Revised 12/30/2018

HUMPBACK WHALE (*Megaptera novaeangliae*): Western North Pacific Stock

NOTE – NMFS is in the process of reviewing humpback whale stock structure under the Marine Mammal Protection Act (MMPA) in light of the 14 Distinct Population Segments established under the Endangered Species Act (ESA) (81 FR 62259, 8 September 2016). A complete revision of the humpback whale stock assessments will be postponed until this review is complete. In the interim, new information on humpback whale mortality and serious injury is provided within this report.

STOCK DEFINITION AND GEOGRAPHIC RANGE

The humpback whale is distributed worldwide in all ocean basins. In winter, most humpback whales occur in the subtropical and tropical waters of the Northern and Southern Hemispheres. Humpback whales in the high latitudes of the North Pacific Ocean are seasonal migrants that feed on euphausiids and small schooling fishes (Nemoto 1957, 1959; Clapham and Mead 1999). The humpback whale population was considerably reduced as a result of intensive commercial exploitation during the 20th century.

A large-scale study of humpback whales throughout the North Pacific was conducted in 2004-2006 (the Structure of Populations, Levels of Abundance, and Status of Humpbacks (SPLASH) project). Initial results from this project (Calambokidis et al. 2008, Barlow et al. 2011), including abundance estimates and movement information, have been reported in Baker et al. (2008, 2013) and are also summarized in Fleming and Jackson (2011); however, these results are still being considered for stock structure analysis.

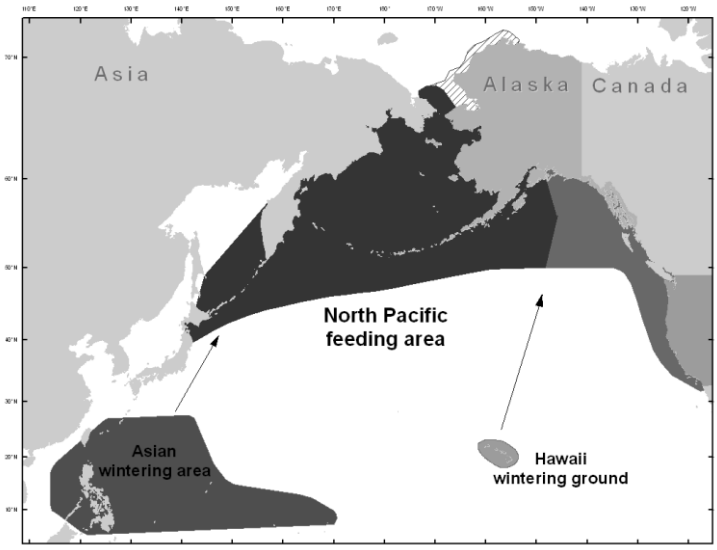

Figure 1. Approximate distribution of humpback whales in the western North Pacific (dark shaded areas). Feeding and wintering grounds are presented above (see text). Area within the hash lines is a probable distribution area based on sightings in the Beaufort Sea (Hashagen et al. 2009). See Figure 1 in the Central North Pacific humpback whale Stock Assessment Report for humpback whale distribution in the eastern North Pacific.

The historical summer feeding range of humpback whales in the North Pacific encompassed coastal and inland waters around the Pacific Rim from Point Conception, California, north to the Gulf of Alaska and the Bering Sea, and west along the Aleutian Islands to the Kamchatka Peninsula and into the Sea of Okhotsk and north of the Bering Strait (Zenkovich 1954, Nemoto 1957, Tomlin 1967, Johnson and Wolman 1984). Historically, the Asian wintering area extended from the South China Sea east through the Philippines, Ryukyu Retto, Ogasawara Gunto, Mariana Islands, and Marshall Islands (Rice 1998). Humpback whales are currently found throughout this historical range (Clarke et al. 2013b), with sightings during summer months occurring as far north as the Beaufort Sea (Hashagen et al. 2009). Most of the current winter range of humpback whales in the North Pacific is relatively well known, with aggregations of whales in Japan, the Philippines, Hawaii, Mexico, and Central America. The winter range includes the main islands of the Hawaiian archipelago, with the greatest concentration along the west side of Maui. In Mexico, the winter breeding range includes waters around the southern part of the Baja California peninsula, the central portions of the Pacific coast of mainland Mexico, and the Revillagigedo Islands off the mainland coast. The winter range also extends from southern Mexico into Central America, including Guatemala, El Salvador, Nicaragua, and Costa Rica (Calambokidis et al. 2008).

Photo-identification data, distribution information, and genetic analyses have indicated that in the North Pacific there are at least three breeding populations (Asia, Hawaii, and Mexico/Central America) that all migrate between their respective winter/spring calving and mating areas and their summer/fall feeding areas (Calambokidis et al. 1997, Baker et al. 1998). Calambokidis et al. (2001) further suggested that there may be as many as six

subpopulations on the wintering grounds. From photo-identification and Discovery tag information there are known connections between Asia and Russia, between Hawaii and Alaska, and between Mexico/Central America and California (Darling 1991, Darling and Cerchio 1993, Calambokidis et al. 1997, Baker et al. 1998). This information led to the designation of three stocks of humpback whales in the North Pacific: 1) the California/Oregon/Washington and Mexico stock, consisting of winter/spring populations in coastal Central America and coastal Mexico which migrate to the coast of California and as far north as southern British Columbia in summer/fall (Calambokidis et al. 1989, 1993; Steiger et al. 1991); 2) the Central North Pacific stock, consisting of winter/spring populations of the Hawaiian Islands which migrate primarily to northern British Columbia/Southeast Alaska, the Gulf of Alaska, and the Bering Sea/Aleutian Islands (Baker et al. 1990, Perry et al. 1990, Calambokidis et al. 1997); and 3) the Western North Pacific stock, consisting of winter/spring populations off Asia which migrate primarily to Russia and the Bering Sea/Aleutian Islands (Fig. 1).

Information from the SPLASH project largely confirms this view of humpback whale distribution and movements in the North Pacific. For example, the SPLASH results confirm low rates of interchange between the three principal wintering regions (Asia, Hawaii, and Mexico). However, the full SPLASH results suggest that the previous view of population structure was inaccurate. The overall pattern of movements is complex but indicates a high degree of population structure. Whales from wintering areas at the extremes of their range on both sides of the Pacific migrate to coastal feeding areas that are on the same side of the Pacific: whales from Asia in the west migrate to Russia and whales from mainland Mexico and Central America in the east migrate to coastal waters off California/Oregon.

The SPLASH data show the Revillagigedo whales are seen in all sampled feeding areas except northern California/Oregon and the south side of the Aleutians. They are primarily distributed in the Bering Sea, Gulf of Alaska, and Southeast Alaska/northern British Columbia but are also found in Russia and southern British Columbia/Washington. The migratory destinations of humpback whales from Hawaii were found to be quite similar, and a number of matches (14) were seen during SPLASH between Hawaii and the Revillagigedos (Calambokidis et al. 2008).

The winter distribution of humpback whales in the Western stock includes several island chains in the western North Pacific. In the Ogasawara Islands, humpback whale sampling during SPLASH was conducted at the three main island groups of Chichi-jima, Haha-jima, and Muko-jima, separated from each other by ~50-70 km. SPLASH sampling in Okinawa (southwest of Honshu) occurred at the Okinawa mainland and Zamami in the Kerama Islands (40 km from the Okinawa mainland), and in the Philippines SPLASH sampling occurred only at the northern tip of the archipelago around the Babuyan Islands. Humpback whales are reported to also occur in the South China Sea north of the Philippines near Taiwan, and east of Ogasawara in the Marshall and Mariana Islands (Rice 1998), but there were no known areas of high density in these regions that could be efficiently sampled.

The SPLASH project also found that whales from the Aleutian Islands and Bering Sea, and perhaps the Gulf of Anadyr and the Chukotka Peninsula on the west side of the Bering Strait in Russia, have an unusually low resighting rate in winter areas compared to whales from other feeding areas. It is believed that some of these whales have a winter migratory destination that was not sampled during the SPLASH project. Given the location of these feeding areas, the most parsimonious explanation would be that some of these whales winter somewhere between Hawaii and Asia, which would include the possibility of the Mariana Islands (southwest of the Ogasawara Islands), the Marshall Islands (approximately half-way between the Mariana Islands and the Hawaiian Islands), and the Northwestern Hawaiian Islands. Subsequent to the SPLASH project, a survey in 2007 documented humpback whales from a number of locations in the Northwestern Hawaiian Islands at relatively low densities (Johnston et al. 2007), but no sampling occurred there during the SPLASH project. Some humpback whales, including mother/calf pairs, have also been found in the Mariana Islands (Hill et al. 2016). Both of these locations are plausible migratory destinations for whales from the Aleutian Islands and Bering Sea. Which stock that whales in these locations would belong to is unknown.

The migratory destination of Western North Pacific humpback whales is not completely known. Discovery tag recoveries have indicated movement of whales between Ogasawara and Okinawa and feeding areas in the Bering Sea, on the southern side of the Aleutian Islands, and in the Gulf of Alaska (Omura and Ohsumi 1964, Nishiwaki 1966, Ohsumi and Masaki 1975). Research on humpback whales at the Ogasawara Islands has documented movements of whales between there and British Columbia (Darling et al. 1996), the Kodiak Archipelago in the central Gulf of Alaska (Calambokidis et al. 2001), and the Shumagin Islands in the western Gulf of Alaska (Witteveen et al. 2004), but no photo-identification studies had previously been conducted in Russia. Individual movement information from the SPLASH study documents that Russia is likely the primary migratory destination for whales in Okinawa and the Philippines but also reconfirms that some Asian whales go to Ogasawara, the

Aleutian Islands, Bering Sea, and Gulf of Alaska (Calambokidis et al. 2008). A small amount of inter-yearly interchange was also found between the wintering areas (Philippines, Okinawa, and Ogasawara).

During the SPLASH study in Russia, humpback whales were primarily found along the Pacific east side of the Kamchatka Peninsula, near the Commander Islands between Kamchatka and the Aleutian Islands, and in the Gulf of Anadyr just southwest of the Bering Strait. Analysis of whaling data shows historical catches of humpback whales well into the Bering Sea and catches in the Bering Strait and Chukchi Sea in August-October in the 1930s (Mizroch and Rice 2007), but no survey effort occurred during SPLASH north of the Bering Strait. Humpback whales are increasingly seen north of the Bering Strait into the northeastern Chukchi Sea (Clarke et al. 2013a, 2013b), with some indication that more humpback whales are seen on the Russian side north of the Bering Strait (Clarke et al. 2013b). Humpback whales are the most commonly recorded cetacean on hydrophones just north of the Bering Strait and occurred from September into early November from 2009 to 2012 (K. Stafford, Applied Physics Laboratory-University of Washington, Seattle, WA, pers. comm.). Other locations in the far western Pacific where humpback whales have been seen in summer include the northern Kuril Islands (V. Burkanov, NMFS-AFSC-MML, pers. comm.), far offshore southeast of the Kamchatka Peninsula and south of the Commander Islands (Miyashita 2006), and along the north coast of the Chukotka Peninsula in the Chukchi Sea (Melnikov 2000).

These results indicate humpback whales from the Western North Pacific (Asian) breeding stock overlap broadly on summer feeding grounds with whales from the Central North Pacific breeding stock, as well as with whales that winter in the Revillagigedos in Mexico. Given the relatively small size of the Asian population, Asian whales probably represent a small fraction of all the whales found in the Aleutian Islands, Bering Sea, and Gulf of Alaska, which are primarily whales from Hawaii and the Revillagigedos. The only feeding area that appears to be primarily (or exclusively) composed of Asian whales is along the Kamchatka Peninsula in Russia. The initial SPLASH abundance estimates for Asia ranged from about 900 to 1,100, and the estimates for Kamchatka in Russia ranged from about 100 to 700, suggesting a large portion of the Asian population migrates to Kamchatka. This also shows that Asian whales that migrate to feeding areas besides Russia would be only a small fraction of the total number of whales in those areas, given the much larger abundance estimates for the Bering Sea and Aleutian Islands (6,000-14,000) and the Gulf of Alaska (3,000-5,000) (Calambokidis et al. 2008). A full description of the distribution and density of humpback whales in the Aleutian Islands, Bering Sea, and Gulf of Alaska is in the Stock Assessment Report for the Central North Pacific stock of humpback whales.

In summary, information from a variety of sources indicates that humpback whales from the Western and Central North Pacific stocks mix to a limited extent on summer feeding grounds ranging from British Columbia through the central Gulf of Alaska and up to the Bering Sea.

NMFS conducted a global Status Review of humpback whales (Bettridge et al. 2015) and revised the ESA listing of the species (81 FR 62259, 8 September 2016); the effects of the ESA-listing final rule on the status of the stock are discussed below.

POPULATION SIZE

In the SPLASH study, fluke photographs were collected by over 400 researchers in all known feeding areas from Russia to California and in all known wintering areas from Okinawa and the Philippines to the coast of Central America and Mexico during 2004-2006. Over 18,000 fluke identification photographs were collected, and these have been used to estimate the abundance of humpback whales in the entire North Pacific Basin. A total of 566 unique individuals were seen in the Asian wintering areas during the 2-year period (3 winter field seasons) of the SPLASH study. Based on a comparison of all winter identifications to all summer identifications, the Chapman-Petersen estimate of abundance was 21,808 (CV = 0.04) (Barlow et al. 2011). A simulation study identifies significant biases in this estimate from violations of the closed population assumption (+5.3%), exclusion of calves (-10.3%), failure to achieve random geographic sampling (+1.5%), and missed matches (+9.8%) (Barlow et al. 2011). Sex-biased sampling favoring males in wintering areas does not add significant bias if both sexes are proportionately sampled in the feeding areas. The bias-corrected estimate is 20,800 after accounting for a net positive bias of 4.8%. This estimate is likely to be lower than the true abundance due to two additional sources of bias: individual heterogeneity in the probability of being sampled (unquantified) and the likely existence of an unknown and unsampled wintering area (-7.2%).

During the SPLASH study, surveys were conducted in three winter field seasons (2004-2006). The total numbers of unique individuals found in each area during the study were 77 in the Philippines, 215 in Okinawa, and 294 in the Ogasawara Islands. There was a total of 20 individuals seen in more than one area, leaving a total of 566 unique individuals seen in the Asian wintering areas (Calambokidis et al. 2008). For abundance in winter or summer areas, a multistrata Hilborn mark-recapture model was used, which is a form of a spatially-stratified model that explicitly estimates movement rates between winter and summer areas. Two broad categories of models were

used making different assumptions about the movement rates, and four different models were used for capture probability. Point estimates of abundance for Asia (combined across the three areas) were relatively consistent across models, ranging from 938 to 1,107. The model that fit the data the best (as selected by AICc) gave an estimate of 1,107 for the Ogasawara Islands, Okinawa, and the Philippines. No confidence limits or coefficients of variation (CVs) were calculated for the SPLASH abundance estimates. Although no other high density aggregations of humpback whales are known on the Asian wintering ground, whales have been seen in other locations, indicating this is likely to represent an underestimate of the stock's true abundance to an unknown degree. This estimate is more than 8 years old and is outdated for use in stock assessments; however, this population increased between estimates in 1991-1993 and 2004-2006 (Calambokidis et al. 2008), and this is still considered a valid minimum population estimate (NMFS 2016).

On the summer feeding grounds, the initial SPLASH abundance estimates for Kamchatka in Russia ranged from about 100 to 700, suggesting a large portion of the Asian population occurs near Kamchatka. No separate estimates are available for the other areas in Russia, the Gulf of Anadyr and the Commander Islands; abundance from those areas is included in the estimate of abundance for the Bering Sea and Aleutian Islands, which ranged from about 6,000 to 14,000. Abundance estimates for the Gulf of Alaska and for Southeast Alaska/northern British Columbia both ranged from 3,000 to 5,000 (Calambokidis et al. 2008).

Minimum Population Estimate

Point estimates of abundance for Asia ranged from 938 to 1,107 (for 2004-2006), but no associated CV was calculated. The 1991-1993 abundance estimate for Asia using similar (though likely less) data had a CV of 0.084. Therefore, it is unlikely the CV of a SPLASH estimate would be greater than 0.300. The minimum population estimate (N_{MIN}) for this stock is calculated according to Equation 1 from the potential biological removal (PBR) guidelines (Wade and Angliss 1997): $N_{MIN} = N/\exp(0.842\times[\ln(1+[CV(N)]^2)]^{½})$. Using the SPLASH population estimate (N) of 1,107 from the best fit model and an assumed conservative CV(N) of 0.300 would result in an N_{MIN} for this humpback whale stock of 865. The 2016 guidelines for preparing Stock Assessment Reports (NMFS 2016) recommend that N_{MIN} be considered unknown if the abundance estimate is more than 8 years old, unless there is compelling evidence that the stock has not declined since the last estimate. This population increased between estimates in 1991-1993 and 2004-2006 (Calambokidis et al. 2008), and this is still considered a valid minimum population estimate.

Current Population Trend

The SPLASH abundance estimate for Asia represents a 6.7% annual rate of increase over the 1991-1993 abundance estimate (Calambokidis et al. 2008). However, the 1991-1993 estimate was for Ogasawara and Okinawa only, whereas the SPLASH estimate includes the Philippines, so the annual rate of increase is unknown.

CURRENT AND MAXIMUM NET PRODUCTIVITY RATES

Utilizing a birth-interval model, Barlow and Clapham (1997) have estimated a population growth rate of 6.5% (SE = 1.2%) for the well-studied humpback whale population in the Gulf of Maine, although there are indications that this rate subsequently slowed (Clapham et al. 2003). Mobley et al. (2001) estimated a trend of 7% per year for 1993-2000 using data from aerial surveys that were conducted in a consistent manner for several years across all of the Hawaiian Islands and were developed specifically to estimate a trend for the Central North Pacific stock. Mizroch et al. (2004) estimated survival rates for North Pacific humpback whales using mark-recapture methods, and a Pradel model fit to data from Hawaii for the years 1980-1996 resulted in an estimated rate of increase of 10% per year (95% CI: 3-16%). For shelf waters of the northern Gulf of Alaska, Zerbini et al. (2006) estimated an annual rate of increase for humpback whales from 1987 to 2003 of 6.6% (95% CI: 5.2-8.6%). The SPLASH abundance estimate for the total North Pacific represents an annual increase of 4.9% over the most complete estimate for the North Pacific for 1991-1993. Comparisons of SPLASH abundance estimates for Hawaii to estimates for 1991-1993 gave estimates of annual increase that ranged from 5.5 to 6.0% (Calambokidis et al. 2008). No confidence limits were calculated for these rates of increase from SPLASH data.

Estimates of observed rates of increase can be used to estimate maximum net productivity rates (R_{MAX}), although in most cases these estimates may be biased low, as maximum net productivity rates are only achieved at very low population sizes. However, if the observed rates of increase are greater than the default value for R_{MAX}, it would be reasonable to use a higher value based on those observations. The rates of increase summarized above include estimates for the North Pacific of 7%, 10%, and 6.6%. Although there is no estimate of R_{MAX} for just the Western stock (i.e., from trends in abundance in the Asia breeding areas), it is reasonable to assume that R_{MAX} for this stock would be at least 7% based on the other observations from the North Pacific. Until additional data

become available for the Western North Pacific humpback whale stock, 7% will be used as R_{MAX} for this stock (Wade and Angliss 1997).

POTENTIAL BIOLOGICAL REMOVAL

PBR is defined as the product of the minimum population estimate, one-half the maximum estimated net productivity rate, and a recovery factor: $PBR = N_{MIN} \times 0.5R_{MAX} \times F_R$. The recovery factor ($F_R$) for this stock is 0.1, the value for cetacean stocks listed as endangered under the ESA (Wade and Angliss 1997; see Status of Stock section below regarding ESA listing status). Using the N_{MIN} of 865 calculated from the SPLASH abundance estimate for 2004-2006, of 1,107 with an assumed CV of 0.300, the PBR is calculated to be 3.0 whales ($865 \times 0.035 \times 0.1$).

ANNUAL HUMAN-CAUSED MORTALITY AND SERIOUS INJURY

Information for each human-caused mortality, serious injury, and non-serious injury reported for NMFS-managed Alaska marine mammals in 2012-2016 is listed, by marine mammal stock, in Helker et al. (in press); however, only the mortality and serious injury data are included in the Stock Assessment Reports. Injury events lacking detailed injury information are assigned prorated values following injury determination guidelines described in NMFS (2012). A summary of information used to determine whether an injury was serious or non-serious, as well as a table of prorate values used for large whale reports with incomplete information, is reported in Helker et al. (in press). The total estimated annual level of human-caused mortality and serious injury for Western North Pacific humpback whales in 2012-2016 is 3 whales: 0.8 in U.S. commercial fisheries, 0.4 in recreational fisheries, 0.2 in unknown (commercial, recreational, or subsistence) fisheries, 0.7 in marine debris, and 0.9 due to other causes (ship strikes, entanglement in a ship's ground tackle, and an intentional unauthorized take); however, this estimate is considered a minimum because there are no data concerning fishery-related mortality and serious injury in Japanese, Russian, or international waters. Assignment of mortality and serious injury to both the Western North Pacific and Central North Pacific stocks of humpback whales, when stock is unknown and events occur within the area where the stocks are known to overlap, may result in overestimating stock specific mortality and serious injury. Potential threats most likely to result in direct human-caused mortality or serious injury of this stock include entanglement in fishing gear and ship strikes due to increased vessel traffic (from increased shipping in higher latitudes with changes in sea-ice coverage).

Fisheries Information

Information for U.S. commercial fisheries in Alaska waters (including observer programs, observer coverage, and observed incidental takes of marine mammals) is presented in Appendices 3-6 of the Alaska Stock Assessment Reports.

In 2012, one humpback whale mortality occurred in the Bering Sea/Aleutian Islands pollock trawl fishery (Table 1; Breiwick 2013; MML, unpubl. data). Since the stock of the whale is unknown, and the event occurred within the area where the Western North Pacific and Central North Pacific stocks are known to overlap, the mortality in this fishery was assigned to both stocks of humpback whales. The estimated average annual mortality and serious injury rate from observed U.S. commercial fisheries in 2012-2016 is 0.2 Western North Pacific humpback whales (Table 1).

Table 1. Summary of incidental mortality and serious injury of Western North Pacific humpback whales due to U.S. commercial fisheries in 2012-2016 and calculation of the mean annual mortality and serious injury rate (Breiwick 2013; MML, unpubl. data). Methods for calculating percent observer coverage are described in Appendix 6 of the Alaska Stock Assessment Reports.

Fishery name	Years	Data type	Percent observer coverage	Observed mortality	Estimated mortality	Mean estimated annual mortality
Bering Sea/Aleutian Is. pollock trawl[a]	2012	obs data	98	1	1.0	0.2 (CV = 0.16)
	2013		97	0	0	
	2014		98	0	0	
	2015		99	0	0	
	2016		99	0	0	
Minimum total estimated annual mortality						0.2 (CV = 0.16)

[a]Mortality and serious injury in this fishery was assigned to both the Western North Pacific and Central North Pacific stocks of humpback whales, since the stock is unknown and the two stocks overlap within the area of operation of the fishery.

Mortality and serious injury due to entanglements in Kodiak Island commercial salmon purse seine gear (1 mortality in 2012), Kodiak Island commercial salmon set gillnet (1 serious injury in 2015, prorated at 0.75), and Bering Sea/Aleutian Islands commercial pot gear (1 mortality in 2015) was reported to the NMFS Alaska Region stranding network and by Marine Mammal Authorization Program (MMAP) fisherman self-reports in 2012-2016 (Table 2; Helker et al. in press). Because observer data are not available for these fisheries, this mortality and serious injury is used to calculate a minimum mean annual mortality and serious injury rate of 0.6 humpback whales in 2012-2016 in these fisheries (Table 2). Since all of these events occurred in the area where the two stocks overlap, this mortality and serious injury was assigned to both the Western North Pacific and Central North Pacific stocks of humpback whales (NMFS 2016).

The minimum estimate of the mean annual mortality and serious injury rate incidental to U.S. commercial fisheries in 2012-2016 is 0.8 Western North Pacific humpback whales (0.2 based on observed fisheries + 0.6 based on other data); however, this estimate is considered a minimum because there are no data concerning fishery-related mortality and serious injury in Japanese, Russian, or international waters.

Reports of swimming, floating, or beachcast humpback whales entangled in fishing gear or with injuries caused by interactions with gear, which may be from commercial, recreational, or subsistence fisheries, are another source of fishery-related mortality and serious injury data (Table 2). These mortality and serious injury estimates result from an actual count of verified human-caused deaths and serious injuries and are minimums because not all entangled animals strand nor are all stranded animals found, reported, or have the cause of death determined. Since all of these events occurred in the area where the two stocks overlap, the mortality and serious injury was assigned to both the Western North Pacific and Central North Pacific stocks of humpback whales. In 2015, two humpback whales (each with a serious injury prorated at 0.75) entangled in Gulf of Alaska recreational pot fisheries (1 in Dungeness crab pot gear and 1 in shrimp pot gear) were reported to the NMFS Alaska Region stranding network, resulting in a minimum mean annual mortality and serious injury rate of 0.4 whales in recreational gear in 2012-2016 (Table 2; Helker et al. in press). The minimum mean annual mortality and serious injury rate from fishery-related gear entanglements and interactions reported to the NMFS Alaska Region stranding network in 2012-2016, in which the events have not been attributed to a specific fishery listed on the MMPA List of Fisheries (82 FR 3655, 12 January 2017), is 0.2 humpback whales (Table 2; Helker et al. in press).

The minimum average annual mortality and serious injury rate due to interactions with all fisheries in 2012-2016 is 1.4 Western North Pacific humpback whales (0.8 in commercial fisheries + 0.4 in recreational fisheries + 0.2 in unknown fisheries).

Table 2. Summary of mortality and serious injury of Western North Pacific humpback whales, by year and type, reported to the NMFS Alaska Region marine mammal stranding network and by Marine Mammal Authorization Program (MMAP) fisherman self-reports in 2012-2016 (Helker et al. in press). All events occurred within the area of known overlap between the Western North Pacific and Central North Pacific humpback whale stocks. Since the stock is unknown, the mortality and serious injury is reflected in the Stock Assessment Reports for both stocks. Injury events lacking detailed injury information are assigned prorated values following injury determination guidelines described in NMFS (2012). A summary of information used to determine whether an injury was serious or non-serious, as well as a table of prorate values used for large whale reports with incomplete information, is reported in Helker et al. (in press).

Cause of injury	2012	2013	2014	2015	2016	Mean annual mortality
Entangled in Kodiak Island commercial salmon purse seine gear	1[a]	0	0	0	0	0.2
Entangled in Kodiak Island commercial salmon set gillnet	0	0	0	0.75	0	0.2
Entangled in Bering Sea/Aleutian Is. commercial pot gear	0	0	0	1	0	0.2
Entangled in Gulf of Alaska recreational Dungeness crab pot gear	0	0	0	0.75	0	0.2
Entangled in Gulf of Alaska recreational shrimp pot gear	0	0	0	0.75	0	0.2
Entangled in Prince William Sound shrimp pot gear*	0	0	1	0	0	0.2
Entangled in marine debris	0.75	0	0.75	0	2	0.7
Entangled in ship's ground tackle	0	1	0	0	0	0.2
Ship strike	1.2	0	1.2	0	0.2	0.5
Intentional unauthorized take	0	0	0	0	1	0.2
Total in commercial fisheries						0.6
Total in recreational fisheries						0.4
*Total in unknown (commercial, recreational, or subsistence) fisheries						0.2
Total in marine debris						0.7
Total due to other sources (entangled in ship's ground tackle, ship strike, intentional unauthorized take)						0.9

[a]MMAP fisherman self-report.

Brownell et al. (2000) compiled records of bycatch in Japanese and Korean commercial fisheries between 1993 and 2000. During 1995-1999, there were six humpback whales indicated as "bycatch." In addition, two strandings were reported during this period. Furthermore, genetic analysis of four samples from meat found in markets indicated that humpback whale meat was being sold. It is not known whether any or all strandings were caused by incidental interactions with commercial fisheries; similarly, it is not known whether the humpback whales identified in market samples were killed as a result of incidental interactions with commercial fisheries. It is also not known which fishery may be responsible for the bycatch. Regardless, these data indicate a minimum mortality level of 1.1 per year (using bycatch data only) to 2.4 per year (using bycatch, stranding, and market data) in the waters of Japan and Korea. Because many mortalities pass unreported, the actual rate in these areas is likely higher. An analysis of entanglement rates from photographs collected for the SPLASH study found a minimum entanglement rate of 31% for humpback whales from the Asia breeding grounds (Cascadia Research NFWF Report #2003-0170-019).

Alaska Native Subsistence/Harvest Information

There were no reported takes of humpback whales from this stock by Native subsistence hunters in Alaska or Russia in 2012-2016.

Other Mortality

In 2015, increased mortality of large whales was observed along the western Gulf of Alaska (including the areas around Kodiak Island, Afognak Island, Chirikof Island, the Semidi Islands, and the southern shoreline of the Alaska Peninsula) and along the central British Columbia coast (from the northern tip of Haida Gwaii to Southern Vancouver Island). NMFS declared an Unusual Mortality Event (UME) for large whales that occurred from 22 May to 31 December 2015 in the western Gulf of Alaska and from 23 April 2015 to 16 April 2016 in British Columbia (https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events, accessed December 2018). Forty-six large whale deaths attributed to the UME included 12 fin whales and 22 humpback whales in Alaska and 5 fin whales and 7 humpback whales in British Columbia. Based on the findings from the investigation, the UME was likely caused by ecological factors (i.e., the 2015 El Niño, Warm Water Blob, and Pacific Coast Domoic Acid Bloom).

Entanglements in marine debris reported to the NMFS Alaska Region stranding network account for a minimum mean annual mortality and serious injury rate of 0.7 Western North Pacific humpback whales in 2012-2016 (Table 2; Helker et al. in press). Ship strikes and other interactions with vessels unrelated to fisheries resulted in a minimum mean annual mortality and serious injury rate of 0.7 humpback whales from this stock in 2012-2016, based on ship strikes (0.5) and entanglement in a ship's ground tackle (0.2) reported to the NMFS Alaska Region stranding network (Table 2; Helker et al. in press). Because all of these events occurred in the area where the stocks overlap, the mortality and serious injury was assigned to both the Western North Pacific and Central North Pacific stocks of humpback whales. These mortality and serious injury estimates result from an actual count of verified human-caused deaths and serious injuries and are minimums because not all entangled animals strand nor are all stranded animals found, reported, or have the cause of death determined.

An intentional unauthorized take of a humpback whale by Alaska Natives in Toksook Bay in 2016 resulted in a mean annual mortality and serious injury rate of 0.2 whales in 2012-2016 (Table 2).

HISTORICAL WHALING

Rice (1978) estimated that the number of humpback whales in the North Pacific may have been approximately 15,000 individuals prior to exploitation; however, this was based upon incomplete data and, given the level of known catches (legal and illegal) since World War II, may be an underestimate. Intensive commercial whaling removed more than 28,000 animals from the North Pacific during the 20th century (Rice 1978). A total of 3,277 reported catches occurred in Asia between 1910 and 1964, with 817 catches from Ogasawara between 1924 and 1944 (Nishiwaki 1966, Rice 1978). After World War II, substantial catches occurred in Asia near Okinawa (including 970 between 1958 and 1961), as well as around the main islands of Japan and the Ogasawara Islands. On the feeding grounds, substantial catches occurred around the Commander Islands and western Aleutian Islands, as well as in the Gulf of Anadyr (Springer et al. 2006).

Humpback whales in the North Pacific were theoretically fully protected in 1965, but illegal catches by the U.S.S.R. continued until 1972 (Ivashchenko et al. 2013). From 1948 to 1971, 7,334 humpback whales were killed by the U.S.S.R., and 2,654 of these were illegally taken and not reported to the IWC (Ivashchenko et al. 2013). Many animals during this period were taken from the Gulf of Alaska and Bering Sea (Doroshenko 2000); however, additional illegal catches were made across the North Pacific, from the Kuril Islands to Haida Gwaii, and other takes may have gone unrecorded. The Soviet factory ship *Aleut* is known to have taken 535 humpback whales during the period 1933-1947 (Ivashchenko et al. 2013).

STATUS OF STOCK

The total estimated annual level of human-caused mortality and serious injury of 3 Western North Pacific humpback whales is equal to the calculated PBR level for this stock (3.0). The minimum estimate of the mean annual U.S. commercial fishery-related mortality and serious injury rate for this stock (0.8 whales) exceeds 10% of the PBR (10% of PBR = 0.3) and cannot be considered insignificant and approaching a zero mortality and serious injury rate. In addition, there is a lack of information about fisheries bycatch from Russia, Japan, Korea, and international waters, as well as earlier evidence of bycatch in Japan and Korea (Brownell et al. 2000: 1.1 to 2.4 whales per year based on bycatch, stranding, and market data). The humpback whale ESA listing final rule (81 FR 62259, 8 September 2016) established 14 Distinct Population Segments (DPSs) with different listing statuses. The DPSs that occur in waters under the jurisdiction of the United States do not equate to the existing MMPA stocks. Some of the listed DPSs partially coincide with the currently defined Western North Pacific stock. Because we cannot manage one portion of an MMPA stock as ESA-listed and another portion of a stock as not ESA-listed, until such time as the MMPA stock delineations are reviewed in light of the DPS designations and Bettridge et al. (2015), NMFS continues to use the existing MMPA stock structure and considers this stock to be endangered and depleted

for MMPA management purposes (e.g., selection of a recovery factor, stock status). As a result, the Western North Pacific stock of humpback whales is classified as a strategic stock.

There are key uncertainties in the assessment of the Western North Pacific stock of humpback whales. New DPSs were recently identified under the ESA; however, stocks have not been revised. The feeding areas of the Western North Pacific stock and the Central North Pacific stock overlap in waters from British Columbia to the Bering Sea, so human-related mortality and serious injury estimates must be assigned to or prorated to multiple stocks. The migratory destination of the Western North Pacific stock is not well understood. The population estimate was based on studies from the Asian wintering grounds; although no other large aggregations of whales are known, the estimate is likely conservative relative to the actual abundance. An estimate of variance is not available. The abundance estimate is calculated using data collected in 2004-2006; however, the population increased between estimates in 1991-1993 and 2004-2006 (Calambokidis et al. 2008), and the N_{MIN} is still considered a valid minimum population estimate (NMFS 2016). Estimates of human-caused mortality and serious injury from stranding data and fisherman self-reports are underestimates because not all animals strand or are self-reported nor are all stranded animals found, reported, or have the cause of death determined.

HABITAT CONCERNS

Elevated levels of sound from anthropogenic sources (e.g., shipping, military sonars) are a potential concern for humpback whales in the North Pacific, but no specific habitat concerns have been identified for this stock. Other potential impacts include possible changes in prey distribution with climate change, entanglement, ship strikes due to increased vessel traffic (e.g., from increased shipping in higher latitudes and through the Bering Sea with changes in sea-ice coverage), and oil and gas activities.

CITATIONS

Baker, C. S., S. R. Palumbi, R. H. Lambertsen, M. T. Weinrich, J. Calambokidis, and S. J. O'Brien. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344:238-240.

Baker, C. S., L. Medrano-Gonzalez, J. Calambokidis, A. Perry, F. Pichler, H. Rosenbaum, J. M. Straley, J. Urban-Ramirez, M. Yamaguchi, and O. von Ziegesar. 1998. Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. Mol. Ecol. 7:695-707.

Baker, C. S., D. Steel, J. Calambokidis, J. Barlow, A. M. Burdin, P. J. Clapham, E. A. Falcone, J. K. B. Ford, C. M. Gabriele, U. González-Peral, R. LeDuc, D. Mattila, T. J. Quinn, L. Rojas-Bracho, J. M. Straley, B. L. Taylor, J. Urbán-R., M. Vant, P. Wade, D. Weller, B. H. Witteveen, K. Wynne, and M. Yamaguchi. 2008. *geneSPLASH*: an initial, ocean-wide survey of mitochondrial (mt) DNA diversity and population structure among humpback whales in the North Pacific. Final Report for Contract 2006-0093-008 to the National Fish and Wildlife Foundation.

Baker, C. S., D. Steel, J. Calambokidis, E. Falcone, U. González-Peral, J. Barlow, A. M. Burdin, P. J. Clapham, J. K. B. Ford, C. M. Gabriele, D. Mattila, L. Rojas-Bracho, J. M. Straley, B. L. Taylor, J. Urbán, P. R. Wade, D. Weller, B. H. Witteveen, and M. Yamaguchi. 2013. Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. Mar. Ecol. Prog. Ser. 494:291-306. DOI: dx.doi.org/10.3354/meps10508 .

Barlow, J., and P. J. Clapham. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology 78(2):535-546.

Barlow, J., J. Calambokidis, E. A. Falcone, C. S. Baker, A. M. Burdin, P. J. Clapham, J. K. B. Ford, C. M. Gabriele, R. LeDuc, D. K. Mattila, T. J. Quinn II, L. Rojas-Bracho, J. M. Straley, B. L. Taylor, J. Urbán R., P. Wade, D. Weller, B. H. Witteveen, and M. Yamaguchi. 2011. Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. Mar. Mammal Sci. 27:793-818.

Bettridge, S., C. S. Baker, J. Barlow, P. J. Clapham, M. Ford, D. Gouveia, D. K. Mattila, R. M. Pace III, P. E. Rosel, G. K. Silber, and P. R. Wade. 2015. Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-540, 240 p.

Breiwick, J. M. 2013. North Pacific marine mammal bycatch estimation methodology and results, 2007-2011. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-260, 40 p.

Brownell, R. L., T. Kasuya, W. P. Perrin, C. S. Baker, F. Cipriano, J. Urban R., D. P. DeMaster, M. R. Brown, and P. J. Clapham. 2000. Unknown status of the western North Pacific humpback whale population: a new conservation concern. Unpubl. report to the International Whaling Commission. 5 p.

Calambokidis, J., G. H. Steiger, J. C. Cubbage, K. C. Balcomb III, and P. Bloedel. 1989. Biology of humpback whales in the Gulf of the Farallones. Report to Gulf of the Farallones National Marine Sanctuary, San Francisco, CA, by Cascadia Research Collective, 218½ West Fourth Avenue, Olympia, WA. 93 p.

Calambokidis, J., G. H. Steiger, and J. R. Evenson. 1993. Photographic identification and abundance estimates of humpback and blue whales off California in 1991-92. Final Contract Report 50ABNF100137 to Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037. 67 p.

Calambokidis, J., G. H. Steiger, J. M. Straley, T. Quinn, L. M. Herman, S. Cerchio, D. R. Salden, M. Yamaguchi, F. Sato, J. Urban R., J. Jacobson, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladrón de Guevara, S. A. Mizroch, L. Schlender, and K. Rasmussen. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Final Contract Report 50ABNF500113 to Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037. 72 p.

Calambokidis, J., G. H. Steiger, J. M. Straley, L. M. Herman, S. Cerchio, D. R. Salden, J. Urbán R., J. K. Jacobsen, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, S. Uchida, G. Ellis, Y. Miyamura, P. Ladrón de Guevara P., M. Yamaguchi, F. Sato, S. A. Mizroch, L. Schlender, K. Rasmussen, J. Barlow, and T. J. Quinn II. 2001. Movements and population structure of humpback whales in the North Pacific. Mar. Mammal Sci. 17(4):769-794.

Calambokidis, J., E. A. Falcone, T. J. Quinn, A. M. Burdin, P. J. Clapham, J. K. B. Ford, C. M. Gabriele, R. LeDuc, D. Mattila, L. Rojas-Bracho, J. M. Straley, B. L. Taylor, J. Urbán R., D. Weller, B. H. Witteveen, M. Yamaguchi, A. Bendlin, D. Camacho, K. Flynn, A. Havron, J. Huggins, and N. Maloney. 2008. SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific. Final Report for Contract AB133F-03-RP-00078, U.S. Dep. Commer., Western Administrative Center, Seattle, WA. Available online: http://www.cascadiaresearch.org/files/publications/SPLASH-contract-Report-May08.pdf . Accessed December 2018.

Clapham, P. J., and J. G. Mead. 1999. *Megaptera novaeangliae*. Mamm. Species 604:1-9.

Clapham, P. J., J. Barlow, M. Bessinger, T. Cole, D. Mattila, R. Pace, D. Palka, J. Robbins, and R. Seton. 2003. Abundance and demographic parameters of humpback whales from the Gulf of Maine, and stock definition relative to the Scotian Shelf. J. Cetacean Res. Manage. 5:13-22.

Clarke, J. T., C. L. Christman, A. A. Brower, and M. C. Ferguson. 2013a. Distribution and relative abundance of marine mammals in the northeastern Chukchi and western Beaufort seas, 2012. Annual Report, OCS Study BOEM 2013-00117. Marine Mammal Laboratory, AFSC, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115.

Clarke, J., K. Stafford, S. E. Moore, B. Rone, L. Aerts, and J. Crance. 2013b. Subarctic cetaceans in the southern Chukchi Sea: evidence of recovery or response to a changing ecosystem. Oceanography 26(4):136-149.

Darling, J. D. 1991. Humpback whales in Japanese waters. Ogasawara and Okinawa. Fluke identification catalog 1987-1990. Final Contract Report, World Wide Fund for Nature, Japan. 22 p.

Darling, J. D., and S. Cerchio. 1993. Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. Mar. Mammal Sci. 1:84-89.

Darling, J. D., J. Calambokidis, K. C. Balcomb, P. Bloedel, K. Flynn, A. Mochizuki, K. Mori, F. Sato, H. Suganuma, and M. Yamaguchi. 1996. Movement of a humpback whale (*Megaptera novaeangliae*) from Japan to British Columbia and return. Mar. Mammal Sci. 12(2):281-287.

Doroshenko, N. V. 2000. Soviet catches of humpback whales (*Megaptera novaeangliae*) in the North Pacific, p. 48-95. *In* A. V. Yablokov and V. A. Zemsky (eds.), Soviet Whaling Data (1949-1979). Center for Russian Environmental Policy, Marine Mammal Council, Moscow.

Fleming, A., and J. Jackson. 2011. Global review of humpback whales (*Megaptera novaeangliae*). U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-474, 206 p.

Hashagen, K. A., G. A. Green, and B. Adams. 2009. Observations of humpback whales, *Megaptera novaeangliae*, in the Beaufort Sea, Alaska. Northwest. Nat. 90:160-162.

Helker, V. T., M. M. Muto, K. Savage, S. Teerlink, L. A. Jemison, K. Wilkinson, and J. Jannot. In press. Human-caused mortality and injury of NMFS-managed Alaska marine mammal stocks, 2012-2016. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-XXX, XXX p.

Hill, M. C., E. M. Oleson, S. Baumann-Pickering, A. M. Van Cise, A. D. Ligon, A. R. Bendlin, A. C. Ü, J. S. Trickey, and A. L. Bradford. 2016. Cetacean monitoring in the Mariana Islands Range Complex, 2015. Prepared for the U.S. Pacific Fleet Environmental Readiness Office. PIFSC Data Report DR-16-01. 36 p. + appendix.

Ivashchenko, Y. V., R. L. Brownell, Jr., and P. J. Clapham. 2013. Soviet whaling in the North Pacific: revised catch totals. J. Cetacean Res. Manage. 13:59-71.

Johnson, J. H., and A. A. Wolman. 1984. The humpback whale, *Megaptera novaeangliae*. Mar. Fish. Rev. 46(4):30-37.

Johnston, D. W., M. E. Chapla, L. E. Williams, and D. K. Mattila. 2007. Identification of humpback whale *Megaptera novaeangliae* wintering habitat in the Northwestern Hawaiian Islands using spatial habitat modeling. Endang. Species Res. 3:249-257.

Melnikov, V. V. 2000. Humpback whales *Megaptera novaeangliae* off Chukchi Peninsula. Russ. J. Oceanogr. 4:844-849.

Miyashita, T. 2006. Cruise report of the sighting survey in the waters east of the Kuril Islands and the Kamchatka Peninsula in 2005. Unpubl. doc. submitted to Int. Whal. Comm. Scientific Committee (SC/58/NPM5).

Mizroch, S. A., and D. W. Rice. 2007. Distribution and movements of humpback whales (*Megaptera novaeangliae*) in the North Pacific Ocean. Presented at the 17th Biennial Conference on the Biology of Marine Mammals, Cape Town, South Africa.

Mizroch, S. A., L. M. Herman, J. M. Straley, D. Glockner-Ferrari, C. Jurasz, J. Darling, S. Cerchio, C. Gabriele, D. Salden, and O. von Ziegesar. 2004. Estimating the adult survival rate of central North Pacific humpback whales. J. Mammal. 85(5):963-972.

Mobley, J. M., S. Spitz, R. Grotefendt, P. Forestell, A. Frankel, and G. Bauer. 2001. Abundance of humpback whales in Hawaiian waters: Results of 1993-2000 aerial surveys. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary. 16 p.

National Marine Fisheries Service (NMFS). 2012. Process for distinguishing serious from non-serious injury of marine mammals. 42 p. Available online: https://www.fisheries.noaa.gov/national/marine-mammal-protection/marine-mammal-protection-act-policies-guidance-and-regulations . Accessed December 2018.

National Marine Fisheries Service (NMFS). 2016. Guidelines for preparing stock assessment reports pursuant to the 1994 amendments to the Marine Mammal Protection Act. 23 p. Available online: https://www.fisheries.noaa.gov/national/marine-mammal-protection/guidelines-assessing-marine-mammal-stocks . Accessed December 2018.

Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. Tokyo 12:33-89.

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. *S*ci. Rep. Whales Res. Inst. 14**:**149-290.

Nishiwaki, M. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling results, p. 172-191. *In* K. S. Norris (ed.), Whales, Dolphins and Porpoises. University of California Press, Berkeley, CA.

Ohsumi, S., and Y. Masaki. 1975. Japanese whale marking in the North Pacific, 1963-1972. Bull. Far Seas Fish. Res. 12:171-219.

Omura, H., and S. Ohsumi. 1964. A review of Japanese whale marking in the North Pacific to the end of 1962, with some information on marking in the Antarctic. Norsk Hvalfangst-Tidende 4:90-112.

Perry, A., C. S. Baker, and L. M. Herman. 1990. Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Rep. Int. Whal. Comm. (Special Issue 12):307-317.

Rice, D. W. 1978. The humpback whale in the North Pacific: distribution, exploitation and numbers, Appendix 4, p. 29-44. *In* K. S. Norris and R. R. Reeves (eds.), Report on a workshop on problems related to humpback whales (*Megaptera novaeangliae*) in Hawaii. U.S. Dep. Commer., Nat. Tech. Info. Serv. PB-280 794. Springfield, VA.

Rice, D. W. 1998. Marine Mammals of the World: Systematics and Distribution. Soc. Mar. Mammal. Spec. Publ. No. 4.

Springer, A. M., G. B. van Vliet, J. F. Piatt, and E. M. Danner. 2006. Whales and whaling in the North Pacific Ocean and Bering Sea: oceanographic insights and ecosystem impacts, p. 245-261. *In* J. A. Estes, R. L. Brownell, Jr., D. P DeMaster, D. F. Doak, and T. M. Williams (eds.), Whales, Whaling and Ocean Ecosystems. University of California Press. 418 p.

Steiger, G. H., J. Calambokidis, R. Sears, K. C. Balcomb, and J. C. Cubbage. 1991. Movement of humpback whales between California and Costa Rica. Mar. Mammal Sci. 7:306-310.

Tomlin, A. G. 1967. Mammals of the USSR and adjacent countries. Vol. 9. Cetacea. Israel Program for Scientific Translations No. 1124, Natl. Tech. Info. Serv. TT 65-50086. Springfield, VA. 717 p. (Translation of Russian text published in 1957.)

Wade, P. R., and R. Angliss. 1997. Guidelines for assessing marine mammal stocks: report of the GAMMS Workshop April 3-5, 1996, Seattle, Washington. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-OPR-12, 93 p.

Witteveen, B. H., J. M. Straley, O. von Ziegesar, D. Steel, and C. S. Baker. 2004. Abundance and mtDNA differentiation of humpback whales (*Megaptera novaeangliae*) in the Shumagin Islands, Alaska. Can. J. Zool. 82:1352-1359.

Zenkovich, B. A. 1954. Vokrug sveta za kitami, Vol. Gosudarstvennoe Izdatel'stvo Geograficheskoi Literatury, Moscow.

Zerbini, A. N., J. M. Waite, J. L. Laake, and P. R. Wade. 2006. Abundance, trends and distribution of baleen whales off western Alaska and the central Aleutian Islands. Deep-Sea Res. I 53(11):1772-1790.