# SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific

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# EXECUTIVE SUMMARY

Humpback whales were hunted commercially in the North Pacific until 1966 and remain on the endangered species list at the time of this report. The degree to which they have recovered from whaling in the North Pacific is difficult to determine because of the lack of accurate abundance estimates for this wide-ranging species. New methods such as photographic identification and analysis of skin and blubber biopsy samples have provided tools to examine the status of humpback whales. These animals undergo one of the longest migrations of any mammal and, within the North Pacific, their population structure and migrations appear to be complex. To effectively study and protect a species that travels widely across international borders requires a high level of collaboration among researchers and governments.

SPLASH (Structure of Populations, Levels of Abundance and Status of Humpbacks) represents one of the largest international collaborative studies of any whale population ever conducted. It was designed to determine the abundance, trends, movements, and population structure of humpback whales throughout the North Pacific and to examine human impacts on this population. This study involved over 50 research groups and more than 400 researchers in 10 countries. It was supported by a number of agencies and organizations including the National Marine Fisheries Service, the National Marine Sanctuary Program, National Fish and Wildlife Foundation, Pacific Life Foundation, Department of Fisheries and Oceans Canada, and Commission for Environmental Cooperation with additional support from a number of other organizations and governments for effort in specific regions. Results presented here include a comprehensive analysis of individual identification photographs. Additional analysis of human impacts, ecosystem markers (e.g., stable isotopes) and the genetic structure of populations are underway or planned pending further funding.

Field efforts were conducted on all known winter breeding regions for humpback whales in the North Pacific during three seasons (2004, 2005, 2006) and all known summer feeding areas during two seasons (2004, 2005). A total of 18,469 quality fluke identification photographs were taken during over 27,000 approaches of humpback whales. After reconciling all within and cross-regional matches (from both the primary match and rechecks), a total of 7,971 unique individuals were cataloged in SPLASH. A total of 6,178 tissue samples were also collected for genetic studies of population structure, with fairly even representation of wintering and feeding areas.

Migratory movements and population structure of humpback whales in the North Pacific were found to be more complex than had been previously described; a high degree of structure, however, was also apparent. Migrations between feeding and wintering areas were documented based on 873 whales that were seen on both a wintering and feeding areas. The overall pattern showed that coastal wintering regions of the western (Asia) and eastern (mainland Mexico and Central America) North Pacific were the primary wintering areas for the lower latitude coastal feeding regions. The wintering areas off Hawaii and the Revillagigedo Archipelago were the primary wintering regions for the more central and northern latitude feeding areas.

Even though the SPLASH study collected data from all known wintering and feeding areas for humpback whales in the North Pacific, the SPLASH data did suggest the likely existence of missing wintering areas that have not been previously described. Humpback whales that feed off the Aleutians and in the Bering Sea were not well represented on any of the sampled wintering areas and must be going to one or more unsampled winter locations. Thus, it is likely that SPLASH has revealed a new breeding ground for humpback whales. While it would be logical to assume that this region would be located in the eastern central North Pacific, the complexities of the migratory pathways revealed here indicate that this is not certain.

Individual whales showed high rates of return to specific wintering and feeding areas, suggesting strong site fidelity to both habitats. Interchange of whales between feeding areas both within and between seasons was unusual and all but a few of these were between adjacent areas. Similarly, whales tended to return to the wintering region they had inhabited previously, although the geographic scale of this varied by region. Whales showed frequent interchange among areas within the Hawaiian Islands but only rarely switched between broader regions. Some wintering areas that were sampled, especially Ogasawara and Baja Mexico, appeared to be transitory areas rather than migratory destinations. These findings are consistent with preliminary analyses of the genetic structure population showing a high degree of maternally-directed fidelity to both breeding and feeding grounds but a complex relationship between seasonal habitats.

Using several methods, the abundance of humpback whales was estimated to be just under 20,000 for the entire North Pacific, an estimate that is about double estimates made previously. The non-stratified Chapman-Petersen estimates of abundance were 18,000 to 21,000. Among geographically stratified models, the model assuming non-Markovian movements with capture probability proportional to sample size across years provided the best overall fit to the data indicated an abundance of 17,558 for wintering areas and 19,056 for the feeding areas. The average of these two estimates (18,302) represented the best estimate of overall abundance of humpback whales in the North Pacific, excluding calves. Over 50% of this population was estimated to winter in Hawaiian waters with large populations also inhabiting Mexican waters. The abundance estimates of humpback whales wintering in Asia and Central America were fairly low (1,000 or less). Among feeding areas, regional estimates differed greatly among models. Average estimates of abundance ranged from about 100-700 for Russia, 6,000-14,000 for the Bering Sea and Aleutians, 3,000-5,000 each for the Gulf of Alaska and the combined Southeast Alaska and Northern British Columbia area, 200-400 for Southern British Columbia-Northern Washington, and 1,400-1,700 for California-Oregon.

The SPLASH estimate represents a dramatic increase in abundance from other post-whaling estimates for the overall North Pacific, yet is consistent with a moderate rate of recovery for a depleted population. Comparison of the SPLASH estimate of 18,302 for all feeding and wintering areas to the estimate of 9,819 obtained for 1991-93 in a previous study suggests a 4.9% annual increase over this 13-year period. Going back to the estimate of 1,400 whales at the end of whaling for humpbacks in 1966, a 6.8% annual increase over the 39-year period would be required to reach the current SPLASH abundance. For Hawaii, three methods were used to compare estimates to determine trends since the early 1990s and yielded very similar annual rate of increase from 5.5 to 6.0%.

While the overall humpback whale abundance and trends in the North Pacific are encouraging, some areas should be of concern, especially Asia. The western-most feeding and wintering areas were distinct from the rest of the North Pacific with a very low level of interchange between Asian wintering or feeding areas and those in the central and eastern North

Pacific. Abundance estimates in this area are low (below historical levels based on the number taken in this region) and whales along the Asian coast appear to be subject to a high level of incidental mortality.

# INTRODUCTION

Humpback whale (*Megaptera novaeangliae*) populations were depleted due to commercial exploitation and are listed as endangered under the Endangered Species Act today. North Pacific humpback whale populations were thought to have numbered about 15,000 prior to commercial exploitation in the twentieth century (Rice 1978), however, this estimate was based on whaling data that may have been inaccurate. Approximate numbers in the North Pacific following the cessation of commercial whaling have been estimated at 1,400 (Gambell 1976) and 1,200 (Johnson and Wolman 1984).

The most recent estimate of North Pacific humpback whale abundance was conducted using capture-recapture statistics with photo-identification data from the early 1990s (Calambokidis *et al.* 1997, 2001, In prep.). This study was a retrospective analysis using data collected between 1990 and 1993 by 16 research groups from all areas of the North Pacific where photo-identification studies had been conducted. It yielded estimates of 6,000- 10,000 whales. This estimate is now 10 years old and a number of areas where whales are now known to be present were not represented in the study. Genetic data derived from biopsy samples also were not part of that study. Data from photo-identification and genetic studies have provided some information on North Pacific stock structure, verifying a high degree of site fidelity to feeding areas and the presence of individuals from multiple feeding areas at each wintering area but few individuals that move between wintering area; however, only limited data exist on the numbers, sizes, and ranges of most feeding areas in the North Pacific (Baker *et al*. 1986, 1993, 1994, 1998; Calambokidis *et al.* 1996, 2001).

We report on the first-ever comprehensive field study of humpback whales throughout the North Pacific. Termed SPLASH (Structure of Populations, Levels of Abundance and Status of Humpbacks), this work was the result of an international collaborative research effort conducted throughout the North Pacific which involved over 50 research groups and more than 400 researchers, and which was supported by a number of agencies and organizations. Primary support for the overall project and specifically for data collection in three of the five field seasons (Winter 2004, Summer 2004, and Summer 2005) came under a contract from NOAA's National Marine Fisheries Service and the National Marine Sanctuary Program. Major support including that to help fund the sampling in Winter 2005 and Winter 2006 came from the National Fish and Wildlife Foundation, Pacific Life Foundation, Department of Fisheries and Oceans Canada, and Commission for Environmental Cooperation. Significant support also came from a number of other organizations and governments for effort in specific regions.

# OVERALL OBJECTIVES

A dedicated sampling program and subsequent analyses of humpback whales at wintering and feeding areas within the North Pacific were conducted to address the following objectives:

- Collect a representative sample of photo-identification photographs of humpback whale populations throughout the North Pacific.

- Collect biopsy samples to provide a better understanding of population structure and migratory interchange using genetic markers.
- Estimate humpback whale overall abundance for the North Pacific basin using capture-recapture models.
- Estimate the abundance of humpback whales for specific wintering and feeding areas.
- Examine trends in abundance.

Additionally, data were gathered to examine human impacts on humpback whales including incidence of entanglement and ship strikes and other population parameters including reproductive rates, mortality rates, age/sex structure, pregnancy rates.

## METHODS AND STUDY DESIGN

SPLASH sampling was conducted by an international collaborative group of more than 50 research groups and 400 researchers coordinated by a Steering Committee that included coordinators for each of the regions (Table 1) sampled, as well as principals in the funding, coordination, and analysis of SPLASH.

*Table 1. Summary of organizations coordinating SPLASH-dedicated surveys and compiling opportunistic data contributions.*

| Research Group | Full Name | Survey Regions |
|---|---|---|
| **Feeding areas** | | |
| ASLC | Alaska Sealife Center | Russia |
| CRC | Cascadia Research | U.S. West Coast, British Columbia, Bering Sea |
| DFOC | Department of Fisheries and Oceans, Canada | British Columbia |
| GBNP | Glacier Bay National Park | Southeast Alaska |
| NGOS | North Gulf Oceanic Society | Northern Gulf of Alaska, Bering Sea |
| NMML | U.S. National Marine Mammal Laboratory | Southeast Alaska, Northern Gulf of Alaska, Western Gulf of Alaska, Bering Sea |
| SWFSC | Southwest Fisheries Science Center | SPLASH cruise of BC, SEAK, Gulf of Alaska, Aleutians and Bering Sea in 2004 and US West Coast in 2005 (CSCAPE) |
| UAFK | University of Alaska Fairbanks | N Gulf of Alaska, W Gulf of Alaska |
| UASE | University of Alaska Southeast | Southeast Alaska |
| **Wintering areas** | | |
| OMC | Ogasawara Marine Center | Asia including Philippines |
| HIWS | Hawaiian. Islands Humpback Whale National Marine Sanctuary. | Hawaii |
| UABCS | Universidad Autonoma de Baja California Sur | Mexico |
| CRC | Cascadia Research | Central America |

Sampling effort was designed to obtain a large and broadly distributed sample from each geographic region including both wintering and feeding areas and was collected in a manner to best achieve random sampling of all age and sex classes. Somewhat different sampling procedures were used on feeding versus wintering areas, particularly the type of research vessel used for sampling area. Data were collected during three seasons at wintering areas (2004, 2005, and 2006) and in two seasons (2004 and 2005) at feeding areas. In all regions, the goal was to apportion effort in a manner that was proportional to the anticipated density of animals. The study was designed to provide broad coverage of all known feeding areas (Figure 1) and wintering areas of humpback whales and within each area to sample as wide a geographic area as possible. Sampling within areas was conducted over a broad time period, especially in the wintering areas, to cover the full duration of the season (Table 2). This approach helped to avoid sampling bias regarding residency time and timing of arrival on the wintering regions.

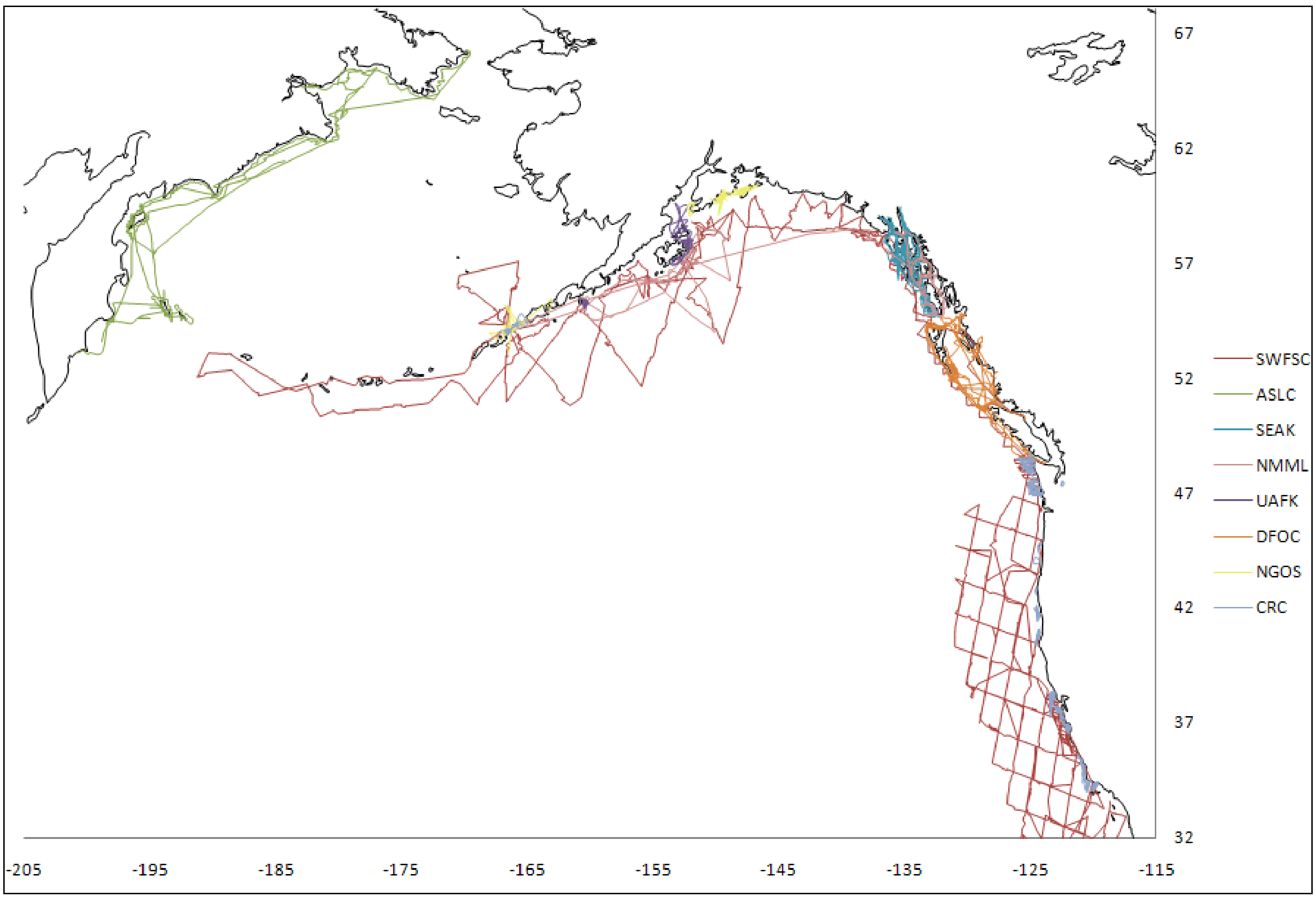


*Figure 1. Survey track lines and effort during surveys of feeding areas in 2004 and 2005.*

*Table 2. Summary of survey effort broken down by season and area.*

| Region | Start Date | End Date | Vessel Days | Research Groups | Fluke Identifica-tions | Fluke Ident/ SPLASH ID | Unique Individ. | Samples |
|---|---|---|---|---|---|---|---|---|
| **Winter 2004** | | | | | | | | |
| Asia-PHI | 26-Feb-04 | 01-May-04 | 33 | WWFP | 56 | 50 | 27 | 3 |
| Asia-OK | 17-Feb-04 | 05-Mar-04 | 12 | OCA | 85 | 72 | 43 | 0 |
| Asia-OG | 10-Jan-04 | 13-May-04 | 47 | OMC | 294 | 205 | 114 | 45 |
| Hawaii | 02-Dec-03 | 12-May-04 | 174 | CFWS, HIWS, HMMC, HWRF, MMRC, OWSI, TDI, WHTR | 1170 | 839 | 697 | 540 |
| MX-REV | 24-Jan-04 | 16-Apr-04 | 169 | COR, HSU, UNAM | 1352 | 1206 | 317 | 151 |
| MX-Baja | 20-Jan-04 | 03-Apr-04 | 60 | UABCS, UNAM | 215 | 183 | 182 | 176 |
| MX-ML | 30-Nov-03 | 08-Apr-04 | 226 | COVISI, FIBB, UNAM | 527 | 417 | 223 | 77 |
| Cent Am | 14-Jan-04 | 22-Mar-04 | 41 | CRC | 27 | 23 | 18 | 12 |
| Total | | | | | 3,726 | 2,995 | 1,621 | 1,004 |
| **Summer 2004** | | | | | | | | |
| Russia | 18-Jul-04 | 19-Aug-04 | 16 | ASLC | 65 | 57 | 40 | 30 |
| W Aleut. | 16-Aug-04 | 22-Aug-04 | 8 | SWFSC | 18 | 15 | 12 | 9 |
| E Aleut. | 21-Jul-04 | 15-Sep-04 | 20 | NMML, SWFSC | 76 | 66 | 51 | 38 |
| Bering | 09-Jun-04 | 10-Sep-04 | 62 | NGOS, NMML, SWFSC | 415 | 302 | 228 | 106 |
| WGOA | 21-Jul-04 | 19-Sep-04 | 29 | NMML, SWFSC, UAFK | 400 | 334 | 223 | 120 |
| NGOA | 07-May-04 | 08-Oct-04 | 209 | NGOS, UAFK, NMML, SWFSC | 1359 | 1174 | 730 | 247 |
| SEAK | 01-May-04 | 14-Dec-04 | 246 | CRC, GBNP, NMML, SWFSC, UASE, UAFB | 1933 | 1566 | 808 | 347 |
| NBC | 01-Jan-04 | 27-Nov-04 | 254 | DFOC, SWFSC | 1050 | 868 | 421 | 106 |
| NWA-SBC | 18-Apr-04 | 23-Nov-04 | 46 | CRC, DFOC, SWFSC | 171 | 106 | 76 | 26 |
| CA-OR | 04-Apr-04 | 13-Dec-04 | 108 | CRC | 598 | 421 | 253 | 65 |
| Total | | | | | 6,085 | 4,909 | 2,842 | 1,094 |
| **Winter 2005** | | | | | | | | |
| Asia-PHI | 17-Feb-05 | 02-May-05 | 60 | WWFP | 86 | 65 | 35 | 6 |
| Asia-OK | 18-Feb-05 | 25-Mar-05 | 20 | OCA | 122 | 114 | 55 | 0 |
| Asia-OG | 27-Dec-04 | 13-May-05 | 53 | OMC | 524 | 292 | 123 | 60 |
| Hawaii | 15-Dec-04 | 29-Apr-05 | 212 | ANZO, CFWS, HAMR, HIWS, HMMC, HWRF, MMRC, OWSI, TDI, WHTR | 1718 | 1102 | 846 | 668 |
| MX-REV | 08-Feb-05 | 22-Apr-05 | 132 | COR, HSU, UNAM | 781 | 568 | 193 | 123 |
| MX-Baja | 08-Jan-05 | 30-May-05 | 103 | CRC, UABCS | 382 | 198 | 157 | 97 |
| MX-ML | 16-Nov-04 | 16-Mar-05 | 261 | COVISI, CRC, FIBB, UNAM | 741 | 462 | 266 | 150 |
| Cent Am | 17-Jan-05 | 18-Mar-05 | 54 | CRC | 82 | 69 | 48 | 15 |
| Total | | | | | 4,436 | 2,870 | 1,723 | 1,119 |
| **Summer 2005** | | | | | | | | |
| Russia | 22-Jun-05 | 14-Aug-05 | 44 | ASLC | 101 | 98 | 72 | 43 |
| Bering | 25-Jun-05 | 10-Sep-05 | 39 | CRC, NGOS, NMML | 755 | 475 | 301 | 164 |
| WGOA | 31-May-05 | 11-Sep-05 | 15 | NMML, UAFK | 284 | 205 | 111 | 81 |
| NGOA | 09-Jan-05 | 25-May-06 | 183 | NGOS, NMML, UAFK | 1117 | 755 | 427 | 292 |
| SEAK | 09-Jan-05 | 11-Jan-06 | 167 | CRC, GBNP, NMML, UASE | 1545 | 1096 | 482 | 145 |
| NBC | 24-Jan-05 | 26-Jan-06 | 236 | DFOC | 826 | 608 | 236 | 56 |
| NWA-SBC | 25-Feb-05 | 27-Dec-05 | 169 | CRC, DFOC, SWFSC | 424 | 329 | 152 | 33 |
| CA-OR | 08-Mar-05 | 05-Dec-05 | 221 | CRC, SWFSC | 848 | 680 | 319 | 74 |
| Total | | | | | 5,900 | 4,246 | 2,100 | 888 |
| **Winter 2006** | | | | | | | | |
| Asia-PHI | 19-Feb-06 | 30-Apr-06 | 79 | WWFP | 88 | 47 | 26 | 0 |
| Asia-OK | 12-Jan-06 | 30-Mar-06 | 95 | OCA | 633 | 424 | 152 | 94 |
| Asia-OG | 27-Nov-05 | 24-May-06 | 63 | OMC | 775 | 285 | 119 | 259 |
| Hawaii | 14-Nov-05 | 30-Apr-06 | 321 | ANZO, CFWS, HAMR, HIWS, HMMC, HWRF, MMRC, OWSI, TDI, WHTR | 3590 | 1488 | 1026 | 1174 |
| MX-REV | 30-Jan-06 | 22-Apr-06 | 159 | COR, HSU, UNAM | 929 | 532 | 186 | 198 |
| MX-Baja | 10-Dec-05 | 17-May-06 | 52 | UABCS | 198 | 120 | 87 | 121 |
| MX-ML | 09-Dec-05 | 31-May-06 | 195 | COVISI, FIBB, UABCS, UNAM | 777 | 475 | 328 | 204 |
| Cent Am | 05-Dec-05 | 19-Mar-06 | 55 | CRC | 101 | 78 | 46 | 23 |
| Total | | | | | 7,091 | 3,449 | 1,970 | 2,073 |
| All seasons total | | | | | 27,238 | 18,469 | 10,256 | 6,178 |
| Unique after internal matches | | | | | | | 7,971 | |

## Data collection methods

*Photo-identification*

Photographs of pigmentation patterns and scarring on the ventral surface of tailflukes, together with serration patterns along the trailing edge (Figure 1), were used to individually identify whales (*e.g.*, Katona *et al.* 1979). To obtain photographs, whales were photographed with digital SLR cameras equipped with telephoto lenses.

*Biopsy sampling*

Skin and attached blubber tissue samples were collected for genetic analysis using a small stainless steel biopsy dart fired from a crossbow or modified rifle or air-powered gun. Each dart was fitted with a flange or "stop" that regulated penetration of the bolt/dart and caused recoil after sampling. Flotation material secured to the shaft of the bolt/dart allowed it to float on the surface and be retrieved after sampling. Crossbows, most commonly with a draw of 68 kg (150 lbs), and veterinary rifles using either compressed air or blank charges with adjustable pressure were used for sample collection. Depending on field conditions, samples were preserved by freezing immediately after sampling or by immersion in a saturated solution of salt (many samples were also stored in ethanol if freezing was not available). At least half of each biopsy tissue sample (skin and attached blubber if blubber is obtained in the sample) was submitted to the marine mammal tissue archive at the Southwest Fisheries Science Center. An initial analysis of population structure using a representative subset of 2,000 samples is underway with funding from National Fisheries and Wildlife Foundation and the Marine Mammal Institute of Oregon State University.

## Regional sampling effort

A variety of approaches were used in the SPLASH sampling summarized in Table 2 and are briefly described by region below. Regional strata were assigned at the outset, based on areas of effort and concentrations of sightings and then modified or pooled based on preliminary results as described in the text. Region names and abbreviations and how they were pooled for the mark-recapture analyses are listed in Table 3.

*Asia*

The winter distribution of humpback whales in the western North Pacific is centered off the Ogasawara Islands, Ryukyu (Okinawa) Islands, Taiwan, the Philippines, and the Mariana Islands. Humpback whales in this geographic region are distributed over a large area along this chain of islands. Past photographic identification has been conducted in this region began in the 1990s (Darling and Mori 1993, Yamaguchi *et al*. 2002, Acebes 2001, Acebes *et al*. 2007). SPLASH effort in this region was coordinated by the Ogasawara Marine Center (Manami Yamaguchi). Sampling was conducted in the following areas: 1) Ogasawara including Chichi-jima, Haha-jima (50km from Chichi-jima) and Muko-jima (70km from Chichi-jima) by OMC, 2) Okinawa including Okinawa mainland and Zamami Islands (40km from Okinawa mainland) by the Okinawa Expo Aquarium, and 3) Philippines around the Babuyan Islands by World Wildlife Fund-Philippines (Acebes *et al*. 2007). Effort was conducted primarily from shore-based small boats.

*Table 3. Summary of area designations and abbreviations used in SPLASH.*

| **Area (subarea)** | **Abbreviation** | **6x6 model abbrev.** |
|---|---|---|
| Russia (pooled regions) | | |
| Kamchatka | Kamchatka | Russia-Kam |
| Commander Islands | Commander Is | Al-Ber |
| Gulf of Anadyr | | Al-Ber |
| Aleutian Islands | Aleut | Al-Ber |
| Western Aleutians | W Aleut | Al-Ber |
| Eastern Aleutians | E Aleut | Al-Ber |
| Bering Sea | Bering | Al-Ber |
| Gulf of Alaska | GOA | GOA |
| Western Gulf of Alaska | WGOA | GOA |
| Northern Gulf of Alaska | NGOA | GOA |
| Southeast Alaska | SEAK | SEAK-NBC |
| Northern British Columbia | NBC | SEAK-NBC |
| Southern British Columbia-Northern Washington | SBC-NWA | SBC-NWA |
| California-Oregon | CA-OR | CA-OR |
| Asia | Asia | Asia |
| Philippines | Asia-PHI | Asia |
| Japan-Okinawa | Asia-OK | Asia |
| Japan-Ogasawara | Asia-OG | Asia |
| Hawaii | HI | HI |
| Kauai | Kauai | HI |
| Oahu | Oahu | HI |
| Penguin Bank | PB | HI |
| Molokai | Molokai | HI |
| Maui | Maui | HI |
| Big Island | Big Is | HI |
| Mexico | MX | |
| Mainland | MX-ML | Mx-Main |
| Baja | MX-Baja | Baja |
| Revillagigedo | MX-REV | Mx-Rev |
| Central America | Cent Am | CentAm |

*Hawaii*

Sampling for the SPLASH project in Hawaii was coordinated and funded by NOAA's Hawaiian Islands Humpback Whale National Marine Sanctuary (Dave Mattila and Alan Ligon). The Sanctuary and its partner, the State of Hawaii, contracted local humpback whale researchers, who have been consistently active in the region, to collect geographically and temporally representative data for SPLASH. These represent eight teams: on Kauai (1), Oahu (1), Penguin Bank (1), Maui (4) and the Big Island (1).

*Mexico*

There are three main winter aggregations in the Mexican Pacific: the southern end of Baja California Peninsula (Baja); central portions of the Pacific coast of mainland Mexico (Mainland); and the Revillagigedo Archipelago (Revillagigedo)(Urban and Aguayo, 1987). Jorge Urbán was the regional coordinator for the field sampling in Mexico. Field sampling in Baja was primarily conducted by UABCS coordinated by Ursula Gonzalez, off mainland Mexico by UNAM and UABCS and off the Revillagigedos by Jeff Jacobsen and included effort by personnel associated with Humboldt State University, Cornell University, and UNAM. The primary platforms for dedicated effort were inflatable boats at Revillagigedo and pangas at mainland and Baja with 2-4 people, with additional effort as part of broader surveys from larger platforms. Most of the effort off mainland Mexico was conducted around Bahia de Banderas with some surveys conducted near the area around the Islas Tres Marias. An important part of the effort in this region was the contribution of two groups who compiled identification photographs obtained opportunistically during whale watching operations in and around Bahia de Banderas. These were COVISI (coordinated by Maria Eugenia Rodriguez and Eduardo Lugo of Wildlife Connections) and FIBB (coordinated by Astrid Frisch of Ecotours de Mexico).

*Central America*

The waters from southern Mexico south along the Central America coast are used as a wintering area for humpback whales coming almost exclusively from feeding areas off California (Steiger *et al.* 1991; Calambokidis *et al.* 2000; Rasmussen *et al.* 2001). Cascadia Research coordinated surveys in this region. To cover this broad low-density area, surveys were conducted in a number of ways: 1) dedicated surveys were made from small chartered boats, 2) a network of local collaborators were set up to obtain opportunistic identifications, and 3) identification photographs were collected during several weeks of surveys in collaboration with Oceanic Society Expeditions trips in southern Costa Rica. Dedicated small-boat surveys were conducted in Guatemala, El Salvador, Nicaragua, and Costa Rica.

*US West Coast including California, Oregon, and Washington*

Surveys conducted along a broad area of the U.S. west coast were coordinated by Cascadia Research and SWFSC using several platforms and with additional contributions from a number of sources included:

1. Dedicated small boat surveys using 5-6m RHIBs based from various harbors all along the coast.
2. CSCAPE cruise conducted by SWFSC in 2005 off the coast of California, Oregon, and Washington.
3. Opportunistic identifications obtained by naturalists, researchers, and boaters including the Naturalist Corps working with the Channel Islands National Marine Sanctuary.
4. SPLASH sampling was conducted in June based from a NOAA ship and deployed RHIB during surveys off Washington conducted with the Olympic Coast National Marine Sanctuary (OCNMS).

Washington and southern British Columbia were treated as a single region because the concentration of whales straddles the border and the same general areas were being sampled from effort originating on either side of the border.

*British Columbia*

DFO coordinated sampling effort in British Columbia which included small-boat surveys, ship surveys and opportunistic identifications. A joint DFO and Cascadia survey aboard the charter vessel *Curve of Time* with two deployed RHIBs was conducted off northern Vancouver Island and off the Queen Charlotte Islands each August. Additional identifications were obtained as a part of ship surveys conducted by DFO generally in spring and fall of each year. Small-boat effort was conducted off northern British Columbia from a variety of vessels that operated widely along the mainland coast or were based at Langara Island. SPLASH effort off southern British Columbia was conducted from a small charter boat operating along the southwest side of Vancouver Island. Surveys were conducted in West Hecate Strait in collaborations with Parks Canada.

*Southeast Alaska – coastal effort*

Three primary research groups collected data in SPLASH in Southeast Alaska: University of Alaska Southeast, Glacier Bay National Park and Preserve and National Marine Mammal Laboratory. UASE vessel charters worked the inside waters of Peril Straits, Lynn Canal, Chatham Strait, Stephens Passage, Frederick Sound and the outside near-shore waters from Dixon Entrance to Cross Sound. Researchers from the Glacier Bay National Park and Preserve surveyed Glacier Bay and Icy Strait. The NOAA vessel *John Cobb* surveyed the inside waters of southern Southeast Alaska.

*Northern and Western GOA*

Coastal effort in the Gulf of Alaska and Aleutians was conducted through a subcontract to the North Gulf Oceanic Survey (NGOS, Craig Matkin) and coordinated by Kate Wynne and Bree Witteveen (UAFK). Sampling was conducted successfully in a number of areas including 1) Prince William Sound and Kenai area, 2) Barren Islands, 3) Kodiak Is. area, 4) Shumagin Islands, and 5) eastern Aleutian Islands.

*Russia*

Surveys for humpback whales on feeding grounds off Russia were conducted primarily based from a larger charter vessel and smaller deployed boats under subcontract to North Pacific Wildlife Consulting LLC (Alexander Burdin). The primary survey areas included Anadyr Gulf, Bering Island, Litke Strate, Karaginsky Island, Dezhnevia Bay and the Commander Islands.

*NMML ship surveys in Alaska waters*

The National Marine Mammal Laboratory (NMML) conducted a range of large-scale ship surveys using the NOAA vessel *Oscar Dyson* and other platforms in the waters off Alaska especially in 2005. These covered broad areas of the Gulf of Alaska, Aleutian Islands, and Bering Sea including offshore areas missed by the coastal-based work described above.

*SWFSC ship surveys - 2004*

A large scale ship survey was conducted in 2004 by SWFSC that encompassed waters off British Columbia, SE Alaska, Gulf of Alaska, Aleutians, and the Bering Sea. This survey provided somewhat systematic coverage of broad portions of the feeding areas of humpback whales, especially in offshore waters.

## Management of regional submissions

At the end of each field season (or incrementally throughout the field season), regional coordinators received copies of all photographs, datasheets, vessel track lines, and tissue samples collected. In some cases, the contributors entered their data into a digital format and provided this to the regional coordinator. Additionally, some contributors reconciled their photographs and provided a set of best flukes for each unique individual that they encountered that season as well as a complete archive of all photographs taken.

Regional coordinators were responsible for the compilation of regional data from a season into a unified database including effort, sighting, identification, and sample data fields requested prior to submission to Cascadia Research. Data were either entered from hard copies of the field notes provided by the contributors, or imported from digital formats. Regional coordinators then reviewed photograph archives from each sighting to identify (or verify) selections of the best photos (fluke, left and right flanks, and tailstocks) of each individual, and these filenames were imported into the database. In most cases, where software was available, a selection of sighting data was also imported into the metadata fields associated with each image file.

The best fluke photographs from each sighting within an area were compared to each other. Regional coordinators included low quality fluke photos in this preliminary match stage to identify as many within area resightings of individual whales as possible. At the completion of regional reconciliation, a copy of the best fluke photograph of each whale for that season was copied into a separate folder, and an area-season working ID number was assigned to each. This number was assigned to all identifications of the whale within the area, and was also updated in database records where the identity of the biopsy sampled whale was known within a sighting. A digital copy of this preliminary catalog was provided to the central matching office, along with the combined data for all contributors from the area. Tissue samples were sent separately to the lab at SWFSC for archiving, extraction, and/or distribution.

The seasonal collection from each area, including archives of all photographs collected, all vessel track lines, the combined regional database, preliminary catalog, and hard copies of the original field datasheets if available, were sent to Cascadia for reference and archiving.

## Data compilation and catalog development

Each regional database was imported into the combined seasonal SPLASH sighting database. SPLASH data were compiled using a Microsoft Access relational database which was designed specifically for the SPLASH project and which was comprised of six related tables for field data. The top tier table contained a record for each vessel survey day that included regional information, contributing organization, personnel, effort type (SPLASH dedicated or opportunistic) and total survey hours. Related to this table by research group (contributing organization), date, and vessel were tables with time and position data for effort-related events, such as changes in environmental conditions and whale sightings. The remaining two tables, which contained records for each individual identified and samples collected during a sighting, were linked to the sightings table by research group, date, vessel, and a unique sighting number for that vessel-day.

Upon receipt, the preliminary catalog was reviewed for metadata completeness and accuracy, and fields were added or reformatted as necessary for each best fluke image to include linked information for research group, photographer, sighting information, and the working ID number of the pictured whale. The preliminary catalog was converted to a digital print layout using the *Fotoslate* plug-in of the *ACDSee* photo management software package. The layout applied custom settings to each image that cropped and adjusted the exposure of each fluke and converted each image to grayscale prior to printing, without actually altering the original image file, thus avoiding any loss in quality that may have resulted from sequentially resaving JPG files.

Layouts were printed with associated metadata on a label. The layouts were cut into individual fluke photos, which were then sorted into the numeric color categories (1-5, from lightest to darkest) that were used to organize all SPLASH collections at the central matching level. Some color categories were further separated into subcategories by proportion of pigmentation and, in the case of all black flukes, by a hierarchical classification of mark types. During this step, incidental matches within a collection were sometimes encountered. If a significant number of internal matches were found, a complete re-reconciliation of the preliminary catalog was undertaken. As part of the initial color-sorting procedure, very poor quality flukes were rejected from the collection.

After sorting and reconciliation, remaining best fluke photos from each region were coded on a scale of 1-5 for five quality features (proportion visible, vertical angle, lateral angle, focus/sharpness, and exposure) and three characteristic features (distinctiveness of the trailing edge, degree of scarring, and presence of killer whale rake marks) using the same process developed previously (Calambokidis *et al*. 1997, 2000). As part of the coding process, each printed fluke photo was verified in the database, and other resightings of the pictured whale were reviewed for accuracy and to verify that the fluke photograph in the preliminary catalog was the best of season. After an entire collection was coded, flukes that received a score of 4 or higher in any quality category or scored 3 in more than three quality categories were rejected (however there were some exceptions to this in the case of small collections, where marginal flukes were included in the match to augment sample size). In most cases, if a rejected fluke was at or near the level of acceptability, all images of the whale from its initial sighting were reviewed to ensure that the best fluke of the sighting had accurately been selected per SPLASH criteria, and in some cases the original best fluke was replaced. All best flukes and rejected flukes were quality coded in the database; known resighting flukes were not coded.

After coding, the best fluke photos were placed in archival-quality clear plastic sleeves within their assigned color category. Any flukes that were known to be from calves (and thus subject to significant change in appearance over time) or which had ambiguous coloration (and were thus difficult to confidently assign to a color category) were flagged in the database and a copy of the photo was placed in a supplemental category at the end of each catalog for special attention during matching. Once assembled, the final catalog was reviewed for consistency in color-coding and quality screening, and each individual was assigned a six-digit SPLASH ID number, which reflected the season and region in which it was assigned to the whale. SPLASH IDs were then updated into all identifications of the whale in the identifications table, and each fluke identification record was classified as either the catalog best for the pictured whale, a regional resighting for that season, or a reject in the coding table.

## Photographic matching

All SPLASH comparisons were conducted manually by a team of six experienced humpback whale fluke matchers. Because it was not feasible to manually compare every whale in every catalog against every other whale as the SPLASH collection became progressively larger, a series of protocols were developed to expedite the matching process. These protocols increased the likelihood of finding matches quickly, removed whales from the match process once found in an earlier catalog, and systematically limited the number of flukes against which each whale was ultimately compared; subsequently they introduced a certain potential to miss matches by exclusion. Extensive collateral data were collected with each comparison to record which photos were actually compared, as well as to later assess any biases in match rate associated with factors such as matcher, fluke color, or collection.

A series of regional catalogs were organized for each season, although the Summer 2004 SWFSC cruise and NMML cruises were combined in a single catalog. Regional catalogs from a current season were sequentially compared against all earlier catalogs[1], prioritizing comparison against the regions of highest known match rates (either from other studies or previous seasonal comparisons). In this way, each regional catalog was always compared first to the same region in a previous year (*e.g.*, Hawaii 2005 against Hawaii 2004), and then to the feeding or wintering area catalogs known to have the highest interchange rates (*e.g*., Hawaii 2005 against SEAK 2004). Once a whale was found in an earlier catalog, the previously assigned SPLASH ID was recorded in the match log, along with the relative quality of the new photo to the previous photograph, and any changes in the fluke itself. If the newer photograph of the whale was of comparable or lesser quality to the older photo and there were no significant changes in the fluke, the newer was covered in its catalog and excluded from further comparison against other collections. If the new fluke photograph was substantially better quality and/or different than the earlier photo, it remained uncovered and continued through the comparison to all other earlier collections.

The fluke photograph being matched was compared to all flukes in the corresponding color category of the earlier catalog, as well as all flukes in the color categories preceding and following, and all flukes in the calf/ambiguous section. Because it was sometimes more difficult to accurately assign color to the darkest flukes, all whales in the 4C section were compared against the 4B section and all the 5 sub-categories, and all whales in the 5 sub-categories were also compared against the 4C section. At matcher discretion, a given fluke was compared to additional color categories beyond those dictated by protocol if either its coloration or quality warranted a broader search.

When comparisons to all previous season catalogs were completed for a current season, the remaining uncovered photos in each regional catalog were compared against each other to identify any same-season movements among whales new to the SPLASH collection. All match logs for the season were compiled in preparation for collapsing catalogs and updating the SPLASH IDs assigned that season to the lower number for all whales that had been identified previously. As a final step to completing a seasonal match, any better/changed photos of whales seen previously were moved into the earliest catalog in which the match was found, photographs of whales seen previously that were not better were moved out of the active matching section of the newer catalog, and whales new to SPLASH were condensed in their current catalog in preparation for the next seasonal comparison. Consequently, there was only ever one active photo of each whale, its best to date, which was being compared against in subsequent seasons.

Upon completion of the final season of matching (Winter 2006), catalogs were not collapsed as in previous seasons. Instead, SPLASH IDs were updated on the photos and in the database, and original catalogs were reconstructed so that selective matches between collections could be conducted using the same photos initially compared. In this way, a whale seen in multiple seasons and regions would be represented by its best of collection photo in every catalog it had been in, but with its unified, lowest SPLASH ID number. Additionally a single

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[1] The one exception to this pattern was Winter 2004, which was compared against Summer 2004, rather than vice versa, to facilitate simultaneous comparisons by multiple matchers working within two collections that were still relatively small.

digital catalog was compiled containing the single best photograph of each individual identified in SPLASH.

## Evaluation of rates of missed matches and double checks

A complete double match of the entire SPLASH collection was not possible due to the number of photographs, so several experiments were conducted to quantify the error rates associated with the initial match. Nine comparisons among collections were completely rechecked: five rechecks were conducted throughout the matching process to verify and refine matching protocols, and four were conducted after the final match was completed.

A more systematic assessment of error rate was included in the final Winter 2006 comparison by “seeding” the Winter 2006 catalogs with 266 known matches to earlier catalogs. The Winter 2006 catalog included roughly 10% “seeds” (relative to its initial size), which were evenly distributed across color categories, quality scores, matching regions, and seasons. The seeded matches were assigned false SPLASH IDs and printed with mock labels so that the matchers were blind to which photographs were seeds. In this way, a rate at which known matches were missed was calculated for each matcher and factors which contributed to a higher than usual miss rate could be identified as Winter 2006 was compared to the 21 previous SPLASH catalogs.

In total 246 of 266 seeded matches were found (92%), consistent with expectations and similar to the match success rate found in a previous study using similar quality scoring criteria as employed here (Calambokidis *et al*. 1997). The average score of the five quality criteria used to rate photographs was only slightly higher (poorer quality) for those that were missed ($n$ = 20, mean = 2.16, SD = 0.28) than those that were found ($n$ = 246, mean = 2.03, SD = 0.33). Although this difference was not significant, the results of specific quality characteristics proved relevant. We looked at the success rate in finding those seeded matches where the photograph was at our cut-off for acceptance; match success rate ranged from high of 96% for photographs with no quality scores at three (the poorest acceptable rating) to a low of 82% when three of the criteria were rated as a three (no more than three scores of three were allowed or the photograph to be included in the SPLASH comparison). The clarity of the photograph (*i.e.,* quality score for focus) appeared to be the most important factor in whether a match was missed, with the largest difference in this category between the photographs where matches were found and those that were missed (mean score of 2.1 vs. 2.6, a highly significant difference, ANOVA, p = 0.005). Similarly, when the quality scores of both the seeded match and the whale it matched to were pooled, both the quality score for exposure and focus were significantly better for whales where the match was found versus those that were missed (ANOVA, p = 0.04 and p = 0.001 for exposure and focus, respectively).

Selective rechecking also indicated an overall match success rate of close to 90% for both initial and secondary comparisons. A total of 148 out of 165 matches were found (90%) in either an initial matching or in a recheck. Two matches were missed due to protocol (color category not checked) and discovered incidentally. The influence of photograph quality was assessed for the remaining 31 missed matches. Photo quality did not appear to be a factor in 10 of 31 missed matches (39%), where both the photo being matched and the catalog photo had better than average quality scores (<1.9) and did not score a 3 in any category. For the remaining 21 cases, 11 misses were attributed to low quality in both photos, 5 involved a low quality photo in the catalog, and 5 were attributed to a low quality photo in hand. No specific quality fault appeared unusually high among missed match photos.

Based on the relatively high success rate in finding matches (at least 90%) no additional exclusions from the analysis were made based on quality. Additional matches that were found in the rechecks were included in the SPLASH sample because a correction factor for missed matches was not being applied.

## ANALYTICAL METHODS

We examined abundances of humpback whales using several capture-recapture methods including simple Chapman/Petersen models and a more complex multi-strata model to estimate the abundance of humpback whales in feeding and wintering areas of the North Pacific in conjunction with calculated migration rates among these areas. We used a geographically stratified mark-recapture model (Hilborn 1990) similar to that used in the past analyses of the 1990-93 humpback photo-identification data (Calambokidis *et al.* 1997). In this approach, parameters for migration between feeding and wintering areas, survival, and capture probability were estimated in a likelihood setting. Abundance was estimated by dividing the number of sampled animals in an area by the estimated capture probability. Details of the methodology as applied to feeding areas in Southeast Alaska are given in Straley *et al.* (In press).

For mark-recapture abundance estimates, known calves were excluded from their first winter and feeding season because these animals can be harder to identify and accurately match. For the Hilborn models we also restricted the number of feeding and wintering areas to six each (with five seasons) as summarized in Table 3. Because the model did not allow for an animal to be seen in multiple areas in the same period, in the event an animal was seen in more than one area it was assigned to the area where it was seen closest to the middle of the season (1 March for wintering areas and 1 August for feeding areas). In the few cases were whales were identified on feeding areas in winter months, they were assigned to the previous or following feeding season using 1 March as a cut-off (even though they may have been submitted and compared as if they were part of a different season).

The Hilborn method estimates the size of a geographically stratified population that moves between areas and sampled during different time periods (Hilborn 1990; Quinn and Deriso 1999, Chapter 10; Calambokidis *et al.* 1997). For a given release group in a given year stratified by area, a model was constructed to predict the matrix of recaptures by release area and recovery area for each time period. In this application, two sets of areas were defined: six wintering areas and six feeding areas, and given time-periods denoted [Winter 2004 (W04), Summer 2004 (S04), Winter 2005 (W05), Summer 2005 (S05), and Winter 2006 (W06)]. It is assumed that survival is equal to 1, because of the short duration of the study (2 years) and thus estimates of abundance would not be appreciably biased. The key information derived from mark recaptures were estimates of capture probabilities and probabilities of movement between different areas. We denoted capture probability as $p_{tj}$ for time period $t$ and capture area $j$.

Two different assumptions about movement were evaluated. The first assumption was that movement followed a Markov process, in which the probability that a mark was in a given area depended on where the mark had been the previous season. This required having two movement matrices: $\Theta_{WS}$ for winter-to-summer movement and $\Theta_{SW}$ for summer-to-winter movement, each of size 6x6. The second assumption was that movement followed a non-Markov process, in which the probability that a mark was in a given area was not dependent on season but rather depended on where the mark had been the previous year. In other words, winter recaptures depended on where the whales had been the previous winter, and summer recaptures depended on where the whales had been the previous summer. This required having two additional movement matrices: $\Theta_{WW}$ for winter-to-winter movement and $\Theta_{SS}$ for summer-to-summer movement.

For this application, there were release groups in each of the first four time periods. The first release group in W04 had four sets of mark-recapture matrices in subsequent time periods, and each subsequent release group had one less mark-recapture matrix. A schematic showing which movement matrices were used in each period is shown in Table 4.

*Table 4. Depiction of which movement matrices were applied to recapture periods for each release group, (a) Markovian movement, (b) Non-Markovian movement.*

| (b) | Recapture period | | | |
|---|---|---|---|---|
| Release group | S04 | W05 | S05 | W06 |
| W04 | $\Theta_{WS}$ | $\Theta_{WW}$ | $\Theta_{SS}$ | $\Theta_{WW}$ |
| S04 | | $\Theta_{SW}$ | $\Theta_{SS}$ | $\Theta_{WW}$ |
| W05 | | | $\Theta_{WS}$ | $\Theta_{WW}$ |
| S05 | | | | $\Theta_{SW}$ |

| (a) | Recapture period | | | |
|---|---|---|---|---|
| Release group | S04 | W05 | S05 | W06 |
| W04 | $\Theta_{WS}$ | $\Theta_{SW}$ | $\Theta_{WS}$ | $\Theta_{SW}$ |
| S04 | | $\Theta_{SW}$ | $\Theta_{WS}$ | $\Theta_{SW}$ |
| W05 | | | $\Theta_{WS}$ | $\Theta_{SW}$ |
| S05 | | | | $\Theta_{SW}$ |

A recursion process was used to follow the movement of the number of marked whales (release group) from a given time period. The release group *k* consisted of newly identified whales not previously seen. The recursion started with a diagonal matrix of releases in each area. Movement was assumed constant over time for parsimony.

For the Markov process, the formula for the predicted number of marked whales in area *j* that came from area *i* at the next season was found from the number of marked whales $M_{m \to i,t}$ in area *i* that came from all areas *m* in year *t*, given by:

$$M_{i \to j,t} = \sum_m M_{m \to i,t} \theta_{WS,i \to j} \quad \text{for winter-to-summer movement,}$$

and $$M_{i \to j,t+1} = \sum_m M_{m \to i,t} \theta_{SW,i \to j} \quad \text{for summer-to-winter movement.}$$

(The time subscript denotes year, so that summer follows winter in the same year $t$, and winter the next year ($t$+1) follows summer.) These equations can be compactly written in matrix notation as $\mathbf{M}_{S,t} = \mathbf{M}_{W,t}\Theta_{WS}$ and $\mathbf{M}_{W,t+1} = \mathbf{M}_{S,t}\mathbf{\Theta}_{SW}$, respectively, in which the subscripts S and W denote summer and winter.

For the non-Markov process, the predicted number of marked whales in the season following release used these same equations. Thereafter, the predicted number of marked whales in winter depended on the previous winter, such that $\mathbf{M}_{W,t+1} = \mathbf{M}_{W,t}\Theta_{WW}$. Similarly, the predicted number of marked whales in summer was determined from $\mathbf{M}_{S,t+1} = \mathbf{M}_{S,t}\Theta_{SS}$.

The predicted number of recaptures was then found by multiplying the predicted number of whales by the capture probability in area $j$, or $m_{i\to j,t} = M_{i\to j,t}\,p_j$. This prediction was then compared to the observed number of marked recaptures from the release group in a likelihood setting to estimate parameters. Estimates of movement and capture probability parameters were obtained numerically by maximizing the likelihood, here assumed to be a product of Poisson distributions. All calculations were done in Excel using its Solver optimizer.

Once capture probabilities were estimated ($\hat{p}_{tj}$) for each area $j$, the general law of estimating abundance (Seber, 1982) was used to produce the estimates of abundance as $\hat{N}_{tj} = n_{tj} / \hat{p}_{tj}$, where $n_{tj}$ is the number of animals examined for marks at time period $t$ in area $j$.

Four different modeling scenarios made different assumptions about how probability of capture varied over time. The first scenario assumed that capture probabilities were constant over time [p(.)]. The second scenario assumed that capture probabilities varied over time [p(t)]. The third scenario assumed that capture probability was proportional to sample size each year [p(n)]. Effectively, model p(n) resulted in a single estimate of abundance for each area, since $N = n/p$. In the Markov case, the fourth scenario was a modification of p(n), in which the capture probability for SBC/NWA was constant over time, in an attempt to constrain it to a realistic value. In the non-Markov case, a fourth scenario was examined for analytical purposes, in which winter capture probabilities were proportional to sample size and summer capture probabilities were constant [p(S.,Wn)]

Model selection followed the procedures outlined in Burnham & Anderson (2002), including the use of AICc (Akaike Information Criterion, corrected, p. 51) as a model comparison statistic. Central to AICc is the calculation of the difference Δ between a given model and the model with the lowest AICc value. Models with Δ < 4 were considered to be very similar, while models with Δ > 10 were considered unlikely to be correct.

## RESULTS AND DISCUSSION

A total of 18,469 fluke identification photographs of acceptable quality were taken during over 27,000 humpback whale approaches. After reconciling all within and cross-regional matches (from both the primary match and rechecks), a total of 7,971 unique individuals were cataloged in SPLASH and 6,178 tissue samples collected (see Table 2). A total of 4,516 individuals were identified at wintering regions in at least one of the three seasons and 4,328 individuals were seen at least once at feeding areas in one of the two years.

### Interchange within wintering areas

Interchange within some wintering regions, like Hawaii, was extensive (Table 5). Although most of the Hawaii sample came from the Maui sub-area, identifications from Big Island and Kauai at the eastern and western end of the region showed a high rate of interchange with Maui. Although there were some indications of subtle differences in migratory destinations among some sub-areas discussed later, for most of the analyses reported here, the Hawaii sub-areas are treated as a single unit.

*Table 5. Rates of interchange among the Hawaii subareas for 2004-2006. Numbers along the diagonal show the total number of unique identifications within that subarea and numbers along upper right portion of the matrix show number of individuals seen in multiple sub-areas.*

| Area | Kauai | Oahu | PB | Molokai | Maui | Big Island |
|---|---|---|---|---|---|---|
| Kauai | 203 | 1 | 0 | 4 | 29 | 2 |
| Oahu | | 89 | 0 | 5 | 20 | 9 |
| PB | | | 34 | 3 | 4 | 3 |
| Molokai | | | | 201 | 61 | 12 |
| Maui | | | | | 1526 | 99 |
| Big Island | | | | | | 507 |

Interchange of whales among the three principal wintering regions sampled (Asia, Hawaii, and Mexico) was relatively low although there were a few animals seen in different major regions in different years (Table 6). Two whales were seen in both Asia (one each in Ogasawara and Philippines) and Hawaii. Similarly, 17 whales were seen in both Hawaii and one of the Mexican wintering sub-areas in different years (14 to the Revillagigedos, 2 to Baja, and 1 to mainland).

Interchange among the three sub-areas of Mexico and Central America was more complex. Of 562 whales from the Revillagigedos included in the SPLASH study, 112 (20%) were sighted at the Revillagigedos in more than one winter season and 48 (8.5%) were resighted at other wintering areas (Table 6). The highest number of wintering area matches was to Baja (22 whales), followed by equal numbers of matches to mainland Mexico and Hawaii (14 each; Table 6). Two whales were sighted at the Revillagigedos and both of the other Mexican wintering sub-areas during the study; no whales were observed at the Revillagigedos and Central America or Asia. The comparable match rates to mainland Mexico and Hawaii is interesting, given that the distance between the Revillagigedos and mainland Mexico (approximately 580km) is only slightly greater than the distance between Isla Socorro and Isla Clarion, the two most separated islands in the Revillagigedos chain (approximately 400km), and the distance between the Revillagigedos and the easternmost of the Hawaiian Islands is 4,600km. No same-season transits were observed between the Revillagigedos and Hawaii, but 3 same-season transits were observed between the Revillagigedos and mainland Mexico. In comparison, there were 22 same-season transits between islands at the Revillagigedos, despite that the majority of the Revillagigedos effort was limited to Isla Socorro only.

A closer connection was found between the whales that winter off Central America and those that winter off Mexico. Central America is the southernmost humpback whale wintering area in the North Pacific, and SPLASH represents the first time a relatively large number of whales from Central America have been compared widely across the ocean basin and especially to a concurrent sample from Mexico. Nine whales from Central America were sighted in mainland Mexico and two whales from Central America were sighted in Baja during the course of the study (Table 6). Three same-season movements between Central America and mainland Mexico were documented. In all cases the whales were sighted first at mainland Mexico and then later in Central America (28, 37, 52 days transit). The average sighting dates of whales seen in both areas (in the same or different seasons) was significantly earlier off mainland Mexico (28 December) than off Central America (5 February) ($t = 3.97$, $P = 0.002$), however this may partly be the result of the timing of effort, which was limited in Central America. The two whales that were photographed in both Baja and Central America were sighted later in the season off mainland Mexico (on 26 and 30 March), suggesting that southbound whales en route to Central America may pass too early in the season to be captured in Baja, or do not spend a significant amount of time in the area. It is also possible that Central America whales vary their migratory route north and southbound.

*Table 6. Interchange among wintering areas 2004-2006. Numbers along the diagonal show the total number of unique identifications within that area and numbers along upper right portion of the matrix show number of individuals seen in multiple areas.*

| **Area** | **Asia-PHI** | **Asia-OK** | **Asia-OG** | **HI** | **MX-REV** | **MX-Baja** | **MX-ML** | **Cent Am** |
|---|---|---|---|---|---|---|---|---|
| Philippines | 77 | 5 | 5 | 1 | 0 | 0 | 0 | 0 |
| Okinawa | | 215 | 10 | 0 | 0 | 0 | 0 | 0 |
| Ogasawara | | | 294 | 1 | 0 | 0 | 0 | 0 |
| Hawaii | | | | 2317 | 14 | 2 | 1 | 0 |
| MX-REV | | | | | 562 | 22 | 14 | 0 |
| MX-Baja | | | | | | 406 | 66 | 2 |
| MX-ML | | | | | | | 690 | 9 |
| Cent Am | | | | | | | | 105 |

## Interchange and movements among and within feeding areas

Even though multiple sightings of the same individuals were made on the feeding areas, most of these showed only infrequent exchanges among areas, which supported an overall conclusion of a high degree of site fidelity to feeding areas. There were cases of this interchange both within and between 2004 and 2005 seasons (Figure 2).

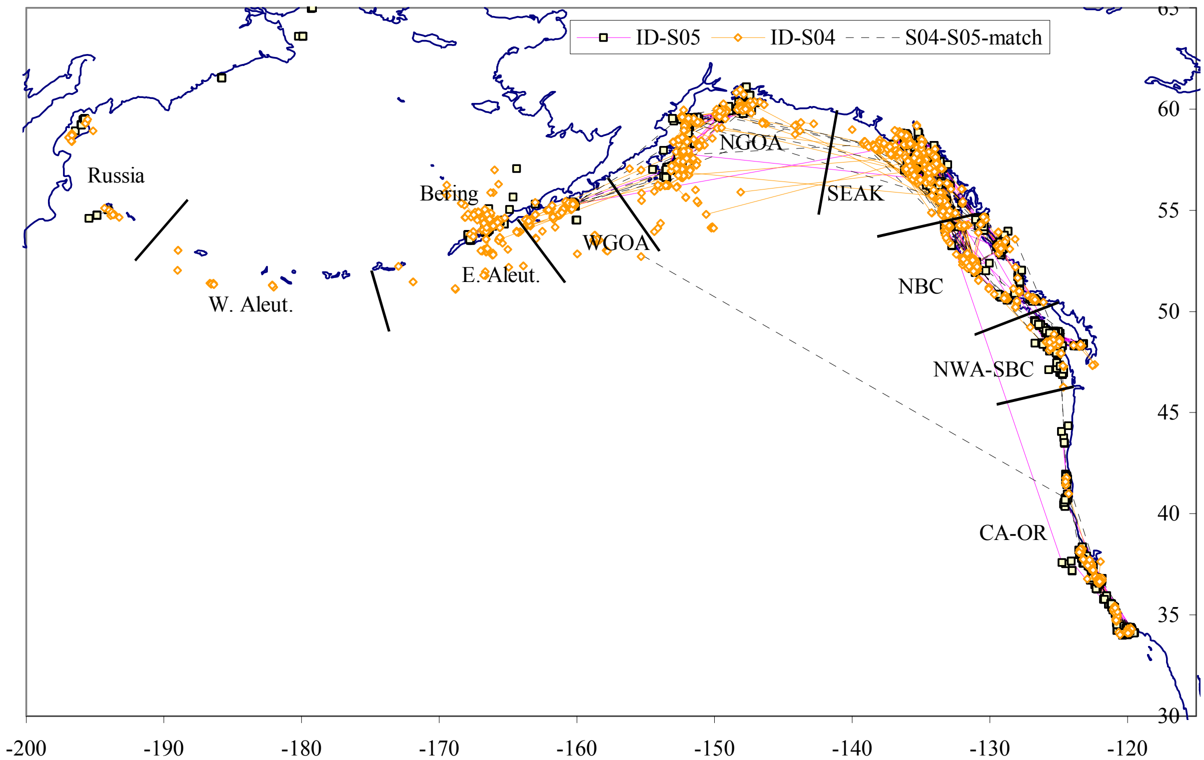


*Figure 2. Summary of resightings of humpback whales on feeding areas both within and between the 2004 and 2005 seasons.*

Same-season movement among the feeding areas was best evaluated in 2004 when survey efforts were broadest due to the four-month SPLASH cruise conducted by SWFSC supplementing more localized effort in British Columbia, SE Alaska, Gulf of Alaska, Aleutians, and Bering Sea (Table 7). Whales that were seen on multiple days were generally resighted in the same area and in only 12 cases were resighting locations more than 400 nmi apart. Overall, most resightings of whales in the feeding areas were within the same area and in only 42 cases were whales seen in different regions. Out of 789 whales seen on more than one day, 42 (5%) were seen in more than one defined area. Even among these 42, all but three were resightings made in adjacent areas. Adjacent areas with relatively high rates of within-season interchange included SE Alaska and N British Columbia (19), SE Alaska and N Gulf of Alaska (10), North and West Gulf of Alaska (4), and Bering Sea and E Aleutians (5).

Interchange between feeding areas was relatively uncommon; most individuals that were sighted in Summer 2004 and 2005 were sighted in the same area in both years (Table 8). Most cross-regional resightings of whales again occurred between adjacent areas. The highest rates of adjacent-area resightings occurred between SE Alaska and N British Columbia, however even here, cross-regional resightings were much less frequent than resightings within each area. Other adjacent areas with intermediate rates of interchange included the N and W Gulf of Alaska and the N British Columbia and S British Columbia/Washington. There were only three examples of shifts in location between years that were farther than the nearest adjacent area: 1) one whale seen in N British Columbia in 2004 and resighted in N Gulf of Alaska in 2005, 2) one whale from SE Alaska in 2004 resighted in W Gulf of Alaska in 2005 and 3) one whale seen of W Gulf of Alaska in 2004 and resighted off California on 18 November 2005, possibly on its southern migration.

*Table 7. Summary of interchange of humpback whales across feeding areas during SPLASH effort in the 2004 feeding season. Numbers along the diagonal indicate photo-IDs in the area.*

| | Russia | W Aleut | Bering | E Aleut | WGOA | NGOA | SEAK | NBC | SBC-NWA | CA-OR |
|---|---|---|---|---|---|---|---|---|---|---|
| Russia | 40 | | | | | | | | | |
| W Aleut | 0 | 12 | | | | | | | | |
| Bering | 0 | 0 | 228 | | | | | | | |
| E Aleut | 0 | 0 | 5 | 51 | | | | | | |
| WGOA | 0 | 0 | 0 | 0 | 223 | | | | | |
| NGOA | 0 | 0 | 0 | 1 | 4 | 730 | | | | |
| SEAK | 0 | 0 | 1 | 0 | 0 | 10 | 808 | | | |
| NBC | 0 | 0 | 0 | 0 | 0 | 1 | 19 | 421 | | |
| SBC-NWA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 76 | |
| CA-OR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 253 |

*Table 8. Interchange among feeding areas based on sightings in 2004 (rows) and 2005 (column headings).*

| | | **2005** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | **Russia** | **Bering** | **WGOA** | **NGOA** | **SEAK** | **NBC** | **SBC-NWA** | **CA-OR** |
| **2004** | **IDs** | **72** | **301** | **111** | **427** | **482** | **236** | **152** | **319** |
| Russia | 40 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aleut-Bering | 291 | 0 | 41 | 0 | 0 | 0 | 0 | 0 | 0 |
| WGOA | 223 | 0 | 0 | 33 | 1 | 0 | 0 | 0 | 1 |
| NGOA | 730 | 0 | 0 | 6 | 119 | 1 | 0 | 0 | 0 |
| SEAK | 808 | 0 | 0 | 1 | 4 | 175 | 16 | 0 | 0 |
| NBC | 421 | 0 | 0 | 0 | 1 | 13 | 74 | 4 | 0 |
| SBC-NWA | 76 | 0 | 0 | 0 | 0 | 0 | 1 | 21 | 1 |
| CA-OR | 253 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 47 |

Identifications from Russian waters came from three distinct areas, the Commander Islands at the western end of the Aleutians, an area off the east side of Kamchatka, and in the Gulf Anadyr at the north end of the Bering Sea. These areas were sampled in both 2004 and 2005 with the exception of the Gulf Anadyr that was sampled only in 2005. All 10 of the resightings of humpback whales in Russian waters between 2004 and 2005 were made within these sub-areas. Nine whales were resighted off Kamchatka between years, and the other was resighted at the Commander Islands (Table 9). While the small sample size would limit the expected number of resightings, the finding that none of the 10 resightings involved interchange among these areas indicated site fidelity within these areas and some degree of separation between them.

*Table 9. Summary of matches made between the three subareas in Russian waters in 2004 and 2005 showing all resightings between years were within the same subarea*

| | | **2004** | |
|---|---|---|---|
| **Area** | | **Commanders** | **Kamchatka** |
| **2005** | **IDs** | **11** | **29** |
| Commander Is | 7 | 1 | 0 |
| Gulf of Anadyr | 27 | 0 | 0 |
| Kamchatka | 38 | 0 | 9 |

## Migrations between wintering and feeding areas

Migrations between feeding and wintering areas were documented based on 873 whales that were seen at both wintering and feeding regions (Table 10, Figure 3). Movement patterns were complex but indicated a high degree of population structure. The overall pattern showed that wintering areas on both sides of the Pacific (Asia in the west and mainland Mexico and Central America in the east) are the primary wintering areas for the lower latitude coastal feeding areas on the same side of the Pacific. The regions off Hawaii and the Revillagigedo Archipelago were the primary wintering areas for the more central- and northern-latitude feeding areas. Within this broad overall pattern, however, were more complex and sometimes surprising movements and structure that are discussed in more detail below.

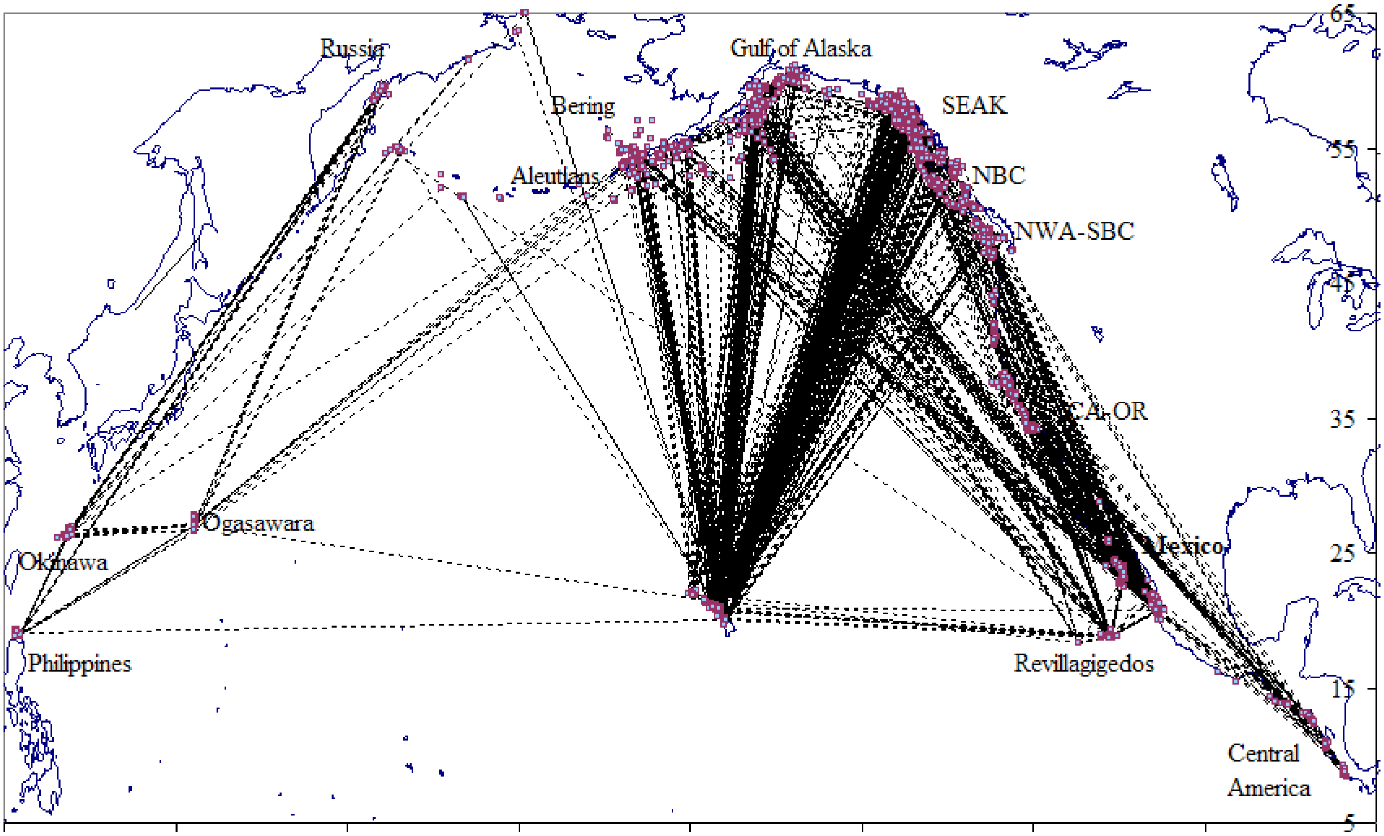


*Figure 3. Locations of SPLASH identifications. Lines connect sequential resightings of the same individual.*

*Table 10. Identifications and connections made between wintering areas (columns) and feeding areas (rows). Seasons are pooled for both wintering and feeding areas. Sum reflects the total of the whales matching between areas and Overall reflects the number of individuals matching to any area (in a few cases the same whale matched to multiple areas).*

| **Region** | | | **Asia-PHI** | **Asia-OK** | **Asia-OG** | **Hawaii** | **MX-REV** | **MX-Baja** | **MX-ML** | **Cent Am** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Daily IDs** | | **151** | **448** | **602** | **3205** | **2009** | **465** | **1222** | **140** | | |
| | | **Unique** | **77** | **215** | **294** | **2317** | **562** | **406** | **690** | **105** | **Sum** | **Overall** |
| Russia | 128 | 102 | 6 | 14 | 5 | 4 | 1 | 0 | 0 | 0 | 30 | 29 |
| Aleutians | 64 | 63 | 0 | 1 | 0 | 4 | 0 | 2 | 0 | 0 | 7 | 7 |
| Bering | 728 | 491 | 0 | 1 | 5 | 44 | 11 | 8 | 11 | 0 | 80 | 77 |
| WGOA | 516 | 301 | 0 | 0 | 2 | 26 | 13 | 7 | 4 | 0 | 52 | 51 |
| NGOA | 1792 | 1038 | 0 | 0 | 1 | 124 | 44 | 20 | 21 | 0 | 210 | 200 |
| SEAK | 2382 | 1115 | 0 | 0 | 0 | 215 | 9 | 3 | 8 | 0 | 235 | 235 |
| NBC | 1183 | 583 | 0 | 0 | 0 | 99 | 8 | 5 | 4 | 0 | 116 | 114 |
| NWA-SBC | 380 | 207 | 0 | 0 | 0 | 20 | 2 | 8 | 22 | 3 | 55 | 53 |
| CA-OR | 881 | 525 | 0 | 0 | 0 | 0 | 0 | 20 | 97 | 26 | 143 | 133 |
| Sum | | | 6 | 16 | 13 | 536 | 88 | 73 | 167 | 29 | 928 | |
| Overall matches | | | 6 | 16 | 13 | 516 | 87 | 70 | 164 | 29 | | 873 |

Some feeding areas in the central North Pacific had very low match rates to any wintering ground (Figure 4). The lowest proportion of animals going to any sampled wintering area occurred in the Aleutian region where only about 11% of the whales identified matched to any wintering area. Humpback whales identified in neighboring areas including the Commanders, Bering Sea, and Western Gulf of Alaska had just slightly higher proportions with 15-17% matching to wintering areas. This is in contrast with areas like SE Alaska where almost all animals go to Hawaii and over 21% match a wintering area, California-Oregon where most animals migrate from mainland Mexico and Central America and over 25% match a wintering area, and Russia where close to 40% match Asian wintering areas. One likely explanation for this pattern is the existence of an unknown wintering ground not sampled in SPLASH that serves as a destination for these animals. We also cannot rule out that this pattern could also be created by a combination of small sample sizes for the Aleutians and Russia feeding areas, under-sampled wintering areas or use of a known wintering ground outside the sampled period, although this seems unlikely given the sampling strategy and the high proportion (>20%) of animals from most wintering areas present on some feeding areas (Russia for the Asia wintering areas, SE Alaska for Hawaii, and California-Oregon for mainland Mexico and Central America).

With the exception of Asian wintering areas, over 15% of animals at wintering areas were identified on feeding areas (Figure 5). At all three Asian wintering areas less than 10% of the identified whales had also been seen on a feeding ground and this was less than 5% for Ogasawara. This supports the idea that the SPLASH sample under-represents the feeding areas that are the main destinations for animals wintering in Asia. This is not too surprising given the limited effort in the difficult to study areas in the western Aleutians, Bering Sea, and waters off Russia.

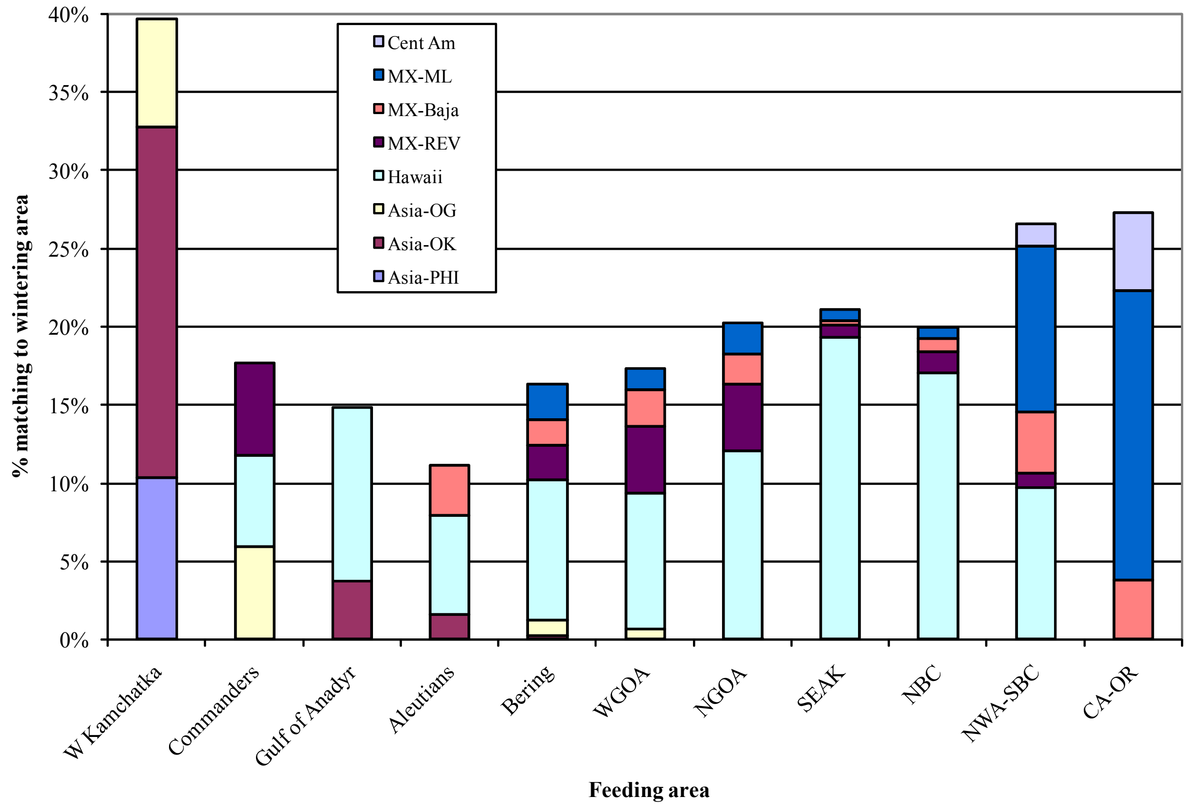


*Figure 4. The proportion of whales on feeding areas that were seen on different wintering areas.*

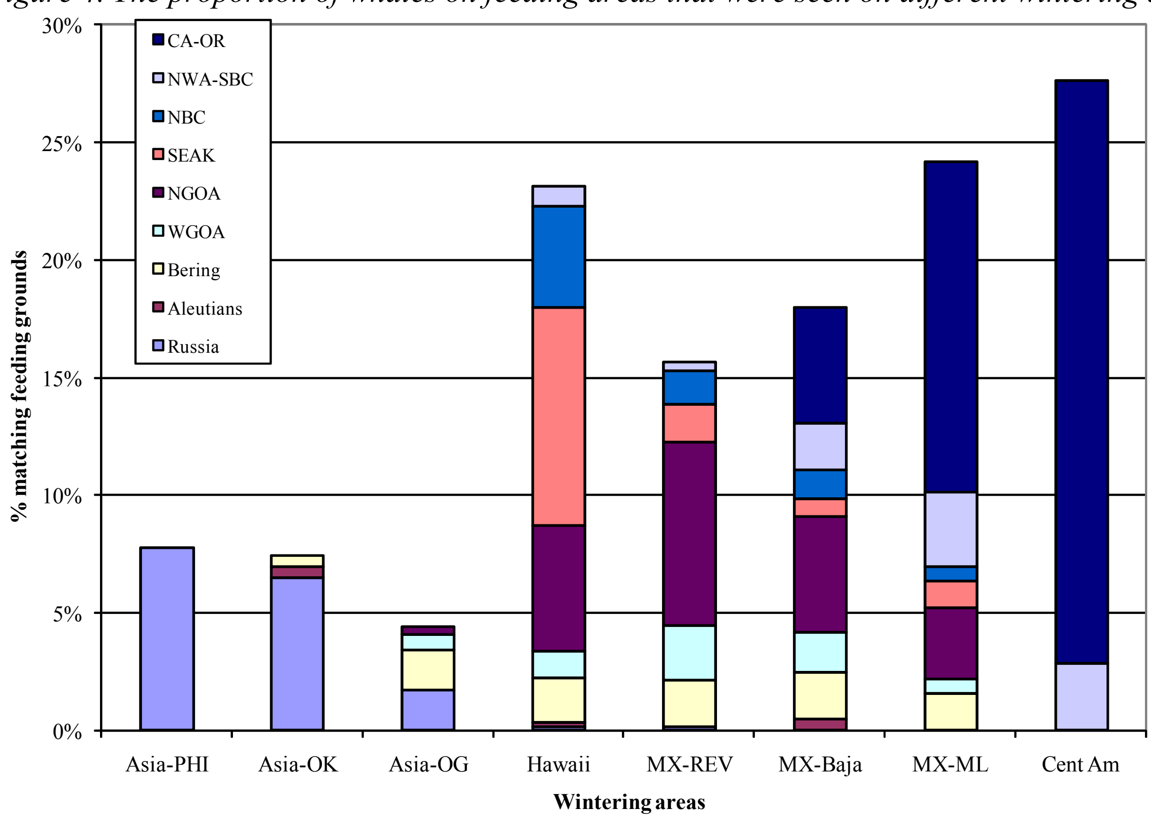


*Figure 5. The proportion of whales on wintering areas that were seen on different feeding areas.*

Humpback whales that were identified on feeding areas in Russian waters migrated primarily to Asian wintering areas, but strong differences in winter destinations existed among whales at the three Russian sub-areas (Table 11). Humpback whales identified along the east side of Kamchatka had high match rates to the three Asian wintering areas (especially Philippines and Okinawa) with 38% of these identified whales having been seen in at least one of these three wintering areas and no matches to Hawaii (Table 11). In sharp contrast, humpback whales identified off the Commander Islands and farther north in the Bering Sea in the Gulf Anadyr, had very low overall incidence of matches to any wintering area, and those that were found included more matches to Hawaii and Mexico than to Asian wintering areas. The match rates and destinations for the animals from the Commanders and northern Russia were much more similar to those for the Aleutians and Bering Sea (US side) than they were for the area off Kamchatka (Table 11). For this reason we used an alternate regional assignment for some of the mark-recapture estimates that reclassified identifications from the Commander Is and the Gulf of Anadyr to the Aleutians and Bering Sea (where they would reasonably belong though across an international border) and categorized the Kamchatka identifications as a separate region.

*Table 11. Summary of migratory destinations of humpback whales from Russian waters showing differences by sub-area and similarities to the Aleutian and Bering areas in US waters.*

| | IDs | Asia-PHI 77 | Asia-OK 215 | Asia-OG 294 | Hawaii 2317 | MX 1558 | Any area | % |
|---|---|---|---|---|---|---|---|---|
| Gulf of Anadyr | 27 | 0 | 1 | 0 | 3 | 0 | 4 | 15% |
| Kamchatka | 58 | 6 | 13 | 4 | 0 | 0 | 22 | 38% |
| Commanders | 17 | 0 | 0 | 1 | 1 | 1 | 3 | 18% |
| All Russia | 102 | 6 | 14 | 5 | 4 | 1 | 29 | 28% |
| | | | | | | | | |
| Aleutians | 63 | 0 | 1 | 0 | 4 | 0 | 7 | 11% |
| Bering | 491 | 0 | 1 | 5 | 44 | 27 | 77 | 16% |

This study also provided the first clear insight into the migratory destinations of whales that winter in the Revillagigedos. Eighty-seven of 562 whales from the Revillagigedos (15.4%) were sighted at a feeding area, a substantial increase in the feeding area matching rates reported from all previous studies of 3% or less. The whales from the Revillagigedos were seen in all sampled feeding areas except California-Oregon and the south side of the Aleutians. The majority of movements observed were to N Gulf of Alaska (n=44) and W Gulf of Alaska (n=13), with match rates declining to the west and east to a low of one match to Russia and two matches to Washington-S British Columbia. The movement observed between the Revillagigedos in March 2005 and the Commander Islands in the Russian Bering Sea in August that same year is the first documented, and represents a minimum migratory distance of 7,925 km.

## Current Abundance

Chapman/Petersen mark-recapture estimates using all pooled regions for each of the five SPLASH seasons yielded consistent abundances increasing from 18,347 to 21,452 (Table 12). While one reason for these increased estimates could be a reflection of an increasing population, the rate of increase is higher than would be expected (see later sections) and such fluctuations over a relatively short time scale may be the result of other sampling factors in conjunction with an increasing population. Because calves (where identified) were excluded in their initial year, these estimates are of the non-calf portion of the population. While these are closed population models and there is some violation to closure from natality and mortality, the time intervals are less than a year so these violations should result in only a small upward bias in the estimates. This would also be offset by the small downward bias introduced by excluding calves.

*Table 12. Chapman/Petersen mark-recapture estimates using pooled regions for each of the five SPLASH seasons. Estimates are based on four successive paired periods alternating between winter and feeding seasons.*

| | Unique Ids | | | | | |
|---|---|---|---|---|---|---|
| **Sample periods** | **n1** | **n2** | **Recapt.** | **Estimate** | **CV** | **CV-Jk*** |
| Winter 2004 - Summer 2004 | 1,588 | 2,724 | 235 | **18,347** | 0.06 | 0.13 |
| Summer 2004 - Winter 2005 | 2,724 | 1,685 | 247 | **18,525** | 0.06 | 0.53 |
| Winter 2005 - Summer 2005 | 1,685 | 2,021 | 169 | **20,052** | 0.07 | 0.20 |
| Summer 2005 - Winter 2006 | 2,021 | 1,930 | 181 | **21,452** | 0.07 | 0.17 |

**Jackknife estimate of variance treating entire regions as samples, somtimes high due to the large influence of eliminating some larger samples like Hawaii*

As expected, mark-recapture estimates based on paired years exclusively from two of the three winter seasons or exclusively from the two summer feeding seasons yielded unrealistically low estimates of abundance (Table 13). Estimates from only winter areas tend to be biased because males are more likely to return and are identified in greater numbers than females (Brown *et al*. 1995, Craig and Herman 1997, 2000, Craig *et al*. 2003) and juveniles are probably underrepresented (Robbins 2007). These biases have been shown to result in dramatic underestimates of abundance (Calambokidis *et al*. 1997, Smith *et al*. 1999). While the sex ratio on the feeding grounds are more representative of the population overall (Clapham *et al*. 1995), the estimate based only feeding areas samples would be biased downward by heterogeneity in capture probability created by the tendency to capture the same animals in the same areas in similar effort in the two years. The knowledge of these biases was the reason the focus for accurate abundance was on estimates using the combination of wintering and feeding areas.

Mark-recapture estimates of abundance and capture probabilities based on the Hilborn model with Markovian movement are compared in Table 14 and key parameters summarized in Tables 15 and 16. These indicated the p(t) model, in which capture probabilities varied over time, had the lowest AIC and AICc scores. However, all four models had AICc scores within 7 of the p(t) model, indicating that none of these models could be ruled out.

*Table 13. Petersen mark-recapture estimates using pooled regions for each of the five SPLASH seasons comparing only Winter to Winter and feeding to feeding for pairs of years.*

| | **Unique Ids** | | | | | |
|---|---|---|---|---|---|---|
| **Sample periods** | **n1** | **n2** | **Recapt.** | **Estimate** | **CV** | **CV-Jk*** |
| Winter 2004 - Winter 2005 | 1,588 | 1,685 | 298 | 8,959 | 0.05 | 0.28 |
| Winter 2005 - Winter 2006 | 1,685 | 1,930 | 278 | 11,668 | 0.05 | 0.31 |
| Summer 2004 - Summer 2005 | 2724 | 2021 | 544 | 10,109 | 0.03 | 0.40 |

**Jackknife estimate of variance treating entire regions as samples*

*Table 14. Comparison of key parameters for four Hilborn models with Markovian movement. Values in bold reflect lowest model score.*

| **Parameter** | **p(.)** | **p(t)** | **p(n)** | **p(n)(2)** |
|---|---|---|---|---|
| log likelihood | -974 | -953 | -976 | -976 |
| Observations | 360 | 360 | 360 | 360 |
| Parameters | 84 | 96 | 84 | 83 |
| Constraints | 12 | 12 | 12 | 12 |
| Unconstrained parameters | 72 | 84 | 72 | 71 |
| AIC | 2,092 | **2,074** | 2,097 | 2,094 |
| BIC | **2,372** | 2,400 | 2,377 | **2,370** |
| AICc | 2,129 | **2,126** | 2,133 | 2,130 |

All of the Hilborn models gave fairly similar estimates of abundance and movement rates for most areas, although there were difficulties with some of the smaller areas, especially the Washington/S British Columbia feeding area. Overall, average estimates for either all feeding or all wintering areas in the four models ranged from about 16,000 to 17,000 (Table 15), with the p(t) model giving estimates of 16,184 for the combined wintering areas and 16,744 for the combined feeding areas. Among wintering areas, Hawaii was estimated at close to 8,000 (approximately half the population), the three Mexican areas totaled about 6,600 (with Revillagigedos and Baja the largest at about 2,600 and Mainland Mexico at about 1,400), Asia was estimated at about 1,000 and Central America at about 500. Among feeding areas, the combined SE Alaska and N British Columbia area had the highest abundance at about 6,000 followed by Gulf of Alaska (about 4,000), Aleutians-Bering Sea (about 3,000), California-Oregon (about 2,000), Russia (encompassing the other feeding areas for the Asia wintering area but not the Aleutians) (~1,200) and Washington/S British Columbia (~200).

A key element of the Hilborn model is the movement rates from wintering to feeding areas and return (Table 16). While many of these movement rates appear quite reasonable and provide the best integrated measure of whale migration between these areas, a few were surprising. In particular, all the models estimated high movement rates between Baja and the Aleutians/Bering Sea areas despite a relatively low number of matches between these areas. This may be a result of the low proportion of animals in the Aleutians/Bering Sea for which a wintering destination was found, forcing the model to adjust for this. One other surprising high movement rate was for Washington/S BC to Central America, which may be an artifact of the

*Table 15. Summary of results of capture probabilities and abundance estimates for four models: 1) p(.) where capture probabilities are constant over time for each region, 2) p(t) where capture probabilities vary over time, 3) p(n) which assumes that capture probability is proportional to sample size each year referenced to Summer 2004 and Winter 2005 (effectively results in a single estimate of abundance), and 4) p(n)(2) same as p(n) except capture probability for SBC/NWA kept constant for Summer 2004 and 2005.*

**Capture probabilities and abundance**

Winter

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Model p(.) | | | | Capture probs p | | | | |
| | Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum |
| All | | 0.241 | 0.114 | 0.073 | 0.044 | 0.202 | 0.088 | |
| | | | | Estimated abundance | | | | |
| | 2004 | 759 | 6103 | 4211 | 4016 | 1038 | 205 | 16331 |
| | 2005 | 866 | 7370 | 2625 | 3419 | 1246 | 512 | 16037 |
| | 2006 | 1190 | 8935 | 2502 | 1882 | 1567 | 512 | 16587 |
| Average | | 938 | 7469 | 3112 | 3105 | 1284 | 409 | 16319 |
| Model p(t) | | | | Capture probs p | | | | |
| | Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum |
| | 2004 | Capture prob's in W04 cannot be estimated | | | | | | |
| | 2005 | 0.217 | 0.122 | 0.080 | 0.079 | 0.221 | 0.128 | |
| | 2006 | 0.256 | 0.110 | 0.065 | 0.025 | 0.191 | 0.071 | |
| | | | | Estimated abundance | | | | |
| | 2004 | Abundance in W04 cannot be estimated | | | | | | |
| | 2005 | 965 | 6872 | 2408 | 1876 | 1140 | 351 | 13612 |
| | 2006 | 1119 | 9196 | 2832 | 3316 | 1658 | 636 | 18757 |
| Average | | 1042 | 8034 | 2620 | 2596 | 1399 | 493 | 16184 |
| Model p(n) | | | | Capture probs p | | | | |
| | Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum |
| | 2004 | 0.171 | 0.084 | 0.117 | 0.072 | 0.149 | 0.037 | |
| | 2005 | 0.195 | 0.101 | 0.073 | 0.061 | 0.179 | 0.092 | |
| | 2006 | 0.268 | 0.123 | 0.069 | 0.034 | 0.226 | 0.092 | |
| | | | | Estimated abundance | | | | |
| | 2004 | | | | | | | |
| | 2005 | 1071 | 8261 | 2637 | 2447 | 1406 | 489 | 16312 |
| | 2006 | 1071 | 8261 | 2637 | 2447 | 1406 | 489 | 16312 |
| Average | | 1071 | 8261 | 2637 | 2447 | 1406 | 489 | 16312 |
| Model p(n) (2) | | | | Capture probs p | | | | |
| | Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum |
| | 2004 | 0.171 | 0.084 | 0.117 | 0.071 | 0.155 | 0.033 | |
| | 2005 | 0.195 | 0.101 | 0.073 | 0.061 | 0.186 | 0.083 | |
| | 2006 | 0.268 | 0.123 | 0.069 | 0.033 | 0.234 | 0.083 | |
| | | | | Estimated abundance | | | | |
| | 2004 | | | | | | | |
| | 2005 | 1071 | 8258 | 2638 | 2452 | 1356 | 542 | 16318 |
| | 2006 | 1071 | 8258 | 2638 | 2452 | 1356 | 542 | 16318 |
| Average | | 1071 | 8258 | 2638 | 2452 | 1356 | 542 | 16318 |

Summer

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Model p(.) | | | | Capture probs p | | | | |
| | Summer | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR | Sum |
| All | | 0.034 | 0.106 | 0.158 | 0.145 | 0.497 | 0.132 | |
| | | | | Estimated abundance | | | | |
| | 2004 | 738 | 2715 | 5825 | 8061 | 145 | 1879 | 19363 |
| | 2005 | 1122 | 3063 | 3332 | 4766 | 274 | 2295 | 14852 |
| Average | | 930 | 2889 | 4578 | 6414 | 209 | 2087 | 17108 |
| Model p(t) | | | | Capture probs p | | | | |
| | Summer | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR | Sum |
| | 2004 | 0.017 | 0.091 | 0.216 | 0.153 | 0.434 | 0.147 | |
| | 2005 | 0.042 | 0.109 | 0.139 | 0.145 | 0.497 | 0.128 | |
| | | | | Estimated abundance | | | | |
| | 2004 | 1464 | 3180 | 4280 | 7622 | 166 | 1690 | 18402 |
| | 2005 | 895 | 2978 | 3795 | 4772 | 274 | 2372 | 15087 |
| Average | | 1179 | 3079 | 4038 | 6197 | 220 | 2031 | 16744 |
| Model p(n) | | | | Capture probs p | | | | |
| | Summer | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR | Sum |
| | 2004 | 0.025 | 0.094 | 0.233 | 0.215 | 0.497 | 0.112 | |
| | 2005 | 0.038 | 0.106 | 0.133 | 0.127 | 0.938 | 0.137 | |
| | | | | Estimated abundance | | | | |
| | 2004 | 989 | 3074 | 3962 | 5427 | 145 | 2206 | 15803 |
| | 2005 | 989 | 3074 | 3962 | 5427 | 145 | 2206 | 15803 |
| Average | | 989 | 3074 | 3962 | 5427 | 145 | 2206 | 15803 |
| Model p(n) (2) | | | | Capture probs p | | | | |
| | Summer | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR | Sum |
| | 2004 | 0.025 | 0.094 | 0.233 | 0.215 | 0.905 | 0.112 | |
| | 2005 | 0.038 | 0.106 | 0.133 | 0.127 | 0.905 | 0.137 | |
| | | | | Estimated abundance | | | | |
| | 2004 | 989 | 3080 | 3963 | 5427 | 80 | 2208 | 15747 |
| | 2005 | 989 | 3080 | 3963 | 5427 | 150 | 2208 | 15817 |
| Average | | 989 | 3080 | 3963 | 5427 | 115 | 2208 | 15782 |

*Table 16. Summary of results of migration rates for four models listed in Table 15. Migration rates total 1 across rows for movement from either summer feeding areas to wintering areas or the return.*

| | | | | S->W | | | | | | | W->S | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model p(.) | Θ | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Ψ | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR |
| | Russia-Kam | 0.990 | 0.010 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.963 | 0.037 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.013 | 0.169 | 0.032 | 0.765 | 0.020 | 0.000 | HI | 0.000 | 0.043 | 0.108 | 0.844 | 0.005 | 0.000 |
| | GOA | 0.002 | 0.169 | 0.734 | 0.070 | 0.026 | 0.000 | Mx-Rev | 0.000 | 0.026 | 0.950 | 0.022 | 0.002 | 0.000 |
| | SEAK-NBC | 0.000 | 0.973 | 0.015 | 0.007 | 0.005 | 0.000 | Baja | 0.000 | 0.695 | 0.108 | 0.027 | 0.013 | 0.157 |
| | SBC-NWA | 0.000 | 0.252 | 0.000 | 0.050 | 0.112 | 0.585 | MX-Main | 0.000 | 0.033 | 0.029 | 0.006 | 0.016 | 0.916 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.149 | 0.708 | 0.143 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.311 | 0.689 |

| | | | | S->W | | | | | | | W->S | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model p(t) | Θ | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Ψ | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR |
| | Russia | 0.989 | 0.011 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.960 | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.013 | 0.165 | 0.035 | 0.766 | 0.021 | 0.000 | HI | 0.000 | 0.044 | 0.111 | 0.838 | 0.006 | 0.000 |
| | GOA | 0.002 | 0.162 | 0.748 | 0.063 | 0.025 | 0.000 | Mx-Rev | 0.000 | 0.027 | 0.948 | 0.022 | 0.003 | 0.000 |
| | SEAK-NBC | 0.000 | 0.972 | 0.017 | 0.007 | 0.005 | 0.000 | Baja | 0.000 | 0.698 | 0.107 | 0.026 | 0.013 | 0.156 |
| | SBC-NWA | 0.000 | 0.249 | 0.000 | 0.052 | 0.114 | 0.584 | MX-Main | 0.000 | 0.034 | 0.028 | 0.006 | 0.016 | 0.915 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.148 | 0.713 | 0.138 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.319 | 0.681 |

| | | | | S->W | | | | | | | W->S | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model p(n) | Θ | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Ψ | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR |
| | Russia | 0.989 | 0.011 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.959 | 0.041 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.013 | 0.168 | 0.036 | 0.764 | 0.019 | 0.000 | HI | 0.000 | 0.045 | 0.113 | 0.838 | 0.004 | 0.000 |
| | GOA | 0.002 | 0.165 | 0.747 | 0.062 | 0.024 | 0.000 | Mx-Rev | 0.000 | 0.027 | 0.950 | 0.021 | 0.002 | 0.000 |
| | SEAK-NBC | 0.000 | 0.973 | 0.016 | 0.007 | 0.004 | 0.000 | Baja | 0.000 | 0.706 | 0.108 | 0.026 | 0.007 | 0.153 |
| | SBC-NWA | 0.000 | 0.282 | 0.000 | 0.054 | 0.110 | 0.553 | MX-Main | 0.000 | 0.035 | 0.030 | 0.006 | 0.011 | 0.918 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.165 | 0.682 | 0.153 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.178 | 0.822 |

| | | | | S->W | | | | | | | W->S | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model p(n) (2) | Θ | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Ψ | Russia-Kam | Al-Ber | GOA | SEAK-NBC | SBC-NWA | CA-OR |
| | Russia | 0.989 | 0.011 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.959 | 0.041 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.013 | 0.167 | 0.036 | 0.765 | 0.019 | 0.000 | HI | 0.000 | 0.045 | 0.113 | 0.839 | 0.003 | 0.000 |
| | GOA | 0.002 | 0.165 | 0.748 | 0.063 | 0.024 | 0.000 | Mx-Rev | 0.000 | 0.027 | 0.950 | 0.021 | 0.001 | 0.000 |
| | SEAK-NBC | 0.000 | 0.973 | 0.016 | 0.007 | 0.004 | 0.000 | Baja | 0.000 | 0.707 | 0.108 | 0.026 | 0.007 | 0.153 |
| | SBC-NWA | 0.000 | 0.276 | 0.000 | 0.051 | 0.104 | 0.569 | MX-Main | 0.000 | 0.036 | 0.030 | 0.006 | 0.010 | 0.918 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.166 | 0.657 | 0.177 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.162 | 0.838 |

small samples and abundance estimates for these two areas, because previous studies have shown a low interchange between these areas (Calambokidis *et al*. 2000, 2001).

Mark-recapture models based on the Hilborn model with non-Markovian movement are compared in Table 17 and key parameters summarized in Tables 18 and 19. These non-Markovian models fitted the data substantially better than the Markovian models, as indicated by the much lower AICc scores. The p(t) and p(n) models fitted the data better than the p(.) and p(S.,Wn) models. The p(n) model had the lowest AICc score, suggesting that capture probabilities were proportional to sample size in all areas.

*Table 17. Comparison of key parameters for four Hilborn models with non-Markovian movement. Values in bold reflect lowest model score.*

| **Parameter** | p(.) | p(t) | p(n) | p(S.,Wn) |
|---|---|---|---|---|
| log likelihood | -489 | -445 | -465 | -491 |
| Observations | 360 | 360 | 360 | 360 |
| Parameters | 156 | 168 | 156 | 156 |
| Constraints | 24 | 24 | 24 | 24 |
| Unconstrained parameters | 132 | 144 | 132 | 132 |
| AIC | 1,243 | **1,177** | 1,193 | 1,245 |
| BIC | 1,756 | 1,737 | **1,706** | 1,758 |
| AICc | 1,397 | 1,371 | **1,348** | 1,400 |

The non-Markovian models gave remarkably similar estimates of abundance in winter both by area and overall, but not in summer. Estimated total abundance ranged from 17,482 to 17,558 for the combined winter areas and from 18,568 to 21,225 for the combined summer feeding areas (Table 18). These abundance estimates are generally higher than for the Markovian models and closer to the pooled-area Petersen estimates. The p(n) model which provided the best overall fit to the data indicated an abundance of 17,558 for wintering areas and 19,056 for the feeding areas. The average of these two estimates (18,302) represents the best estimate of overall abundance of humpback whales in the North Pacific.

Among wintering areas, Hawaii was estimated at near10,000 or about 57% of the population, the three Mexican areas totaled 6,000-7,000 (with Baja the largest at about 5,000 and Revillagigedos and Mainland Mexico at about 750), Asia was estimated at about 1,000 and Central America at about 500 whales. Among feeding areas, regional estimates differed greatly among models. Average estimates of abundance ranged from about 100-700 for Russia, 6,000-14,000 for the Bering Sea and Aleutians, 3,000-5,000 each for the Gulf of Alaska (W and N) and the combined SE Alaska and N British Columbia area, 200-400 for Washington/S British Columbia , and 1,400-1,700 for California-Oregon Movement rates from summer to winter areas were similar among models (Table 19). Clear associations occurred between certain pairs of feeding and wintering areas (Russia/Asia, SE AK/Hawaii, CA-OR/Baja), but the Aleutians/Bering Sea, Gulf of Alaska, and S British Columbia/N Washington whales had more varied wintering destinations (Table 19).

*Table 18. Modeling results based on non-Markov movement. The first scenario assumed that capture probabilities were constant [p(.)]. The second scenario assumed that capture probabilities varied over time [p(t)]. The third scenario assumed that capture probability was proportional to sample size each year [p(n)]. Effectively, model p(n) resulted in a single estimate of abundance for each area, since N = n/p and the fourth scenario was examined for analytical purposes, in which winter capture probabilities were proportional to sample size and summer capture probabilities were constant [p(S.,Wn)]*

**Capture probabilities and abundance**

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model p(.) | | | Capture probs p | | | | | | | | Capture probs p | | | | |
| Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum | Summer | Russia-Kam | Al-Ber | GOA | AK-NBC | BC-NWA | CA-OR | Sum |
| All | 0.234 | 0.095 | 0.279 | 0.024 | 0.346 | 0.109 | | All | 0.044 | 0.048 | 0.142 | 0.214 | 0.290 | 0.166 | |
| | | | Estimated abundance | | | | | | | | Estimated abundance | | | | |
| 2004 | 781 | 7332 | 1106 | 7298 | 608 | 166 | 17290 | 2004 | 565 | 5997 | 6516 | 5445 | 248 | 1498 | 20268 |
| 2005 | 892 | 8853 | 689 | 6214 | 729 | 414 | 17791 | 2005 | 859 | 6765 | 3728 | 3219 | 469 | 1830 | 16868 |
| 2006 | 1225 | 10733 | 657 | 3420 | 917 | 414 | 17366 | | | | | | | | |
| Average | 966 | 8973 | 817 | 5644 | 751 | 331 | 17482 | Average | 712 | 6381 | 5122 | 4332 | 358 | 1664 | 18568 |
| | | | MX: | 7213 | | | | | | | | | | | |
| Model p(t) | | | Capture probs p | | | | | | | | Capture probs p | | | | |
| Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum | Summer | Russia-Kam | Al-Ber | GOA | AK-NBC | BC-NWA | CA-OR | Sum |
| 2004 | Capture prob's in W04 cannot be estimated | | | | | | | 2004 | 0.338 | 0.016 | 0.392 | 0.443 | 0.220 | 0.222 | |
| 2005 | 0.208 | 0.103 | 0.285 | 0.039 | 0.371 | 0.186 | | 2005 | 0.386 | 0.034 | 0.158 | 0.220 | 0.299 | 0.175 | |
| 2006 | 0.249 | 0.090 | 0.271 | 0.014 | 0.333 | 0.089 | | | | | | | | | |
| | | | Estimated abundance | | | | | | | | Estimated abundance | | | | |
| 2004 | Abundance in W04 cannot be estimated | | | | | | | 2004 | 74 | 17546 | 2356 | 2635 | 327 | 1119 | 24058 |
| 2005 | 1004 | 8150 | 674 | 3798 | 679 | 242 | 14547 | 2005 | 99 | 9642 | 3334 | 3132 | 455 | 1731 | 18393 |
| 2006 | 1152 | 11346 | 674 | 5817 | 952 | 505 | 20445 | | | | | | | | |
| Average | 1078 | 9748 | 674 | 4807 | 816 | 373 | 17496 | Average | 86 | 13594 | 2845 | 2883 | 391 | 1425 | 21225 |
| | | | MX: | 6297 | | | | | | | | | | | |
| Model p(n) | | | Capture probs p | | | | | | | | Capture probs p | | | | |
| Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum | Summer | Russia-Kam | Al-Ber | GOA | AK-NBC | BC-NWA | CA-OR | Sum |
| 2004 | 0.165 | 0.069 | 0.452 | 0.039 | 0.270 | 0.043 | | 2004 | 0.250 | 0.027 | 0.273 | 0.370 | 0.380 | 0.146 | |
| 2005 | 0.189 | 0.083 | 0.282 | 0.033 | 0.324 | 0.107 | | 2005 | 0.381 | 0.031 | 0.156 | 0.219 | 0.718 | 0.178 | |
| 2006 | 0.259 | 0.101 | 0.269 | 0.018 | 0.408 | 0.107 | | | | | | | | | |
| | | | Estimated abundance | | | | | | | | Estimated abundance | | | | |
| 2004 | 1107 | 10103 | 681 | 4471 | 777 | 420 | 17558 | 2004 | 100 | 10534 | 3375 | 3156 | 189 | 1702 | 19056 |
| 2005 | 1107 | 10103 | 681 | 4471 | 777 | 420 | 17558 | 2005 | 100 | 10534 | 3375 | 3156 | 189 | 1702 | 19056 |
| 2006 | 1107 | 10103 | 681 | 4471 | 777 | 420 | 17558 | | | | | | | | |
| Average | 1107 | 10103 | 681 | 4471 | 777 | 420 | 17558 | Average | 100 | 10534 | 3375 | 3156 | 189 | 1702 | 19056 |
| | | | MX: | 5928 | | | | | | | | | | | |
| Model p(S.,Wn) | | | Capture probs p | | | | | | | | Capture probs p | | | | |
| Winter | Asia | HI | Mx-Rev | Baja | MX-Main | CentAm | Sum | Summer | Russia-Kam | Al-Ber | GOA | AK-NBC | BC-NWA | CA-OR | Sum |
| 2004 | 0.165 | 0.069 | 0.452 | 0.039 | 0.270 | 0.043 | | 2004 | 0.044 | 0.048 | 0.142 | 0.214 | 0.290 | 0.166 | |
| 2005 | 0.189 | 0.083 | 0.282 | 0.033 | 0.324 | 0.107 | | 2005 | 0.044 | 0.048 | 0.142 | 0.214 | 0.290 | 0.166 | |
| 2006 | 0.259 | 0.101 | 0.269 | 0.018 | 0.408 | 0.107 | | | | | | | | | |
| | | | Estimated abundance | | | | | | | | Estimated abundance | | | | |
| 2004 | 1107 | 10100 | 681 | 4470 | 777 | 420 | 17555 | 2004 | 565 | 5997 | 6516 | 5445 | 248 | 1498 | 20269 |
| 2005 | 1107 | 10100 | 681 | 4470 | 777 | 420 | 17555 | 2005 | 858 | 6765 | 3728 | 3219 | 469 | 1830 | 16870 |
| 2006 | 1107 | 10100 | 681 | 4470 | 777 | 420 | 17555 | | | | | | | | |
| Average | 1107 | 10100 | 681 | 4470 | 777 | 420 | 17555 | Average | 712 | 6381 | 5122 | 4332 | 359 | 1664 | 18570 |
| | | | MX: | 5928 | | | | | | | | | | | |

*Table 19. Migration rates for four Non-Markov models described in Table 18.*

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | S->W | | | | | | | W->S | | | | | | | S->S | | | | | | | | W->W | |
| Model p(.) | ΘSW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm | ΘWS | ssia-Kam | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘSS | Russia | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘWW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm |
| | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.724 | 0.276 | 0.000 | 0.000 | 0.000 | 0.000 | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.972 | 0.028 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.030 | 0.480 | 0.016 | 0.459 | 0.015 | 0.000 | HI | 0.000 | 0.316 | 0.295 | 0.377 | 0.012 | 0.000 | Al-Ber | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | HI | 0.000 | 0.996 | 0.003 | 0.000 | 0.001 | 0.000 |
| | GOA | 0.005 | 0.524 | 0.030 | 0.425 | 0.016 | 0.000 | Mx-Rev | 0.000 | 0.451 | 0.476 | 0.063 | 0.010 | 0.000 | GOA | 0.000 | 0.000 | 0.989 | 0.005 | 0.000 | 0.005 | Mx-Rev | 0.000 | 0.096 | 0.717 | 0.162 | 0.025 | 0.000 |
| | SEAK-N | 0.000 | 0.875 | 0.013 | 0.106 | 0.006 | 0.000 | Baja | 0.000 | 0.474 | 0.254 | 0.071 | 0.041 | 0.160 | SEAK-N | 0.000 | 0.000 | 0.023 | 0.965 | 0.011 | 0.000 | Baja | 0.000 | 0.022 | 0.017 | 0.860 | 0.088 | 0.013 |
| | SBC-NW | 0.000 | 0.509 | 0.000 | 0.299 | 0.152 | 0.040 | MX-Mai | 0.000 | 0.180 | 0.091 | 0.025 | 0.047 | 0.658 | SBC-NW | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | MX-Mai | 0.000 | 0.000 | 0.000 | 0.339 | 0.614 | 0.047 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.588 | 0.173 | 0.239 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.092 | 0.908 | CA-OR | 0.000 | 0.000 | 0.000 | 0.000 | 0.013 | 0.987 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.076 | 0.924 |
| | | | | S->W | | | | | | | W->S | | | | | | S->S | | | | | | | | W->W | | | |
| Model p(t) | ΘSW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm | ΘWS | ssia-Kam | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘSS | Russia | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘWW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm |
| | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.049 | 0.951 | 0.000 | 0.000 | 0.000 | 0.000 | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.970 | 0.030 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.029 | 0.476 | 0.016 | 0.464 | 0.015 | 0.000 | HI | 0.000 | 0.562 | 0.163 | 0.262 | 0.013 | 0.000 | Al-Ber | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | HI | 0.000 | 0.996 | 0.003 | 0.000 | 0.001 | 0.000 |
| | GOA | 0.005 | 0.526 | 0.030 | 0.424 | 0.015 | 0.000 | Mx-Rev | 0.000 | 0.717 | 0.232 | 0.040 | 0.011 | 0.000 | GOA | 0.000 | 0.000 | 0.989 | 0.006 | 0.000 | 0.005 | Mx-Rev | 0.000 | 0.095 | 0.718 | 0.161 | 0.025 | 0.000 |
| | SEAK-N | 0.000 | 0.876 | 0.013 | 0.105 | 0.006 | 0.000 | Baja | 0.000 | 0.669 | 0.122 | 0.045 | 0.042 | 0.122 | SEAK-N | 0.000 | 0.000 | 0.022 | 0.967 | 0.011 | 0.000 | Baja | 0.000 | 0.021 | 0.017 | 0.860 | 0.089 | 0.013 |
| | SBC-NW | 0.000 | 0.505 | 0.000 | 0.308 | 0.151 | 0.036 | MX-Mai | 0.000 | 0.330 | 0.051 | 0.017 | 0.050 | 0.552 | SBC-NW | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | MX-Mai | 0.000 | 0.000 | 0.000 | 0.342 | 0.613 | 0.044 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.619 | 0.173 | 0.208 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.103 | 0.897 | CA-OR | 0.000 | 0.000 | 0.000 | 0.000 | 0.013 | 0.987 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.068 | 0.932 |
| | | | | S->W | | | | | | | W->S | | | | | | S->S | | | | | | | | W->W | | | |
| Model p(n) | ΘSW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm | ΘWS | ssia-Kam | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘSS | Russia | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘWW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm |
| | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.054 | 0.946 | 0.000 | 0.000 | 0.000 | 0.000 | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.970 | 0.030 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.030 | 0.482 | 0.016 | 0.459 | 0.014 | 0.000 | HI | 0.000 | 0.505 | 0.200 | 0.288 | 0.007 | 0.000 | Al-Ber | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | HI | 0.000 | 0.996 | 0.003 | 0.000 | 0.001 | 0.000 |
| | GOA | 0.005 | 0.540 | 0.031 | 0.410 | 0.015 | 0.000 | Mx-Rev | 0.000 | 0.653 | 0.295 | 0.045 | 0.007 | 0.000 | GOA | 0.000 | 0.000 | 0.989 | 0.006 | 0.000 | 0.005 | Mx-Rev | 0.000 | 0.095 | 0.724 | 0.158 | 0.024 | 0.000 |
| | SEAK-N | 0.000 | 0.887 | 0.013 | 0.095 | 0.006 | 0.000 | Baja | 0.000 | 0.626 | 0.153 | 0.050 | 0.025 | 0.145 | SEAK-N | 0.000 | 0.000 | 0.022 | 0.973 | 0.005 | 0.000 | Baja | 0.000 | 0.019 | 0.018 | 0.873 | 0.077 | 0.013 |
| | SBC-NW | 0.000 | 0.507 | 0.000 | 0.313 | 0.140 | 0.040 | MX-Mai | 0.000 | 0.264 | 0.062 | 0.019 | 0.028 | 0.628 | SBC-NW | 0.000 | 0.573 | 0.000 | 0.000 | 0.427 | 0.000 | MX-Mai | 0.000 | 0.000 | 0.000 | 0.373 | 0.578 | 0.049 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.597 | 0.162 | 0.241 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.050 | 0.950 | CA-OR | 0.000 | 0.000 | 0.000 | 0.000 | 0.007 | 0.993 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.063 | 0.937 |
| | | | | S->W | | | | | | | W->S | | | | | | S->S | | | | | | | | W->W | | | |
| Model p(S.,V | ΘSW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm | ΘWS | ssia-Kam | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘSS | Russia | Al-Ber | GOA | SEAK-N | SBC-NW | CA-OR | ΘWW | Asia | HI | Mx-Rev | Baja | MX-Mai | CentAm |
| | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.724 | 0.276 | 0.000 | 0.000 | 0.000 | 0.000 | Russia | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | Asia | 0.970 | 0.030 | 0.000 | 0.000 | 0.000 | 0.000 |
| | Al-Ber | 0.030 | 0.482 | 0.016 | 0.459 | 0.014 | 0.000 | HI | 0.000 | 0.316 | 0.295 | 0.377 | 0.012 | 0.000 | Al-Ber | 0.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | HI | 0.000 | 0.996 | 0.003 | 0.000 | 0.001 | 0.000 |
| | GOA | 0.005 | 0.540 | 0.031 | 0.410 | 0.015 | 0.000 | Mx-Rev | 0.000 | 0.451 | 0.476 | 0.063 | 0.010 | 0.000 | GOA | 0.000 | 0.000 | 0.990 | 0.005 | 0.000 | 0.005 | Mx-Rev | 0.000 | 0.095 | 0.724 | 0.158 | 0.024 | 0.000 |
| | SEAK-N | 0.000 | 0.887 | 0.013 | 0.095 | 0.006 | 0.000 | Baja | 0.000 | 0.474 | 0.254 | 0.071 | 0.041 | 0.160 | SEAK-N | 0.000 | 0.000 | 0.023 | 0.965 | 0.011 | 0.000 | Baja | 0.000 | 0.019 | 0.018 | 0.873 | 0.077 | 0.013 |
| | SBC-NW | 0.000 | 0.507 | 0.000 | 0.313 | 0.140 | 0.040 | MX-Mai | 0.000 | 0.180 | 0.091 | 0.025 | 0.047 | 0.657 | SBC-NW | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | 0.000 | MX-Mai | 0.000 | 0.000 | 0.000 | 0.373 | 0.578 | 0.049 |
| | CA-OR | 0.000 | 0.000 | 0.000 | 0.597 | 0.162 | 0.241 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.092 | 0.908 | CA-OR | 0.000 | 0.000 | 0.000 | 0.000 | 0.013 | 0.987 | CentAm | 0.000 | 0.000 | 0.000 | 0.000 | 0.063 | 0.937 |

Movement rates from winter to summer areas were not as similar among models but usually were within 10% of each other. In contrast with summer to winter movement, whales in most areas in the winter had multiple destinations in the summer. There was one important difference among models that greatly affected estimates of model parameters and abundance. Two destination areas (Russia, Al-Ber) were confounded in the Asia recaptures. For models p(.) and p(S.Wn), most Asia whales were estimated to move to Russia. However, for models p(t) and p(n), most Asia whales were estimated to move to the Al-Ber area. This caused the probability of capture in the Al-Ber area to drop and increased its estimate of abundance. Site fidelity from winter to winter and from summer to summer was generally near 1 for the same area (Table 19). The only exception was the set of three Mexico areas, which had an appreciable amount of interchange.

Movement rates from the non-Markovian models were often much different than for the Markovian models. This follows in part from the Aleutian-Bering Sea sampling problem described above, in that the higher abundance in that area requires movement from wintering areas. It appears that there are several combinations of movement parameters and capture probabilities that explain the data equally well. Additional modeling and analysis will be necessary to delineate area-specific knowledge.

The Petersen estimates using pooled-region winter and feeding areas yielded consistently higher estimates than the geographically stratified Hilborn models. The Petersen estimate could be biased upward if sampling of different feeding areas and different wintering areas occurred disproportionately in a manner that biased the number of recaptures downward. This appears to be the case in the western North Pacific, where we had a relatively thorough sample but where feeding areas were not well sampled (based on the low proportion of the animals on the Asian wintering areas that had been seen on any feeding area).

## Previous estimates of abundance and determination of trends

A number of estimates have been made for humpback whale abundance in some of the areas covered by SPLASH. North Pacific humpback whale populations were estimated to be at about 15,000 prior to commercial exploitation in the twentieth century (Rice 1978), however, this estimate was based on whaling data that may have been inaccurate. Approximate numbers in the North Pacific after the end of commercial whaling were estimated at about 1,400 (Gambell, 1976) and 1,200 (Johnson and Wolman 1984). Barlow (1994b) suggested that abundance was greater than 3,000 whales in the early 1990s.

The only other basin-wide mark-recapture abundance estimate was the NPAC study made using post-hoc analysis from photo-identification photographs taken from 1990 to 1993 (Calambokidis *et al*. 1997). These estimates were determined using several geographically stratified capture-recapture models that yielded estimates of 6,000 (models using wintering areas only and subject to male bias) to 10,000 (models using wintering and feeding areas). The primary limitations of the NPAC study were the lack or limited coverage of many known wintering and feeding areas. This included no samples from feeding areas in the western North Pacific and only limited coverage of feeding areas in the central North Pacific. There was also no coverage of some critical wintering areas including the Philippines and Central America, and in most years, the samples from Mexico were incomplete or only from one or two of the three main subareas.

Despite limitations in past estimates of humpback whales abundance in the North Pacific, the SPLASH results can selectively be compared to some of those estimates to examine rates of annual increase (Table 20). For the overall North Pacific, comparison of the most complete NPAC estimate using all feeding and wintering areas was 9,819. Over the 13-year span between these two studies, a 4.9% annual increase would be required to reach the best total estimate from SPLASH. Going back to the estimate of 1,400 whales at the end of whaling for humpbacks in 1966, a 6.8% annual increase over the 39-year period would be required to reach the current SPLASH abundance.

For several key sub-areas, a reasonable quantitative comparison could be made to SPLASH estimates. For Hawaii, three methods were used to compare estimates to determine trends based on NPAC and while the absolute abundance in these estimates had certain biases, the annual rates of increase were very similar and ranged from 5.5 to 6.0% (Table 20). Asia was more problematic because of differences in sampling but the winter-winter mark-recapture estimates between NPAC and SPLASH indicated a 6.7% rate of increase. This estimate could be biased upwards because of the more complete sampling effort in SPLASH (including sampling the Philippines).

*Table 20. Estimates of annual increases in humpback whale abundance based on comparison to previous estimates and those with similar methods. Primary basis for 1991 to 1993 estimates is from NPAC study (Calambokidis et al. 1997, 2001) with recalculation of abundances to match samples described in table.*

| Region/basis | Previous | | Current | | Yr | Annual |
|---|---|---|---|---|---|---|
| | Yr | Estimate | Yr | Estimate | span | incr. |
| **Total N Pacific estimates** | | | | | | |
| Hilborn best NPAC to best SPLASH | 1991-93 | 9,819 | 2004-06 | 18,307 | 13 | 4.9% |
| Rice to best SPLASH Hilborn | 1966 | 1,400 | 2004-06 | 18,307 | 39 | 6.8% |
| **Hawaii estimates** | | | | | | |
| Adj. year Petersen NPAC to SPLASH | 1991-93 | 3,556 | 2004-06 | 7,120 | 13 | 5.5% |
| Hilborn – Wint/Feed NPAC-SPLASH | 1991-93 | 3,760 | 2004-06 | 8,034 | 13 | 6.0% |
| Petersen using SEAK marks | 1991-93 | 5,151 | 2004-06 | 10,425 | 13 | 5.6% |
| **Asia** | | | | | | |
| Adj year Petersen NPAC to SPLASH | 1991-93 | 405 | 2004-06 | 943 | 13 | 6.7% |

SPLASH estimates will provide a much better basis for both the regional stock definitions and abundances currently used by NMFS in their Stock Assessment reports (Carreta *et al*. 2007). The minimum population estimate for humpback whales for the Eastern North Pacific stock of humpback whales is 1,158 whales (Carreta *et al*. 2007) using the capture-recapture estimates by Calambokidis *et al*. (2004a) with an increasing trend in numbers of 6-7%/year. Abundance for the Central North Pacific was 3,698 (Angliss and Outlaw 2007) using capture-recapture estimates from Calambokidis *et al*. (1997). Population trends for this region were estimated to increase at 10%/year (Mizroch *et al*. 2004) and 6.6%/year (Zerbini *et al*. 2006). Estimates for the Western North Pacific were 367 (Angliss and Outlaw 2007) using capture-recapture estimates from Calambokidis *et al*. (1997).

## Comparison to past regional estimates of abundance

There were also earlier estimates of humpback whale abundance for Hawaii that can not be quantitatively compared to SPLASH because these involved even less complete sampling or different methods. In the early 1980s, abundance was estimated at about 900-1400 whales (Darling *et al*. 1983, Darling and Morowitz 1986, Baker and Herman 1987) using photo-identification data applied to discovery rates (Darling and Morowitz 1986) or a weighted Petersen mark-recapture model (Baker and Herman 1987). Later estimates were made using photo-identification techniques or aerial survey line-transect data that estimated about 3,000-5,000 whales in Hawaiian waters in the 1990s (Calambokidis *et al*. 1997, Cerchio 1998, Mobley *et al*.). Mobley *et al*. (1999, 2001) showed increasing numbers of whales and estimated a 7% increase between 1993 and 2000.

While a quantitative comparison of SPLASH estimates to past estimates could not be made for Mexico, two separate abundance estimates were made for the Mexican waters in the early 1990s. Using a modified model of the Jolly-Seber population model, Urbán *et al*. (1999) estimated that in 1991 there were 1813 (95% CI: 918-2505) whales in the coastal stock and 914 (CI: 590-1193) whales in the Revillagigedo Archipelago stock. Calambokidis *et al*. (1997) found disparate results using two different estimation models; 1,600 whales for all Mexican waters were estimated using the Darroch method and 4,200 whales using the Chapman/Petersen method, citing problems with uneven sampling between areas in Mexico and concluding that the true abundance of about 2,200-2,800 whales was likely between these two estimates, and more consistent with the estimate of Urbán *et al*. (1999). An increase from about 2,500 whales in the early 1990s to the SPLASH estimate of 5,928 would be consistent with a 6.9% rate of annual increase, but should be interpreted cautiously given the variability in the earlier estimates.

While other estimates prior to NPAC and SPLASH are not available for Asia, whaling data provides some indications that there was a much larger population present there than even the current SPLASH estimates. Whalers killed large numbers of humpback whales in these areas: 3,277 animals were killed between 1910 and 1965; 970 of these were killed off Okinawa primarily between 1958 and 1961, 817 were killed off Ogasawara between 1924 and 1944 (Nishiwaki 1959, Rice 1978).

Estimates of humpback whale abundance along the US West Coast from SPLASH (1,702 for California-Oregon from best Hilborn model) agree with other recent estimates of this region. Abundance has been estimated using aerial (Forney *et al*. 1995) and ship line-transect surveys (Barlow 1995, 2003, Barlow and Gerodette 1996, Calambokidis and Barlow 2004, Forney *et al*. 1995, Barlow and Forney 2007) and using photo-identification data to make capture-recapture estimates (Calambokidis *et al*. 1990, 2004a, Calambokidis and Barlow 2004). Abundances 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% per 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 between California and Washington (including northern Washington; Barlow and Forney 2007).

Humpback whale abundance estimates off the Washington coast have been made from vessel line-transect surveys and capture-recapture from photo-identification research and are generally consistent with the low estimates of fewer than 500 for the Washington- S British Columbia from SPLASH. Forney (2007) estimate the number of humpback whales off N Washington/S British Columbia at 208 (CV=0.28) in 2005Vessel 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 resighting animals multiple times (Calambokidis *et al*. 2004b). Capture-capture estimates showed the number of whales increasing from about 100 to 200 from 1995 to 2002 (Calambokidis *et al*. 2004b).

There have been a number of past estimates of humpback whales for SE Alaska but these did not include the wide geographic coverage of SPLASH and yielded much lower estimates than SPLASH. Early estimates of abundance for Southeast 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. The most recent estimate was conducted in 2000 where abundance for northern Southeast Alaska was 961 (95% CI 657-1076) humpback whales (Straley *et al*. In Press).

Recent estimates of humpback whale abundance from other areas in Alaska have been even more limited. Vessel line-transect surveys long the Aleutian chain (west of St Matthew Island, north of the 200m bathymetric contour, south of the US/Russia boundary) estimated 1,175 (95% CI:197-7009) whales for this entire central Bering Sea region; however, sightings in this study were too clumped to provide a reliable estimate. Zerbini *et al*. (2006) estimated 1,652 whales (95% CI:1142-2398) along the Aleutian Islands and the Alaska Peninsula (from Kenai to Unimak Pass including Kodiak, the Shumagin Islands and north of Unimak Pass). 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).

Although little is known regarding the distribution and numbers of humpback whales summering off the Russian Far East, historic whaling records and recent field observations suggest that this region serves as one of the migratory destinations for some portion of the North Pacific population (Doroshenko 2000, Melnikov 2000). In general, humpback whales are thought to occur in relatively coastal waters between the northern Chukotka Peninsula and the southern Kamchatka Peninsula. Recent records have noted small numbers of whales (< 30) off Chukotka, Olutorsky Cape, Karaginskiy Island and the Commander Islands.

# CONCLUSION

The SPLASH project shows that humpback whales in the North Pacific have substantially recovered from whaling to a current population size of approximately 20,000. All areas with sufficient data show growing populations since the end of whaling in the 1960s and since the last substantial study of their abundance in the early 1990s. The SPLASH study also shows, for the first time, the detailed patterns of humpback whale migrations between their feeding areas in the North and their wintering areas in the South. Mysteries remain however, and SPLASH data reveals the likely existence of an undiscovered wintering area for many of the whales that feed in the Commander and Aleutian Islands and in the Bering Sea. This report is just the first of what is expected to be many publications to examine the SPLASH data in more detail.

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