to 1.0, so the last movement probability is found by subtracting the sum of the others from 1.0. If there are $i$ strata, the number of estimated movement parameters is equal to $i * (i -1)$, so that for 3 strata, there are 6 estimated movement parameters, and for 4 strata there are 12 estimated movement parameters, et cetera.

With six summer areas and four winter areas, there are a total of ten strata and therefore potentially 90 movement parameters for each time step. However, many of the movement parameters are actually fixed to 0.0 to represent movements that cannot occur. For example, winter area to winter area movements cannot occur, and any summer area to summer area movements cannot occur. This essentially means the model assumes all whales migrate somewhere between seasons; all whales in winter areas move to summer areas for the summer, and all whales in summer areas move to winter areas for the winter.

Therefore, there are only 24 movement parameters each time step, whether representing winter to summer movements or summer to winter movements. For example, a whale in a specific winter area can move to any of 6 different summer areas, so there are 6 movement parameters (5 of which are estimated). Multiplying by 4 areas, this results in 24 parameters, of which 20 are estimated. Similarly, there are 24 movement parameters for summer to winter, 18 of which are estimated. If movement parameters are assumed constant over time (except in time-steps when fixed to 0.0), this leads to a total of 48 separate movement parameters, 38 of which are estimated.

With five time occasions, there are a total of four movements that occur. Two movement models were specified. The simpler was a random model, essentially describing a Markov process where whales moved randomly from a summer area to a winter area, and vice versa, with no memory of previous known movements, but with movement rates constant through time.

The second model included a form of memory of previous movements, implemented through the use of groups based on sighting histories. In this model, the first movement was random (winter 2004 to summer 2004), as in the Markov model.

However, for each of the next three movements, whales were grouped according to their sighting histories to help predict their movement, under the assumption that there is a memory to the movements of the whales, and they are more likely to return to a place they have previously been seen. Therefore, the groups were based on three occasions – where whales were seen (if seen) in their first two winters and in their first summer. Where a whale is in its first winter can help predict where it will go for its second or third winter.  If not seen in the first winter, where it is seen in its second winter can help predict where it will go in its third winter. Similarly, where a whale was seen it its first summer will help predict where it will go in its second summer (there is no third summer, so there is no second case for summer).

For any possible winter to summer transition there are 3 possibilities (groups). For example, for whales in Hawaii consider their possible movement to the Gulf of Alaska:
> 1. Whales which were not previously seen in summer, so there is no basis for predicting their movement, so this is the naïve case.
> 2. Whales which were previously seen in summer in the Gulf of Alaska, so this group would have a covariate predicting for a return movement to the Gulf of Alaska.
> 3. Whales which were previously seen in summer somewhere other than the Gulf of Alaska, so this group would have a covariate predicting against a movement to the Gulf of Alaska.

Similarly, there are 3 possibilities for each of the other 5 possible transitions from Hawaii, so there are a total of 18 movement parameters from Hawaii, 15 of which are estimated. Summing across all 4 winter areas results in 72 total winter to summer movement parameters, 60 of which are estimated.

The same process applies to movements from each summer area to a winter area. For each summer area, there are 3 possible movement parameters to each winter area (analogous to the 3 possibilities described above), for a total of 12 movement parameters, 9 of which are estimated. Summing across all 6 summer areas results in a total of 72 total summer to winter movement parameters, 54 of which are estimated.

Because the movement parameters are not time-dependent, there are three capture history groups that would be given the same covariate – whales seen somewhere in the first winter but not second, whales seen somewhere in the second winter but not first, and whales seen in a winter area in both the first and second winters.

The different models were compared using AICc.  Abundance for each stratum was estimated by dividing the number of identified whales in the stratum by the estimated capture probability.

**RESULTS**

*Model selection*
For the winter area closed population analysis, a model with different capture probability in each stratum and each year was selected.  For the summer areas, the model with different capture probability in each stratum was selected.  For the multi-strata model, the best model included the non-Markov movement model with capture probability varying across strata and time. The non-Markov movement model (essentially, with memory) fit the data much better than the Markov random model (with no memory).  This reflects the strong fidelity individual whales show to specific winter and summer areas.

*Winter-Winter estimates*
Hawaii and Mexico had the largest number of identifications, with well over 500 in each of the three seasons, with 244 and 317 total matches, respectively, between seasons (Table 2).  Asia had between 183 and 287 identifications in each year, with 121 total matches between seasons. In Central America, there were only 17 to 42 identifications in each year, with only 7 total matches between seasons (Table 3). Capture probabilities were highest in Asia and Mexico (~0.23 to 0.32), ~0.09 in Hawaii, and lowest in Central America (~0.05-0.08) (Table 3).   Abundance from the Chapman-Petersen model was estimated to be about 8,100 in Hawaii, 3300 in Mexico, 1100 in Asia, and 400 in Central America, for a total of ~13,000 whales (Table 4).  Abundance from the Chao model was estimated to be about 10,000 in Hawaii, 5,000 in Mexico, 1,900 in Asia, and 500 in Central America (Table 4), for a total of ~17,000 whales.

Over the course of the study, Asia showed a substantial increase in identifications in each year (182 in 2004, 204 in 2005, and 287 in 2006), and capture probability increased over time as well. Hawaii also showed a substantial increase in identifications in each year (657 in 2004, 833 in 2005, and 1005 in 2006); capture probability in Hawaii increased each year in the CP model, but did not increase in the MS model.  The number of whales identified in Mexico did not show as large a proportional change between years; it was higher (678) in 2004, but very similar in 2005 (581) and 2006 (580).  The number of whales identified in Central America was lower in 2004 (17), but was similarly higher in 2005 (41) and 2006 (42).

*Summer-Summer estimates*
The greatest number of identifications occurred in Southeast Alaska/Northern British Columbia(1593), followed by  Gulf of Alaska (1295), Aleutian Islands/Bering Sea (575), California/Oregon (502), Southern British Columbia/Northern Washington (182), and Kamchatka (54) (Table 5). Capture probabilities were highest (0.29 to 0.39) in Southeast Alaska/Northern British Columbia, Kamchatka, Southern British Columbia/Northern Washington, and  Gulf of Alaska, and were intermediate in Aleutian Islands/Bering Sea and California/Oregon (0.12 to 0.19) (Table7).  Estimates of abundance were greater than a thousand in most of the

strata, including  Gulf of Alaska (3,148), Southeast Alaska/Northern British Columbia (3,005), Aleutian Islands/Bering Sea (2,348), and California/Oregon (1,555) (Table 8). The relatively smaller stratum of Southern British Columbia/Northern Washington had an estimate of 412, and the estimate for Kamchatka was 103. The total of all summer-summer estimates was 10,572.

There were differences in capture probability from year to year in many of the strata. Kamchatka, Aleutian Islands/Bering Sea, and SBC/WA had higher capture probability in 2005, whereas Gulf of Alaska and Southeast Alaska/Northern British Columbia had lower capture probabilities in 2005.  This can be seen in the number of whales identified. For example, in the Gulf of Alaska 769 whales were identified in 2004 but only 372 were identified in 2005. Similarly, in Southeast Alaska/Northern British Columbia 897 whales were identified in 2004 but only 426 whales were identified in 2005.  Given that both years had a similar amount of effort, this result is surprising.

*Multi-strata model estimates*
In the winter areas, capture probabilities were highest in Mexico (0.21 to 0.16) and Asia (0.20 to 0.26), followed by Hawaii (0.09 to 0.08) and Central America (0.15 to 0.09) (Table 4). Abundance estimates were highest for Hawaii (11,398), followed by Mexico (3,264), Asia (1,059), and Central America (411) (Table 5, Fig. 3).

In the summer/breeding areas, capture probability was highest in the Gulf of Alaska (0.72 in 2004 and 0.18 in 2005).  Capture probabilities were relatively high in Southern British Columbia/Northern Washington (0.15 and 0.15), Southeast Alaska/Northern British Columbia (0.15 and 0.15), and Aleutian Islands/Bering Sea (0.13 and 0.13), and were lower in California/Oregon (0.06 and 0.08) and Kamchatka (0.02 and 0.05).  Abundance estimates were highest for Southeast Alaska/Northern British Columbia(6,137), followed by California/Oregon (3,734), Aleutian Islands/Bering Sea (2,427),  Gulf of Alaska (2,089), Kamchatka (1,111), and Southern British Columbia/Northern Washington (307) (Table 8, Fig. 4).

The capture probabilities sometimes varied substantially between the MS and CP models, making the abundance estimates quite different as well. For example, the capture probability estimates in Kamchatka under the multi-strata model were 0.02 and 0.05 in 2004 and 2005, respectively, whereas the Lincoln-Peterson estimates were 0.24 and 0.37.  In each case, to estimate abundance the inverse of capture probability is multiplied by the same number of identifications, so the abundance is proportionally higher for lower capture probabilities. For Kamchatka, average abundance over 2004-05 was 1,111 (CV=0.37) for the MS model and 103 (CV=0.23) for the CP model, an order of magnitude difference. Overall, in the summer areas, capture probability from the multi-strata model was substantially lower than from the Lincoln-Peterson model for three of the strata (Kamchatka, Southeast Alaska/Northern British Columbia, California/Oregon), somewhat higher for one stratum (SBC/WA), similar in one stratum (Aleutian Islands/Bering Sea ) and

substantially higher in one stratum ( Gulf of Alaska).  In the winter areas, capture probability was lower in the multi-strata model in Hawaii, and was similar in the other three areas. Because there were more identifications in Hawaii, the sum of abundance was higher for the multi-strata model.

*Movement patterns*

The movement parameters can be used to examine the migratory destination of whales from a specific region.  For the multi-strata model with non-random movements, the naïve movement parameters represent an estimate of the migratory destination of all whales from a specific region.  Starting with the winter areas, a high proportion (0.94) of Asian whales move to feeding grounds off Kamchatka in Russia, with the rest moving to the Aleutian Islands and Bering Sea. The majority of Hawaiian whales move to feeding areas in Southeastern Alaska and northern British Columbia (0.85), but others go to the Gulf of Alaska (0.08), the Aleutian Islands and Bering Sea (0.06), and a small proportion go to southern British Columbia and Washington (0.01).  The majority of Mexican whales move to California/Oregon (0.75), with with the rest moving to the Gulf of Alaska (0.10), the Aleutian Islands and Bering Sea (0.09), Southeast Alaska and northern British Columbia (0.05), and southern British Columbia/northern Washington (0.03).  The majority of Central American whales move to feeding areas in Oregon/California (0.91), with the rest going to southern British Columbia and Washington (0.09).

The estimates of movement from summer areas to winter areas also represents the breeding population composition on the feeding grounds, so it will be described in that way. All whales in Kamchatka are estimated to be from the Asia breeding population. The majority of whales in the Aleutian Islands and Bering Sea are from the Hawaiian breeding population (0.87), with some whales from the Mexican (0.11) and Asian (0.02) breeding populations, but note that these estimates are not very precise.  The majority of whales from the Gulf of Alaska are also from the Hawaiian breeding population (0.89), with some whales from the Mexican breeding population (0.11), and a very small proportion from the Asia (<0.01) breeding population.  Nearly all of the whales from Southeastern Alaska and northern British Columbia are from the Hawaiian breeding population (0.94), with a few whales from the Mexican breeding population (0.06). The majority of whales in southern British Columbia and Washington are from either the Hawaiian breeding population (0.53) or Mexico (0.42), with a few whales from Central American (0.05). Finally, the majority of whales in California/Oregon are from the the Mexican breeding population (0.90), with the remainder from Central American (0.10)

The non-naïve movement estimates (e.g., the probability of moving to a specific Winter area when previously seen in that area) are tabled in the Supplementary materials. In general, the probability of moving to an area where previously seen was quite high; in most cases it was greater than 0.95.

**DISCUSSION**

*1 Overview of abundance*
The results of this study provide the first geographically stratified  look at humpback whale abundance throughout most of the North Pacific.  As expected, in winter the largest abundance was found in Hawaii (N=11,398, CV=0.04), with the second largest in Mexico (N=3,264, CV=0.06). Both the Asia (N=1,059, CV=0.08) and Central America N=411, CV=0.30) winter areas had much smaller abundance. In summer the feeding areas in Alaska and northern British Columbia support the majority of the North Pacific population; these areas include the Aleutian Islands/Bering Sea (N=2,427, CV=0.20), the Gulf of Alaska (2,089, CV=0.0.09), and Southeastern Alaska/northern British Columbia (N=6,137, CV=0.07).  The abundance estimate for southern British Columbia/northern Washington was small at 307 (CV=0.23); this is not surprising as the area occupied by the whales is of relatively small spatial extent.  Abundance in California/Oregon was estimated to be 3,734 (CV=0.11). The first abundance estimate for the Kamchatka feeding area was N=1,111 (CV=0.37). Overall, it is interesting to note that the abundance from the broad oceanographic areas in the central part of the humpback's range is large, whereas abundance from the continental margins of the North Pacific, on both coasts, is relatively small. In particular, the two breeding populations from the continental margins, Asia and Central America, are relatively small (~1,000 and 400 whales, respectively), and are thus of greater conservation concern.

*2. Migratory destinations*
The Alaska and northern British Columbia feeding areas all have a strong migratory link (Psi > 0.86) to Hawaii (with the link between Southeastern Alaska/northern British Columbia and Hawaii (Psi=0.94) particularly high.  In return, nearly all Hawaiian whales migrate to Alaska and northern British Columbia. The sum of the abundance estimates for the three Alaska and northern British Columbia feeding areas is 10,653, which is similar to the estimate for Hawaii (11,398).

The migratory destination of whales that breed in Mexico is the most diverse, with whales going to all feeding areas except Kamchatka, with the higher proportion going to the California/Oregon (Psi=0.75). Nearly all Central American whales migrate to California/Oregon to feed (Psi=0.92), but the California/Oregon feeding area is primarily composed of whales from Mexico (0.90), reflecting the much greater abundance in Mexico than in Central America. The sum of the abundance estimates for Mexico and Central America is 3,675, with 2,761 estimated to migrate to California/Oregon. This is somewhat lower than the estimate for California/Oregon (3,734), and represents a slight miss-match between estimated winter and summer abundance, and their connections.

The strongest migratory connection was between the Kamchatka feeding area (Psi=1.0 to move to Asia) and the Asia breeding area (Psi =0.92 to move to Kamchatka). Consistent with this, abundance was estimated to be nearly identical in

both locations, with an estimate of 1,111 in Kamchatka, and an estimate of 1,059 in Asia. The Kamchatka – Asia link represents the nearest thing to a pure winter and summer area stock, where all the whales in the winter area are from the same summer area, and vice versa.  Overall, it can be seen that nearly all feeding areas appear to have a primary winter destination that is either Asia (Kamchatka), Hawaii (Aleutian Islands and Bering Sea, the Gulf of Alaska, and Southeastern Alaska and northern British Columbia), or Mexico and Central America (noting the whales migrating to Central America first migrate through Mexican waters).  The one exception is Southern British Columbia/northern Washington, which appears to have a nearly even mix between the migratory destination of Alaska and northern British Columbia whales (Hawaii) and the destination of California/Oregon whales (Mexico and Central America).

Note that movements of humpback whales have been documented between summer and winter areas that have estimated movement rates of 0.0 in this study, including a movement between Japan and British Columbia (Darling et al. 1996).  The interpretation of those events from this study is that either such movements did not occur during the years 2004-06, or occurred at such a low rate they were not detected in this study.

An analysis of the proportion of whales from each summer area that were identified in any winter area showed that whales from the Aleutian Islands and Bering Sea had the lowest probability of being seen on a winter area (Calambokidis et al. 2008). One interpretation of this result is that some of those whales go to an unknown (and un-sampled) winter area.  Subsequent to the SPLASH project, a survey in 2007 documented humpback whales from a number of locations in the Northwestern Hawaiian Islands at relatively low densities (Johnson et al. 2007), but no sampling occurred there during the SPLASH project. Some humpback whales, including mother/calf pairs, have also been found in the Marianas Islands (Hill et al. 2016). Both of these locations are plausible migratory destinations for whales from the Aleutian Islands and Bering Sea.

There were also summer areas that were not sampled, or at least sampled very well, during the SPLASH project, due to both a lack of resources in some cases and a lack of knowledge of the distribution of whales at the time.  Friday et al. (2013) showed sightings of humpbacks in places in the Bering Sea that were not well surveyed, especially the northern side of the Alaska Peninsula, and also a few sightings on the northern Bering Sea shelf.  However, the number of sightings before the SPLASH project was low, and the decision was made to preferentially cover areas with historical records of humpback whale catches, such as the south side of the Aleutians Islands.  Recent surveys (2009-2012) have also had sightings and acoustic detections of humpbacks in the Chukchi Sea, north of the Bering Strait, both in Russia along the north side of the Chukotka Peninsula, and also on the US side especially near Point Hope (Clark et al. 2013); SPLASH surveys covered the Bering Strait portion of the Chukotka peninsula but did not have enough ship-time to go to the north side of the peninsula, and no survey effort occurred in the US portion of

the Chukchi Sea. Japanese surveys have also shown an offshore feeding area for humpback whales east of Hokkaido and the Kuril Islands (and southwest of the western Aleutian Islands, another area not surveyed during SPLASH due to limited resources (e.g., Matsuoka et al. 2012). Although the SPLASH survey was by far the most expansive survey of humpback whale feeding areas in the North Pacific, it is clear that future surveys would ideally survey more extensively in the western North Pacific, Chukchi Sea, and Bering Sea.

*3. Regional estimates of abundance and comparison to previous estimates*
In this section, we compare the multi-strata and within-season estimates with previous abundance estimates for each region.

Central America
The MS estimate for Central America is 411 (CV=0.30), with the CP estimate similar, and the Chao estimate was slightly larger at 511 (CV=0.35). There are no previous estimates of abundance for the Central America breeding population.  This breeding population is small, but it is encouraging that the population is more than just a couple of hundred whales.

Mexico
The MS estimate for Mexico is 3,264 (CV=0.06), the CP estimate is similar at 3,327 (0.04), and the Chao estimate is substantially larger at 4,910 (CV=0.10). Two separate abundance estimates were made for Mexican waters in the early 1990s, where Urbán et al. (1999) estimated that in 1991 there were 1,813 (95% CI 918-2505) whales in Mainland Mexico and 914 (95% CI 590-1193) whales in the Revillagigedo Archipelago. For the same time period, Calambokidis et al. (1997) estimated 1,600 whales and 4,200 whales from two different methods, and concluded the true abundance was about 2,200-2,800, consistent with Urbán et al. (1999).  This suggests the Mexican population has increased slightly between the 1990s and the 2000s.

Hawaii
The MS estimate for Hawaii is 11,398, (CV=0.04), the CP estimate is substantially lower, and the Chao estimate is 9,920 (CV=0.09). The most recent previous estimates of abundance for Hawaii were from the 1990s from both photo-identification mark-recapture and aerial survey line-transect surveys. Those estimates were about 3,000-5,000 whales (Calambokidis et al. 1997, Cerchio 1998, Mobley et al. 1999, 2001).  Mobley estimated the population was increasing at 7%/year, so a population of ~11,000 could reflect that continued increase. A breeding population of this size represents approximately half of all the humpback whales in the North Pacific, as estimated by Barlow et al. (2011).

Asia
From these analyses, the MS estimate for Asia is 1,059 (CV=0.08), the CP estimate is slightly larger, and the Chao estimate is substantially larger at 1,907 (CV=0.165) . In

Asia, abundance was previously estimated for 1991-93 as 394 (CV = 0.08) (Calambokidis et al. 1997); this was an estimate for the Ogasawara Islands and Okinawa, but no data from the Philippines or other areas were included. The estimate here is more than twice as large as the previous estimate. Part of this increase could be due to the inclusion of the Philippines, rather than an increase in the population, but this is unlikely to account for the total difference.  For a like-to-like comparison to the earlier estimate, the analyses were repeated without the Philippines SPLASH data; the CP estimate for Okinawa/Ogasawara is 1,025 (CV=0.07), and the Chao estimate is 1,614 (CV=0.11), indicating the population did increase between 1991-93 and 2004-06. It is encouraging that this relatively small breeding population is apparently showing signs of increase, and no longer numbers just a few hundred animals.

California/Oregon
The summer population in California/Oregon has an MS estimate of 3,734, with the CP estimate substantially lower at 1,555. Several estimates of abundance have previously been made for California from photo-identification data.  Abundance estimated off central California in the 1980s were about 300 animals (Dohl et al. 1993, Calambokidis et al. 1990).  In the early 1990s estimates were about 600 whales (Calambokidis et al. 1993, Barlow 1995), and increased at about 8%/year to just below 1000 whales by 1997 (Calambokidis and Barlow 2004). Since 1998, mark-recapture estimates for this area have been more variable with a dramatic drop in abundance in 1999-2001 followed by a rapid increase driven by an apparent influx of new animals that had not been seen in the area previously (Calambokidis et al. 2004a, 2005). Line-transect surveys estimated 1,769 (CV=0.16) animals for surveys pooled between 1991 and 2005 for California, Oregon, and Washington (Barlow and Forney 2007). The new SPLASH abundance estimate is higher than previous estimates.

Southern British Columbia/Northern Washington
The MS abundance estimate for this area was relatively low at 307 whales. Humpback whale abundance estimates off the Washington coast have been previously made from vessel line-transect surveys and capture-recapture from photo-identification research and are generally consistent with the low estimate from SPLASH. Forney (2007) estimated the number of humpback whales off N Washington/S British Columbia at 208 (CV=0.28) in 2005.  Vessel line-transect surveys just in the northern Washington area estimated about 100 whales between 1995 to 2000; however, the estimate in 2002 was substantially higher (562, CV=0.21), although this high estimate may be biased due to re-sighting animals multiple times (Calambokidis et al. 2004b). Capture-recapture estimates showed the number of whales increasing from about 100 to 200 from 1995 to 2002 (Calambokidis et al. 2004b), so an estimate of 307 may indicated continued population growth in this area.

Southeastern Alaska/Northern British Columbia

The MS abundance estimate for this area was relatively large at 6,137. There have been a number of past estimates of humpback whales for Southeast Alaska but these did not include the wide geographic coverage of SPLASH and yielded much lower estimates than SPLASH. Early estimates of abundance for Southeastern Alaska were about 300 whales from 1979 to 1983 (Baker et al. 1985). In 1986, Baker et al. (1992) estimated 547 whales (95% CL: 504-590). Straley (1994) estimated 404 humpback whales from 1985 through 1992. Abundance in 2000 for northern Southeastern Alaska was estimated at 961 (95% CI 657-1076) humpback whales (Straley et al. 2009). Photo-identification data of humpbacks utilizing B.C. waters, either as a migration corridor or for feeding, from 1992-2006, resulted in a best estimate of 2,145 animals (95% confidence limits 1, 970-2,331; Ford et al. 2009). Combining the Straley et al. (2009) estimate with British Columbia results in about 3000 whales for a similar time period, still considerably less than the SPLASH estimate, although note that the SPLASH Lincoln-Petersen estimate was also about 3000 whales.  It is possible that the increased geographic coverage of the region led to the higher estimate, or that the multi-strata model reduced heterogeneity that has led to negatively biased estimates.

Gulf of Alaska
Photo-identification studies have estimated 100-200 in Prince William Sound and Kenai Peninsula waters (Waite et al. 1999, von Ziegesar et al. 2000), 100-150 in the Barren Islands (G. Strong, pers. comm.), 300-500 in Kodiak waters (Waite et al. 1999), and 410 in the Shumagin Islands (Witteveen et al. 2004), totaling about 1200 whales, somewhat less than the MS estimate of 2,089.  Zerbini et al (2006) estimated 2,648 (CV=0.16) humpback whales in the nearshore waters of the Gulf of Alaska and eastern Aleutian Islands (from Kenai to Amchitka Pass) in 2001-2003, with 2,266 of that total found in survey blocks in the Gulf of Alaska, not too different than the SPLASH estimate presented here. Given that humpback whales are found offshore, and that the Zerbini et al (2006) estimate did not include Prince William Sound, it is somewhat surprising that the SPLASH estimate is not higher for this area. Note that the SPLASH CP estimate was higher, at 3,148.

Aleutian Islands/Bering Sea
From line-transect surveys Moore et al. (2000) estimated abundance of humpback whales in the central Bering Sea as 1,175 humpback whales (95% CI: 197-7,009) in 1999, though Moore et al. (2002) suggested these sightings were too clumped in the central-eastern Bering Sea to be used to provide a reliable estimate for the area. In the eastern Aleutian Islands the estimate from Zerbini et al. (2006) totaled 382 humpback whales found in survey blocks in the Aleutian Islands. Abundance estimates for humpback whales in the eastern Bering Sea shelf for 2002, 2008 and 2010 were 231(CV=0.63), 436(CV=0.45), and 675 (CV=0.80), respectively (Friday et al. 2012).  The SPLASH MS estimate of 2,427 is higher than these estimates. However, the SPLASH estimate covers a much wider area, including portions of Russia (Gulf of Anadyr, Commander Islands), and the western Aleutians.

Kamchatka, Russia

For Kamchatka, average abundance over 2004-05 was 1,111 for the MS model. Abundance has not previously been estimated here, so this represents the first estimate of abundance for this feeding area. Note that the CP estimate was only 103, suggesting the MS model accounted for substantial capture heterogeneity. This could potentially result if whales occurred in areas not sampled well in summer, such as offshore waters.

*4. Total abundance compared to Barlow et al. (2011) estimates*
The intent of this analysis was to estimate abundance for each geographical area, not for the entire North Pacific. However, it is worth comparing the totals calculated here with the estimate for the entire North Pacific from these same data by Barlow et al. (2011), where the data were pooled across geographic locations.  For the winter areas, their Chapman-Peterson estimates for Breeding-Breeding comparisons were 8,959 and 11,668 (Table 6, Barlow et al. 2011).  Calculating separate Chapman-Peterson estimates by geographic area and summing them gave a total of 12,999 here (Table 5), somewhat higher than in Barlow et al. (2011).  For the summer areas, their estimate for a Feeding-Feeding comparison was 10,109 (Table 6, Barlow et al. 2011), compared to a sum across summer areas here of 10,572 (Table 8), which is very similar.   It is not surprising that the regional Chapman-Peterson estimates are subject to the same negative bias as the pooled estimate, and likely for the same reasons.  As expected, because they account for individual heterogeneity in capture probability, the Chao estimates were much larger than the Chapman-Peterson estimates, totaling 17,256.

Barlow et al. (2011) considered their best estimate of abundance (before bias corrections) as 21,808 (CV=0.04), based on a pooled summer vs. pooled winter sample.  This is most analogous to the multi-strata model results here, which also used both summer and winter identifications in a single analysis.  The total estimate from the multi-strata analysis here was 16,132 for the winter areas (Table 5) and 15,805 for the summer areas (Table 8), which are nearly identical.  The multi-strata analysis results in a larger summed abundance for the entire North Pacific than the within-season CP estimates, but they are still lower than the Barlow et al. (2011) estimate. It is not obvious why this is the case.  For four areas, the multi-strata analysis produced a much larger (and presumably better) estimate of abundance than the within-season estimates calculated here, including areas such as Kamchatka (1,111 vs. 103), , Southeast Alaska/Northern British Columbia(6,137 vs 3,005), Hawaii (11,398 vs 8,097), and California/Oregon (3,734 vs 1,555).  However, for five other areas (Asia, Mexico, Central America, Aleutian Islands/Bering Sea, southern British Columbia/northern Washington) the MS and CP estimates were fairly similar.  The one anomaly was the Gulf of Alaska where the MS estimate was lower than the CP estimate (2,089 vs. 3,148).

It is also interesting that the Chao estimates were mostly larger than the MS estimates – in two cases remarkably so. The MS estimate for Asia was 1,059 but the Chao estimate was 1,907, and the MS estimate for Mexico was 3,264 but the Chao

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estimate was 4,910. The Hawaii Chao estimate was somewhat smaller than the MS estimate, and the Central America estimate was slightly larger. The total for the Chao estimates was larger at 17,256 compared to 16,132 but is still smaller than the Barlow et al. (2011) estimate of 21,808.

Another check on internal consistency of the MS model results was calculated by prorating summer abundance estimates to winter areas via movement parameter estimates, and vice versa (Figs. 3-4).  The prorated winter estimates are very similar for Asia and Central America, but the Hawaii estimate is slightly lower and the Mexico estimate is slightly higher (Fig. 3).  The prorated summer estimates show more divergence.  The estimates for Kamchatka and southern British Columbia/northern Washington are nearly identical. However, the estimates for the Aleutian Islands/Bering Sea and the Gulf of Alaska are much lower, and the estimate for Southeast Alaska/northern British Columbia is much higher (~10,000 versus ~6,000).  One interpretation of this is that the model has underestimated the proportion of whales moving from Hawaii to Aleutian Islands/Bering Sea and the Gulf of Alaska, and has over-estimated the proportion of whales moving from Hawaii to Southeast Alaska/northern British Columbia. Other than this, the estimated summer abundance, winter abundance, and movements between summer and winter are internally consistent with one another.

The explanation for why the analyses using both summer and winter data are higher than analyses using only summer or only winter data likely has to do with capture heterogeneity within a single region, meaning that individual whales have different capture probabilities, which violates one assumption of the Chapman-Peterson estimator. Although there is likely capture heterogeneity in both the summer areas as well as the winter areas, it is thought that the capture heterogeneities in each season are different, and therefore when combined in a feeding-breeding ground mark-recapture, they do not cause as large a negative bias.  In contrast, in comparing two samples with the same heterogeneity in capture probability, such as the breeding-breeding ground comparison, there can be substantial negative bias. Similarly, the Chao estimator, though based only on winter data, explicitly accounts for individual heterogeneity in capture probability.

For example, a similar bias was seen during the YONAH humpback whale project in the North Atlantic which also involved sampling on both the feeding and breeding grounds. Winter samples (genetic identifications) in the West Indies were used to estimate abundance using a Chapman 2-sample estimator applied to a breeding-breeding ground comparison for the two YONAH years of 1992 and 1993.  The estimate of the population was 7,698 (Palsboll et al. 1997). In contrast, a similar estimator using genetic identifications from feeding ground data (from the Gulf of Maine, Canada, and Greenland) as the mark, and the West Indies breeding ground as the recapture, resulted in an estimate of 10,752 (CV = 6.8%) (Stevick et al. 2003), which was substantially higher. This was attributed to substantial heterogeneity in capture probability on the breeding grounds.  Indeed, when the data were separated into male and female datasets, the estimate for males was 4,894 whereas the

estimate for females was 2,804, even though the sex ratio is known to be approximately equal on the feeding grounds.  It is thought that this is due to females having a relatively short duration on the breeding ground and perhaps also arriving and leaving outside the period of sampling; in contrast, males have a longer duration that spans most or all of the breeding season. Interestingly, doubling the males-only estimate of 4,894 (assuming a 50:50 sex ratio in the population) leads to a population estimate of 9,788, which was only slightly lower than the feeding-breeding ground estimates.

Barlow et al. (2011) similarly concluded that a feeding-breeding ground comparison was more robust and provided a higher estimate of abundance than breeding-breeding ground comparisons, which had a strong negative bias. The migration between the feeding ground and breeding ground effectively randomizes the sampling in the two areas. This approach also avoids many of the sources of heterogeneity that would result from sampling in only one seasonal habitat (Smith et al. 1999). Moreover, Barlow et al. (2011) demonstrated this effect through simulation. They found that if individual heterogeneity was the same in the marked sample as in the recaptured sample, this introduced negative bias of 21% in their example (based on the SPLASH project throughout the North Pacific, which was analogous to the YONAH project in its scope). In contrast, they found that using the same range of heterogeneity in capture probability but with different values in different samples (as would be true in a feeding-breeding ground comparison) resulted in a very small bias. Note that the total of the MS estimates was 24% and 49% higher than the total of the CP estimates in winter and summer, respectively, suggesting it is possible that the MS estimates are higher simple because they correct for substantial individual heterogeneity in capture probability.  Barlow et al. (2011) also investigated sex-biased sampling, as apparently occurs on the breeding ground, but again found that bias from this effect is small if one of the two capture occasions is unbiased with respect to sex, as should be the case on the feeding grounds.

In summary, the multi-strata estimates should be less subject to bias from capture heterogeneity, which has been shown to lead to substantial biases.  The sum from the multi-strata model is much higher (although still lower than the pooled abundance from Barlow et al. 2011), which fits with this known direction of substantial bias.  The multi-strata estimates also use all the data (from both summer and winter), rather than estimating abundance from just part of the data. Given this, it seems reasonable to conclude that the multi-strata estimates calculated here are more accurate than the within-season Chapman-Peterson estimates. The one exception is the Gulf of Alaska, where the MS estimate is substantially lower. However, it is more difficult to decide whether the Chao or MS estimates are better. Both models produce valid estimates of abundance, but from different datasets (one winter-only identifications, and the other from all winter-summer data combined). Both estimation methods account for heterogeneity in capture probability, but in different ways.  Again, it seems sensible to use all the data and therefore favor the MS estimates, but on the other hand the Chao estimates are simpler (using only

winter data), and are therefore not correlated with the estimation of capture probability in summer areas and movements between areas.  For consistency, when using the estimates of movements between winter and summer areas, it would be sensible to use the corresponding MS model abundance estimates rather than the Chao estimates.

Barlow et al. (2011) performed simulations to estimate bias in their estimate of overall abundance from sources other than individual heterogeneity or sex biases. Their result is not strictly applicable to the results here, as the bias estimates were calculated for a pooled Summer-Winter Chapman-Peterson estimate.  However, it is interesting to note that two of the main potential biases that would effect the multi-strata results here, exclusion of calves in samples (-10.5% bias) and missed matches (+9.3%) have biases that nearly offset each other.

*5. Cconservation and management Implications*
This analysis provides estimates of abundance for North Pacific humpback whales throughout their range in the North Pacific, both in winter areas and summer areas. Having estimates of abundance for these areas is important for management. Humpback whales were listed as Endangered under the US ESA because the populations were severely depleted by commercial whaling. Based partly on the genetic results from the SPLASH project (Baker et al. 2013), it has been proposed to designate four Distinct Population Segments of humpback whales in the North Pacific, corresponding to the four winter area strata used in this analysis[1].  Although the overall abundance of North Pacific humpback whales is relatively large, two of the winter populations, Asia and Central America, are relatively small as their abundance estimates are less than 2000 whales and 1000 whales, respectively. Both of these populations migrate to relatively smaller feeding areas than do the other two winter populations, Hawaii and Mexico. Additionally, both of the smaller populations occur on the margins of their respective continents, and are potentially exposed to more risks from human activities than the populations with more open ocean migratory routes.

North Pacific humpback whales have a complicated migration. In many cases whales from a winter population mix with whales from other breeding populations in their feeding areas.  The reverse is always true – whales from each of the feeding area strata used here mix with whales from at least one other feeding ground in their winter area. As noted above, the migratory connection between Asia and Kamchatka comes the closest to a pure stock where the breeding population contains whales from only a single feeding area, and vice versa. Many of the threats to humpback whales (but not all), such as deaths from entanglement in fishing gear or by collisions with ships, occur in the feeding areas, so it is also important to understand

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[1] 80 FR 22304 Endangered and Threatened Species; Identification of 14 Distinct Population Segments of the Humpback Whale (*Megaptera novaeangliae*) and Proposed Revision of Species-Wide Listing; Proposed Rule

local abundance in those areas to evaluate the effect of those takes on local abundance. Moreover, this paper provides the first estimates of breeding population composition on the feeding grounds. From those estimates it is possible to estimate the probability that a whale killed in, for example, the Gulf of Alaska, comes from one of the smaller breeding populations, such as Asia. Mortalities of whales from the two smaller breeding populations are obviously of greater conservation concern.

In the US humpback whales are also managed under the MMPA. MMPA population stocks of humpback whales in the North Pacific are primarily based on the winter areas, with a California/Oregon/Washington stock based on the Mexican breeding area, a Central North Pacific stock based on the Hawaii breeding area, and a Western North Pacific stock based on the Asia breeding areas. If the proposed Distinct Population Segments under the ESA are finalized, it is likely that population stocks under the MMPA will be revised to represent similar units. In that case, abundance estimates from the winter areas could represent the abundance of the MMPA population stocks.

Efforts to reconstruct the population trajectories of North Pacific humpback whales as they recover from their depletion from commercial whaling have been made difficult by the complicated migratory behavior.  Most (but not all) humpback whales that were killed by commercial whaling were killed in their feeding areas, with most of the catches occurring in the 1950s and 1960s, but the catches were not distributed equally throughout their range.  Therefore, it is important to consider the effect of catches within each area. With respect to the winter areas, during the 20th century whaling operations killed ~3,600 whales in Asia, with just a few hundred killed in Russia (Ivashchenko et al. 2015). This contrasts with current abundance that is not much more than ~1,100 (MS estimate) or ~1,900 (Chao estimate), suggesting the Asia breeding population could still be at low levels relative to historic population size.  Although no whaling occurred in Hawaii, over 16,000 whales were killed in the 20th century in the Aleutian Islands and Bering Sea, Gulf of Alaska, and Southeast Alaska/Northern British Columbia (Ivashchenko et al. 2015), the primary feeding areas of the Hawaii population (though some of those whales killed would have been from the Mexico breeding population).  With an estimated abundance of ~11,000, this suggests it is possible the Hawaii population may have recovered close to carrying capacity.  Some whaling did occur in Mexico with ~2,200 whales killed in Baja from shore stations in early 20th century, along with major catches in their feeding areas in the Aleutian Islands and Bering Sea, Gulf of Alaska, Southeast Alaska, and California throughout the 20th century (Ivashchenko et al. 2015). With an abundance of ~3,000 (MS estimate) or ~5,000 (Chao estimate), it is unclear if the Mexico breeding has recovered to close to historical levels or not.  There was no substantial whaling in Central America, but this breeding population was subject to whaling in their feeding area, with large number of humpback whales killed in California. Those catches presumably consisted of whales from both Central America and Mexico. The small population size of the Central America population suggests this breeding population may still be recovering.

With respect to the summer areas, relatively few whales were killed in whaling operations in Russia, but the substantial number of whales killed in Asia (the primary source of whales in Kamchatka) suggests the Kamchatka population may not have recovered to historical population levels.  In the 20th century whaling operations killed >7,000 whales in the Aleutian Islands and Bering Sea, with nearly 5,000 of those after World War II (Ivashchenko et al. 2015).  A current abundance of 2,400 suggests humpback whales may not have recovered to historical population levels in this area. In the 20th century whaling operations killed 4,500 whales in the Gulf of Alaska, with ~2,750 of those after World War II (Ivashchenko et al. 2015).  A current abundance of 2,000 also suggests humpback whales may not have recovered to historical population levels in this area. In the 20th century whaling operations killed ~4,000 whales in Southeast Alaska/northern British Columbia, primarily before World War II.  A current abundance of ~6,000 suggests humpback whales may have recovered to historical population levels in this area. Whaling operations killed ~4,000 whales in southern British Columbia and Washington, with nearly all of those before World War II (Ivashchenko et al. 2015).  A current abundance of only 300-400 suggests humpback whales may still be well below historical population levels in this area. Whaling from primarily coastal whaling stations killed ~4,600 whales in California, with ~1,600 in the 19th century, ~2,100 in the early 20th century, primarily from the Moss Landing and Trinidad whaling stations (Clapham et al. 1991), and ~900 after World War II, with an additional 2,200 whales killed in Baja, Mexico. A current abundance of 3,200 in CA/OR makes it unclear whether humpback whales have recovered to historical population levels in this area.

It will be important to carry out an actual quantitative assessment of depletion level for North Pacific humpback whale populations by modeling historical population size. To estimate the depletion level of the winter and summer areas, it is necessary to have estimates of migratory destination, such as calculated here, in order to allocate feeding areas catches to the breeding populations. Although it will still be a complicated modeling exercise, the results of this analysis will now allow such an analysis to be conducted, such as has been done for Southern Hemisphere humpback whale populations (e.g., Ross-Gillespie et al. 2014).   These analyses can involve simultaneous modeling of several or all breeding populations in a spatially explicit model. Such analyses, sometimes termed back-calculations, can be used to estimate historical carrying capacity, and where current populations are relative to that carrying capacity. Moreover, it is likely that mechanisms of density-dependence would primarily act on the feeding areas, where prey can become limiting. It is not inconceivable that winter area habitat could be limited as well, but it does not appear to be the case for humpback whales in the North Pacific, where the only requirements for breeding and calving habitat seem to be warm, somewhat sheltered waters that contain other humpback whales.  Therefore, a spatially explicit back-calculation model for North Pacific humpback whales requires abundance estimates from both winter areas and summer areas, as well as the migratory connections between them.

**ACKNOWLEDGEMENTS**

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Table 1.  Summary of photo-identifications by sampling areas pooled across all years of the SPLASH project.  Total IDs (in the last column and row) represents the total number of unique identifications in that sampling area across all years. Other numbers represent the total number of matches between summer and winter areas across all years.

| Sample Area | Phillipines | Okinawa | Ogasawara | Hawaii | Mexico | Cent Am | Total IDs |
|---|---|---|---|---|---|---|---|
| Kamchatka | 5 | 14 | 7 | | | | 54 |
| Comm. Is. | | | 1 | 1 | 1 | | 17 |
| Gulf of Anadyr | | 1 | | 3 | | | 25 |
| WAI | | 1 | | 2 | | | 11 |
| EAI | | | | 2 | | | 49 |
| Bering Sea | | 3 | 5 | 43 | 32 | | 512 |
| WGOA | | | 2 | 26 | 24 | | 301 |
| NGOA | | | 1 | 124 | 85 | | 1038 |
| SEA/NBC | | | | 215 | 20 | | 1115 |
| SBC/NWA | | | | 20 | 32 | 3 | 207 |
| CA/OR | | | | | 117 | 26 | 525 |
| Total IDs | 77 | 215 | 294 | 2317 | 1658 | 105 | |

Table 2. Whale identifications in each stratum and year for winter areas. The number of matches between years are also shown, where M04-05 is the number of matches between 2004 and 2005.

| Stratum | 2004 | 2005 | 2006 | M4-5 | M5-6 | M4-6 | M4-5-6 |
|---|---|---|---|---|---|---|---|
| Asia | 183 | 205 | 287 | 19 | 45 | 21 | 18 |
| Hawaii | 661 | 838 | 1016 | 81 | 86 | 45 | 16 |
| Mexico | 692 | 593 | 582 | 100 | 58 | 80 | 41 |
| Central Am | 18 | 45 | 45 | 3 | 3 | 1 | 0 |

Table 3a. Capture probabilities (*p*, with CV in parentheses) for winter areas from the Winter-Winter Chapman-Petersen analysis.

| Stratum | 2004 | | 2005 | | 2006 | |
|---|---|---|---|---|---|---|
| Asia | 0.159 | (0.10) | 0.178 | (0.09) | 0.251 | (0.08) |
| Hawaii | 0.081 | (0.07) | 0.103 | (0.06) | 0.124 | (0.06) |
| Mexico | 0.204 | (0.05) | 0.175 | (0.06) | 0.174 | (0.06) |
| Central Am | 0.039 | (0.41) | 0.095 | (0.37) | 0.097 | (0.37) |

3b. The number of unique whale identifications in each area (*n*) in 2005 and 2006, along with estimated capture probabilities (*p*, with SE in parentheses) for winter areas from the Multi-strata analysis.

| | *n* | | *P* | |
|---|---|---|---|---|
| Stratum | 2005 | 2006 | 2005 | 2006 |
| Asia | 205 | 287 | 0.201 (0.029) | 0.261 (0.024) |
| Hawaii | 838 | 1016 | 0.086 (0.078) | 0.078 (0.004) |
| Mexico | 593 | 582 | 0.208 (0.158) | 0.158 (0.013) |
| Central Am | 45 | 45 | 0.149 (0.087) | 0.087 (0.035) |

Table 4. Abundance estimates for winter areas, defined as $n/p$. $N_{multi}$ is the estimate from the Multistrata model using both winter and summer data, $N_{CP}$ is the estimate from the Chapman-Peterson winter-winter model, and $N_{Chao}$ is the estimate from the Chao winter-winter model. In each case, CV is the Coeffecient of Variation. Total is the total abundance summed across all strata.

| Stratum | $N_{multi}$ | CV | $N_{CP}$ | CV | $N_{Chao}$ | CV |
|---|---|---|---|---|---|---|
| Asia | 1,059 | 0.084 | 1,143 | 0.068 | 1,907 | 0.165 |
| Hawaii | 11,398 | 0.042 | 8,097 | 0.055 | 9,920 | 0.090 |
| Mexico | 3,264 | 0.058 | 3,327 | 0.043 | 4,910 | 0.095 |
| Central Am | 411 | 0.30 | 431 | 0.339 | 519 | 0.353 |
| Total | 16,132 | | 12,999 | | 17,256 | |

Table 5. Whale identifications in each stratum and year for summer areas. The number of matches between years are also shown, and unique IDs is the total number of whales identified in that stratum across the two years.

| Stratum | 2004 | 2005 | Matches | Unique IDs |
|---------|------|------|---------|-----------|
| Kamchatka | 16 | 29 | 9 | 36 |
| AI/BER | 249 | 286 | 40 | 495 |
| GOA | 769 | 372 | 154 | 987 |
| SEA/NBC | 897 | 426 | 270 | 1053 |
| SBC/NWA | 49 | 110 | 23 | 136 |
| CA/OR | 200 | 254 | 48 | 406 |

Table 6a. Number of unique whale identifications ($n$) in each year, and capture probabilities ($p)$ for summer areas from the Multistrata model analysis.

| | $n$ | | $p$ | |
|---|------|------|------|------|
| | 2004 | 2005 | 2004 | 2005 |
| Kamchatka | 25 | 38 | 0.018 (0.0102) | 0.046 (0.012) |
| AI/Ber | 289 | 326 | 0.129 (0.049) | 0.1256 (0.021) |
| GOA | 923 | 528 | 0.719 (0.163) | 0.182 (0.015) |
| SEA/NBC | 1167 | 690 | 0.150 (0.016) | 0.154 (0.009) |
| SBC/NWA | 72 | 136 | 0.284 (0.148) | 0.378 (0.099) |
| CA/OR | 248 | 303 | 0.064 (0.0118) | 0.084 (0.010) |

6b. Number of unique whale identifications ($n$) in each year, and capture probabilities ($p)$ for summer areas from the Chapman-Peterson model analysis.

| | $n$ | | $p$ | | se($p$) | |
|---|------|------|------|------|------|------|
| | 2004 | 2005 | 2004 | 2005 | 2004 | 2005 |
| Kamchatka | 25 | 38 | 0.244 | 0.371 | 0.070 | 0.098 |
| AI/Ber | 289 | 326 | 0.123 | 0.139 | 0.018 | 0.020 |
| GOA | 923 | 528 | 0.293 | 0.167 | 0.020 | 0.012 |
| SEA/NBC | 1167 | 690 | 0.388 | 0.232 | 0.018 | 0.012 |
| SBC/NWA | 72 | 136 | 0.175 | 0.323 | 0.033 | 0.055 |
| CA/OR | 248 | 303 | 0.159 | 0.194 | 0.021 | 0.025 |

Table 7.  Estimates of abundance for summer areas, with estimates from the Multistrata model ($N_{multi}$) and the Chapman-Peterson summer-summer model ($N_{CP}$). In each case, CV is the Coeffecient of Variation. Total is the total abundance summed across all strata.

| Stratum | $N_{multi}$ | CV | $N_{CP}$ | CV |
|---|---|---|---|---|
| Kamchatka | 1,111 | 0.371 | 103 | 0.230 |
| AI/Ber | 2,427 | 0.199 | 2,348 | 0.137 |
| GOA | 2,089 | 0.089 | 3,148 | 0.062 |
| SEA/NBC | 6,137 | 0.070 | 3,005 | 0.042 |
| SBC/NWA | 307 | 0.264 | 412 | 0.156 |
| CA/OR | 3,734 | 0.107 | 1,555 | 0.119 |
| Total | 15,805 | | 10,572 | |

Table 8.  Movement probabilities for the multi-strata model.
a. Probability of moving from each winter area (on left) to each summer area (as columns).  The CV of the estimate is in parentheses.

| Area moving from | Area moving to | | | | | |
|---|---|---|---|---|---|---|
| | Kamchatka | AI/Bering | GOA | SE/NBC | SBC/WA | OR/CA |
| Asia | 0.936 (0.04) | 0.064 (0.48) | 0.000 | 0.000 | 0.000 | 0.000 |
| Hawaii | 0.000 | 0.062 (0.26) | 0.078 (0.19) | 0.849 (0.14) | 0.010 (0.39) | 0.000 |
| Mexico | 0.000 | 0.091 (0.40) | 0.096 (0.38) | 0.052 (0.24) | 0.025 (0.43) | 0.736 (0.06) |
| Central America | 0.000 | 0.000 | 0.000 | 0.000 | 0.086 (0.12) | 0.914 (0.06) |

b. Probability of moving from each summer area (on left) to each winter area (as columns).  The CV of the estimate is in parentheses.

| Area moving from | Area moving to | | | |
|---|---|---|---|---|
| | Asia | Hawaii | Mexico | Central America |
| Kamchatka | 1.000 (0.01) | 0.000 | 0.000 | 0.000 |
| AI/Bering | 0.022 (0.49) | 0.865 (0.02) | 0.113 (0.25) | 0.000 |
| GOA | 0.005 (0.001) | 0.890 (0.01) | 0.105 (0.16) | 0.000 |
| SE/NBC | 0.000 | 0.939 (0.17) | 0.061 (0.03) | 0.000 |
| SBC/WA | 0.000 | 0.529 (0.15) | 0.419 (0.14) | 0.052 (0.91) |
| OR/CA | 0.000 | 0.000 | 0.896 (0.16) | 0.104 (0.45) |

Figure 1. Regional Strata for the analysis, with summer areas in blue and winter areas in green.  Within Asia, subareas are connected with thin green lines, representing Okinawa ("A"), Philippines ("B"), and Ogasawara ("C").  Within the Aleutian Islands and Bering Sea, a thin blue line connects the Gulf of Anadyr subarea ("D") to the rest of the area. The polygons roughly enclose where survey effort occurred for each area.
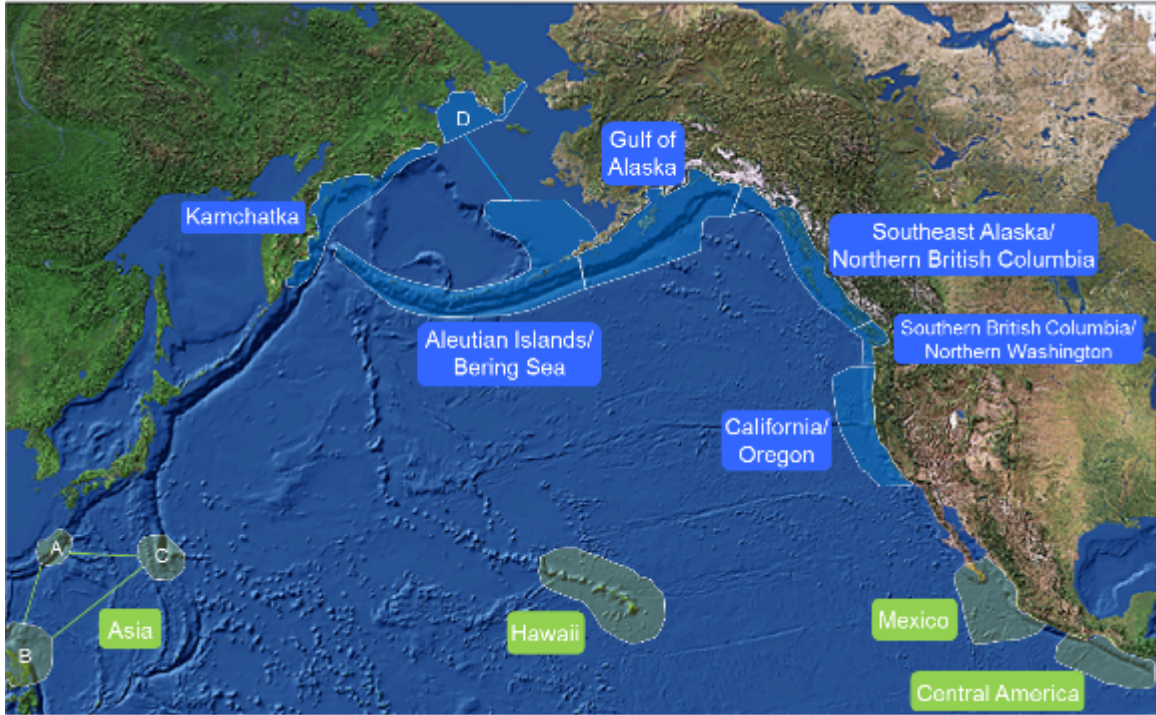
Figure 2. Abundance by area for summer (blue) and winter (green) areas, with 95% log-normal confidence limits in parentheses. Also shown are the estimated migratory destinations for each summer area (representing the breeding population composition found in the summer area), with the width of the arrow proportional to the percentage of whales in the feeding area that move to that winter/breeding area. Exact estimates are in Table 9. Areas are as in Figure 1.
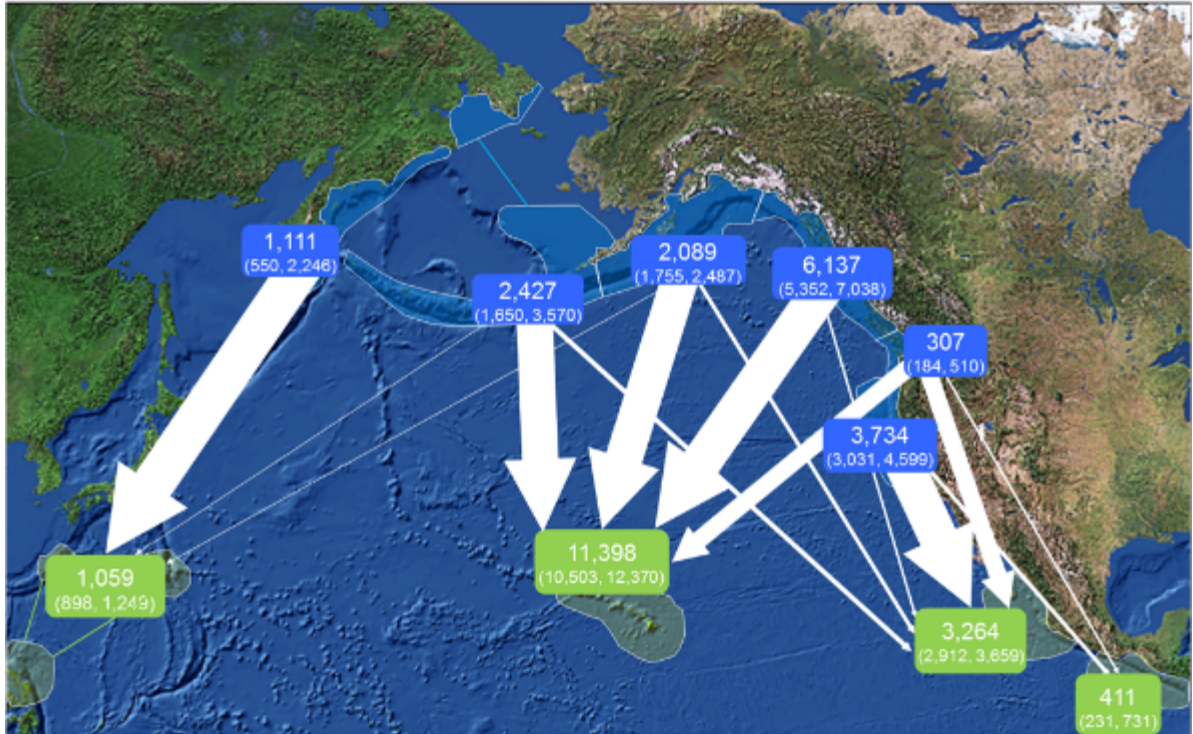
Figure 3. Comparison of summer abundance estimates, including the Multistrata estimates (N_MS), estimates extrapolated from the Multistrata winter abundance prorated by migration rates (N_MS_prorated), and the summer-summer Chapman-Peterson model estimates (N_CP).
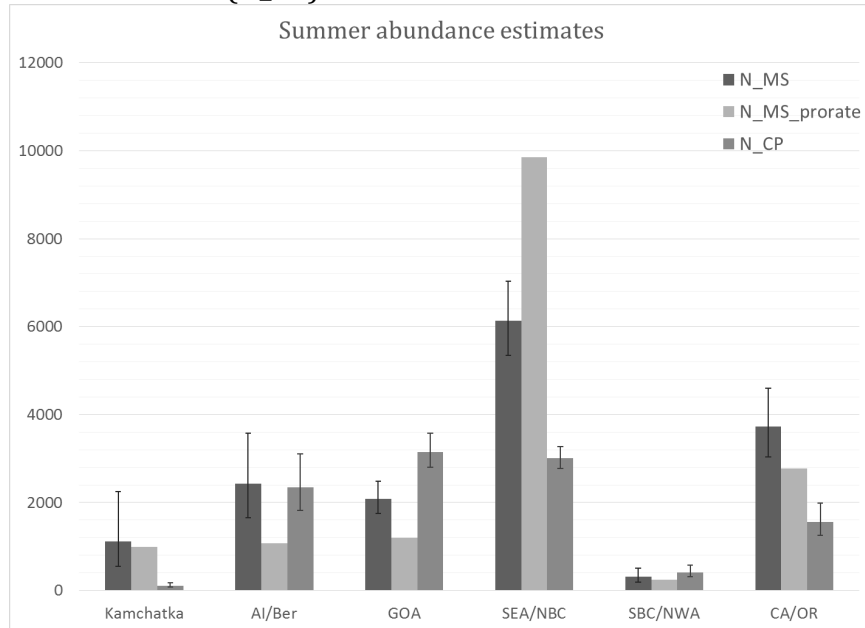


Figure 4. Comparison of winter abundance estimates, including the Multistrata estimates (N_MS), estimates extrapolated from the Multistrata summer abundance prorated by migration rates (N_MS_prorated), the Chao Mth winter-winter estimates (N_Chao), and the winter-winter Chapman-Peterson model estimates (N_CP).