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Abstract

Oregon State University has conducted satellite tagging on humpback whales (*Megaptera novaeangliae*) at several locations in the North Pacific Ocean over the period 1995–2016. Here we provide a brief summary of these data sets and describe how they are being used to address questions about migration, habitat use, residence time, navigation and orientation. In addition, we identify ways in which these data can be used for management in relation to the implementation of the new Distinct Population Segments designation under the Endangered Species Act and the threats affecting these populations throughout their migration routes.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are widely distributed in the North Pacific Ocean, with a total population currently estimated at over 21,000 animals (Barlow et al. 2011). Photographic matches have shown that most whales tend to return to the same general feeding and breeding areas from year to year (Calambokidis et al. 2001, Calambokidis et al. 2008), while geographic structuring in mitochondrial DNA has further indicated that this process is driven by strong maternal fidelity to the feeding areas and by natal fidelity to the breeding areas (Baker et al. 2013). However, occasional movements between breeding areas have been documented (Darling and Jurasz 1983, Darling and Cerchio 1993, Salden et al. 1999, Forestell and Urbán 2007), which together with a comparatively weak differentiation in nuclear DNA, are indicative of male-biased gene flow (Baker et al. 2013), apparently related to the tendency for males to prospect widely for females (Mobley and Herman 1985, Forestell and Urbán 2007).

Our understanding of the biological processes driving the annual migration between feeding and breeding areas in the North Pacific comes primarily from studies conducted in Hawaii. Humpbacks are abundant there from mid-December through early April, reaching peak numbers in February and March, when most females are believed to go into estrus (Darling 2009). The pattern of male activity around females suggests that the peak in ovulation for non-pregnant females is from December to early February, while a secondary peak from mid-February to March appears to be the result of pregnant females from the previous winter going into estrus after giving birth. Mating occurs during the brief period (a few days) when females are receptive, so most individuals (certainly most females) may be present in Hawaii for only a few weeks (Darling 2009). Thus, we might expect that a typical adult female that has spent spring, summer and part of the fall in the high-latitude feeding areas may migrate to Hawaii (a distance of ~4,000-5,000 km) in late fall (say, late November), arrive there 30-40 days later (late December), remain in Hawaii for 20-30 days (40 days if rearing a calf) while looking for a mate, and then undertake the return migration to finally arrive in the feeding area at the beginning of spring (mid-March) of the following year. The pattern of male residence in Hawaii is possibly similar, although the most dominant ones may spend significantly longer (up to 91 days) (Darling 2009), which would, in part, account for the observed biased sex ratio in the breeding areas. However, to date only sparse or incomplete data exist on the migration cycle of individual animals to corroborate this picture.

Indeed, despite having been intensively studied for several decades, many questions remain about humpback whale movement patterns at local to large scales. The most outstanding questions include: do humpbacks change their movement patterns during the different phases of their annual cycle (breeding, migrating, foraging) in measurable ways? How long does a complete migration take and how long do animals spend in each phase? Can we reconcile the traditional paradigm of a temporally ordered migration by age/sex class with the emerging notion of a continuous turnover of animals arriving and departing the breeding area throughout the winter season? Do males and females have different migratory patterns (including routes), as some genetic data suggest? What kind of orientation cues do they use in the open ocean to navigate between the breeding and feeding areas?

While traditional photo-identification studies can provide information on migratory destinations and suggest minimum travel times based on the dates of the photographs (if taken in the same year), they cannot provide information about the actual routes followed by the animals or about their migratory behavior while *en route*. Satellite telemetry, on the other hand, provides spatially explicit information about migration routes, as well as accurate estimates of travel speeds and departure and arrival times at the migratory destinations. The development of suitable electronic tags and tag-attachment methods on whales has overcome significant logistical and technological challenges in the past 30 years (Mate et al. 2007), and satellite telemetry is now a viable technique for studying questions about whale movements across vast ocean expanses on a routine basis. From 1995 to 2000, Oregon State University (OSU) developed the initial technology necessary to track whales for long distances via the Argos satellite system with UHF radio tags, as reported in Mate et al. (1998) and Mate et al. (2007). In the years since, OSU has continued to develop this technology, while also conducting new tagging on humpback whales in the North Pacific. This paper provides a summary of these efforts to date.

HUMPBACK WHALE SATELLITE TAGGING IN THE NORTH PACIFIC

Summary of published information

The history of remote tracking of humpback whales with radio-frequency implantable tags in the North Pacific dates back to the late 1970s, as recently reviewed by Mizroch et al. (2011). These early efforts occurred prior to the inception of the technology for monitoring radio tags from satellites, so tracking relied on surface monitoring of VHF signals using an automatic radio direction finder (Schevill and Watkins 1966, Watkins 1978, 1979, 1981, Watkins et al. 1980). As part of a collaboration between Woods Hole Oceanographic Institution, the National Marine Fisheries Service, and The Johns Hopkins University, five whales were tagged in southeastern Alaska in 1976 and 1977, and two whales were tagged in Prince William Sound, Alaska, in 1978. The southeastern Alaska whales were tracked for periods of up to 6 days and 75 km, while the Prince William Sound whales were tracked for 16 days (Watkins et al. 1981, Mizroch et al. 2011).

As part of the development of the technology for tracking large whales via satellite, OSU conducted tagging operations on humpback whales in Hawaii between 1995 and 2000 (total tags deployed: n=58). In the first year, OSU was successful in tracking two animals of unknown sex that headed almost due north in the direction of the Aleutian Islands, traveling for 1,610 km and 1,860 km in 14.7 and 17 days, respectively, at an average speed of 4.5 km/h (Mate et al. 1998). A third animal (a mother with a calf) also was tracked for 670 km in 4.5 days, moving northward at an average speed of 6.2 km/h (Mate et al. 1998). In subsequent years, several more animals were tracked, revealing the complete migration from Hawaii to feeding areas off Kamchatka, the Aleutians, and southeastern Alaska with unprecedented detail (Mate et al. 2007). The trajectories of partial tracks (from tags that failed early) also pointed in the direction of the various known feeding areas for Hawaiian humpbacks, and hinted at the complex nature of their movements and navigational capabilities in the open ocean. For instance, one animal used the Kermit-Roosevelt Seamount as an apparent feeding station halfway through the migration, and subsequently changed its direction of travel from a presumed destination in southeastern Alaska to one in the Aleutians (Mate et al. 2007) (Figure 1).

Within Hawaii, the tracking data revealed the pattern of inter-island movements from Kaua'i to O'ahu to Maui Nui (i.e., the group of islands comprised by Maui, Molokai, Lāna'i, and Kaho'olawe; also known as the "four-islands region"), including the whales' use of the windward side of the islands and of the offshore Penguin Bank; areas where traditional fieldwork is precluded due to prevalence of high winds (Mate et al. 1998, Mate et al. 2007). These data further indicated that the whales' remaining residence time in the islands after tagging was, on average, only 13.4 days regardless of the month of tagging (December, February, March or April) (Mate et al. 1998), lending support to earlier studies that found that there is a rapid turnover of individuals in the breeding area during the winter season (Craig et al. 2003, Darling 2009).

In 2003, OSU tagged 11 whales in the Revillagigedo Islands, an oceanic archipelago off Mexico, including a mother-calf pair that was tracked to the Gulf of Alaska for a total duration of 150 days (Lagerquist et al. 2008) (Figure 2). Another animal arrived in British Columbia, while the trajectories of three other partial tracks suggested a destination in the Aleutians (Lagerquist et al. 2008). These tracks indicated average speeds of 4 km/h during migration (Lagerquist et al. 2008). The tracking data also demonstrated extensive use of areas adjacent to the Mexican mainland by the animals tagged at the Revillagigedos before initiating migration to the high-latitude feeding areas (Lagerquist et al. 2008) (Figure 2).

Summary of unpublished information

In addition to the studies summarized in the previous section, OSU has conducted humpback whale tagging at several locations in the North Pacific, as follows: southeastern Alaska (1997: n=10; 2014: n=20; 2015: n=17), Cabo San Lucas, Mexico (1998: n=7), central California (2004: n=8; 2005: n=7), Aleutian Islands (2008; n=5), Hawaii (2015: n=20), and central Oregon (2016: n=3).

The total number of tags deployed by OSU during the period 1995-2016 is 166, and it represents one of the largest tracking data sets for any humpback whale population (Figure 3). Of this total, 147 tags (89%) provided at least 1 valid location, 110 tracks (66%) were longer than 7 days, and 43 tracks (26%) were longer than 30 days. For all tags with at least 1 valid location the average duration and distance were 30 days and 1,793 km, respectively. The longest tracking duration and distance were 178 days and 10,732km, respectively. The total tracking duration and distance for all tags combined was 4,576 days and 263,619 km, respectively. The number of complete migrations, from deployment in a breeding area to arrival in a feeding area (or vice versa), was 12 (7%), while two more tags had nearly complete migrations. Sex was determined for 33 females and 41 males, while the remaining 92 animals were of unknown sex.

Ongoing work

We have applied state-space models (SSM) on 92 of these tracks to generate optimized locations at regular intervals. In addition, the SSM provide an inferred behavioral mode (resident or migratory) at each location. We are using these data to investigate the patterns of movement and speed during the different phases of migration, and to address other questions about long-distance migration in humpback whales (see Introduction). In addition, the period of time from tagging to the initiation of migration allows us to estimate the minimum residence time in the breeding and feeding areas, and to identify departure and arrival dates, based on the SSM-derived behavioral mode. Finally, the tracking data further provide valuable information about distribution and use within the breeding and feeding areas that are difficult to document with other methods like sighting or acoustic surveys.

Management applications

A recent revision of the species-wide listing under the Endangered Species Act (ESA) led to the division of the global humpback whale population into 14 Distinct Population Segments (DPS) based on the location of distinct breeding areas (Bettridge et al. 2015, Federal Register 2016a, b). Four DPSs were identified for the North Pacific: Western North Pacific (including Okinawa/Philippines and an unidentified breeding area in the western North Pacific); Hawaii; Mexico (including mainland Mexico and the Revillagigedo Islands); and Central America. The corresponding ESA status is “Endangered” for both the Western North Pacific and the Central America DPSs, “Threatened” for the Mexico DPS, and “Not Listed” for the Hawaii DPS (Federal Register 2016a, b). As a result, there is an urgent need for information on areas of high use by whales from these different DPSs, and their overlap with shipping traffic, fishing grounds, and areas of military operation, in order to prioritize management actions to mitigate the impact from these activities.

Satellite tracking data are particularly useful for informing the implementation of the ESA process, including the identification of areas of high use throughout the migration range, and confirmation of DPS with genetic analyses from biopsy samples of the tagged animals (Figure 3). In addition to ongoing analyses with existing data, OSU plans to conduct further tagging off Oregon in the near future that would augment our information on the movements of the Endangered Central America DPS along the western coast of North and Central America. Additional locations where tagging would be particularly relevant to the DPS process during future efforts include the Western Pacific and Hawaii (especially areas that have received less or no attention like Kauai and the Northwest Hawaiian Islands).

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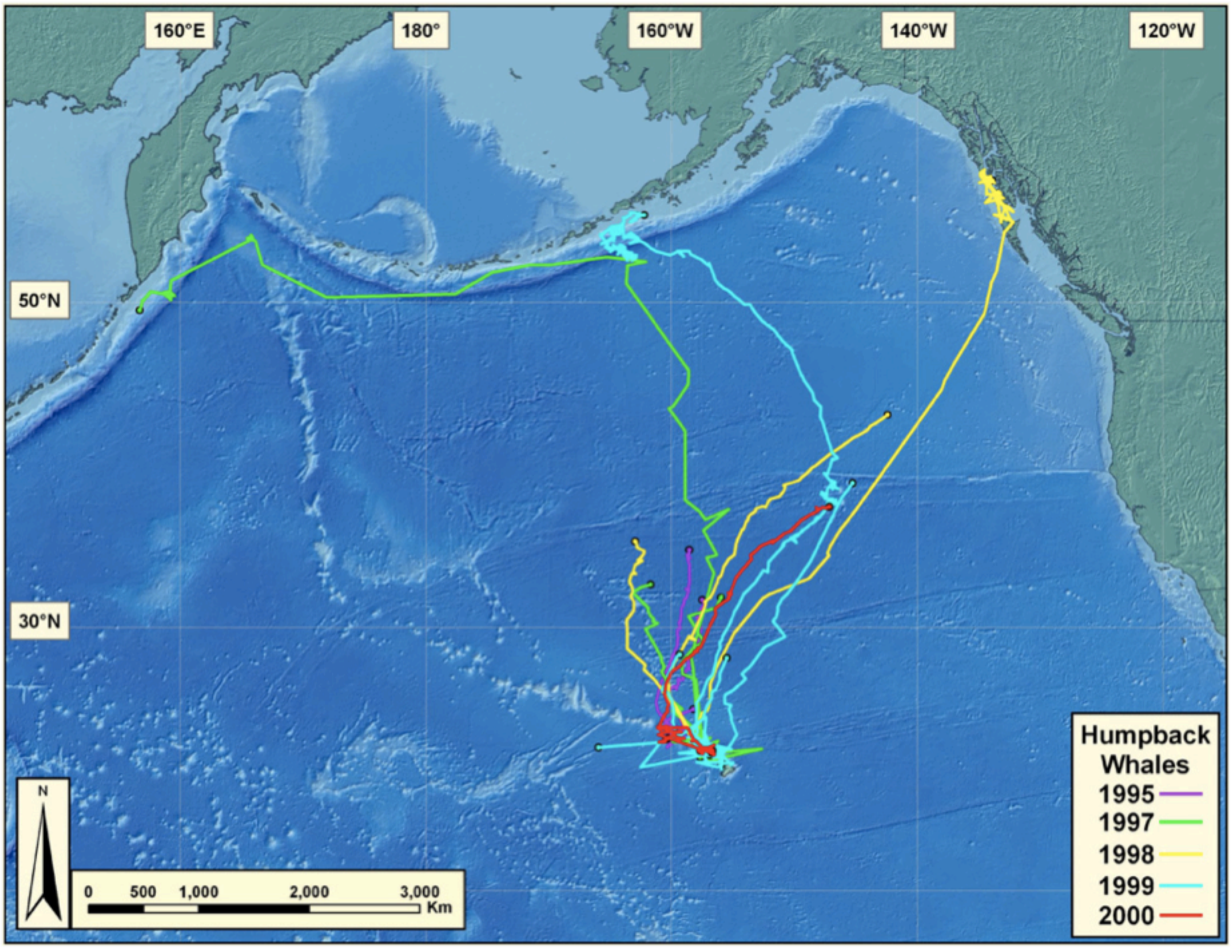

Figure 1. The Argos tracks of humpback whales tagged by OSU in Hawaii between 1995 and 2000, as published in Mate et al. (2007), showing migratory destinations in Kamchatka, the Aleutian Islands, and southeastern Alaska.

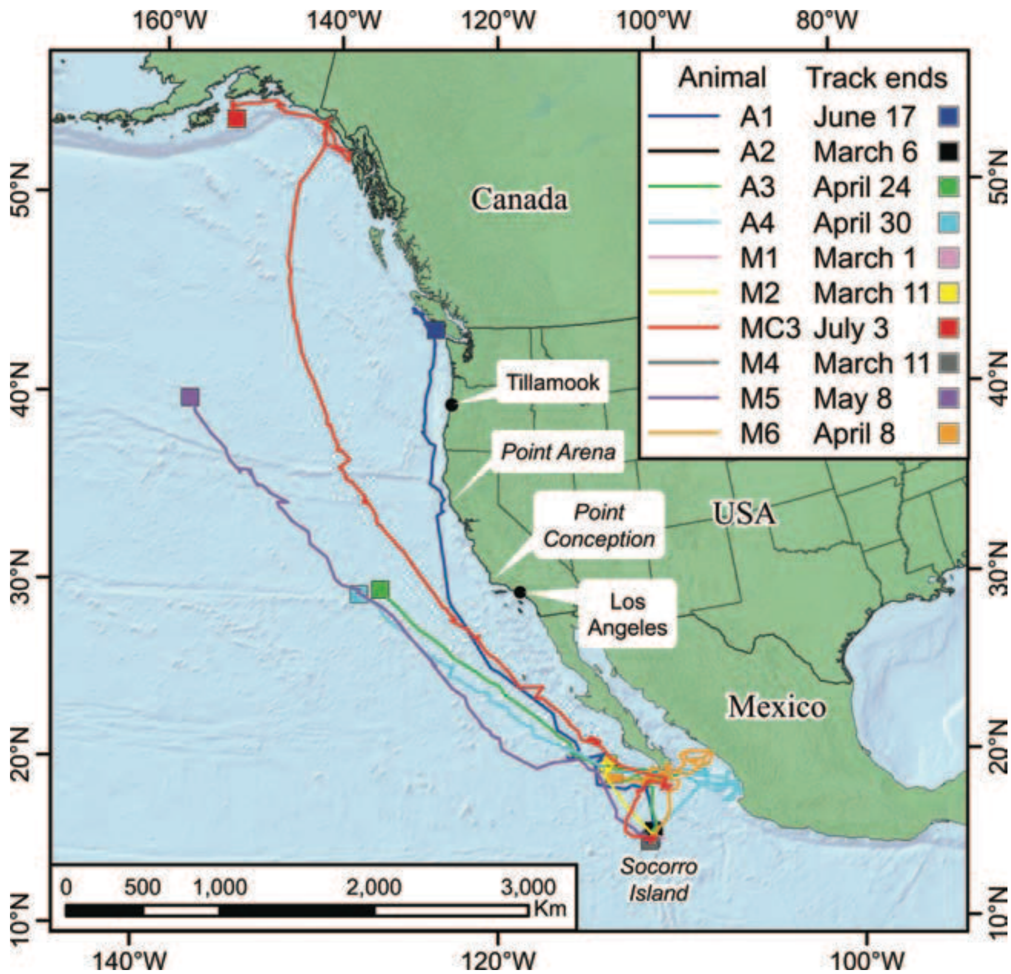

Figure 2. The Argos tracks of 11 humpback whales satellite tagged by OSU at the Revillagigedo Islands off Mexico in 2003, as published in Lagerquist et al. (2008), showing migratory destinations in the Gulf of Alaska, British Columbia, and possibly the Aleutian Islands.

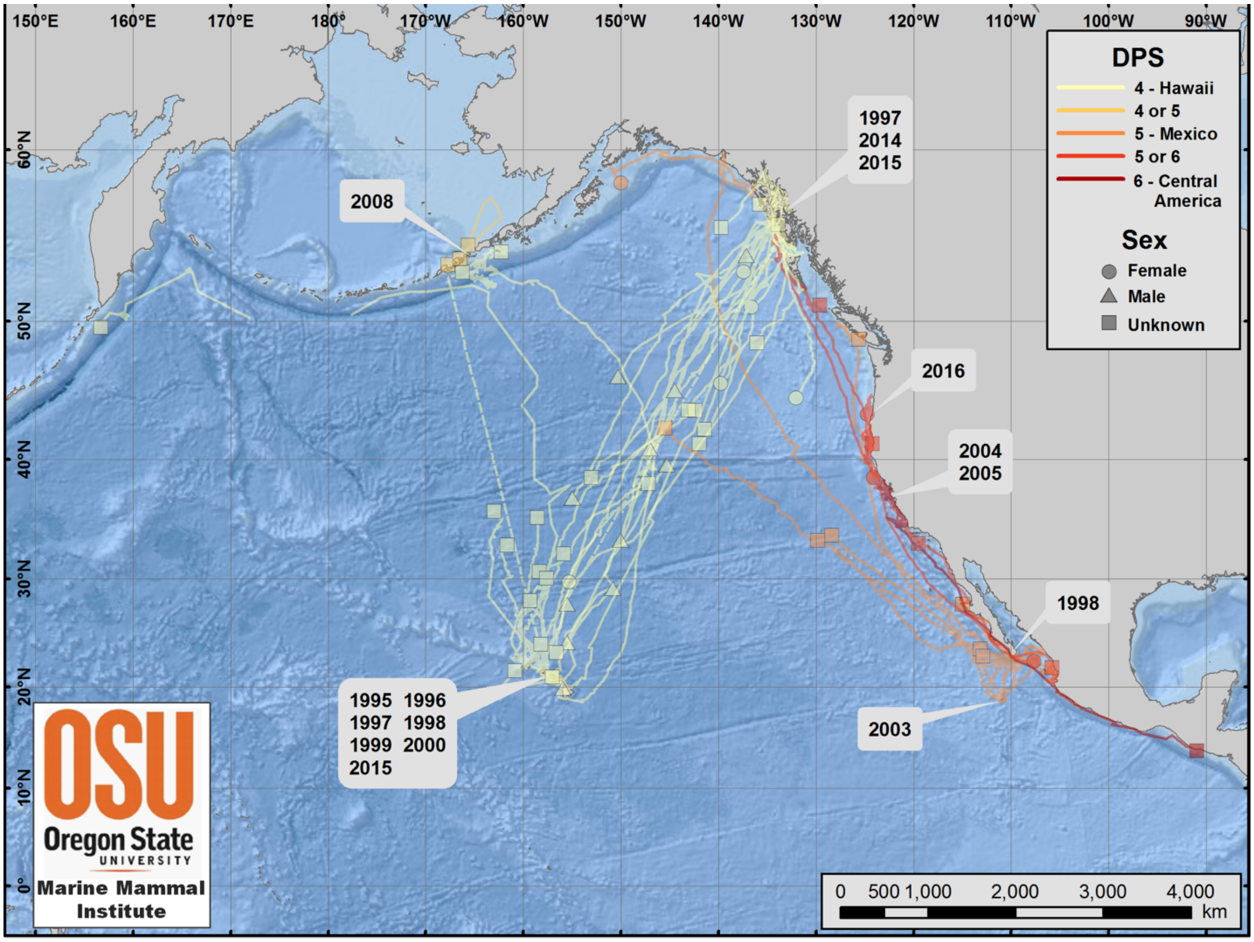

Figure 3. The Argos tracks of 166 humpback whales tagged by OSU in the North Pacific between 1995 and 2016. Years are indicated at each site where tagging has been conducted. Some of these tracks have appeared in Mate et al. (1998), Mate et al. (2007), and Lagerquist et al. (2008). Track color indicates preliminary assignment to DPS. Biopsy samples from 74 of these tagged animals have been collected for genetic confirmation of DPS. [Note: this figure was created for the purpose of discussion at the International Whaling Commission "Workshop on the Comprehensive Assessment of North Pacific Humpback Whales," 18-21 April 2017, Seattle, Washington, USA. Please do not cite or reuse this figure or its contents without the express consent of the authors].