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Migratory destinations of humpback whales that feed off California, Oregon and Washington

John Calambokidis[1,*], Gretchen H. Steiger[1], Kristin Rasmussen[1], Jorge Urbán R.[2], Kenneth C. Balcomb[3], Paloma Ladrón de Guevara P.[4], Mario Salinas Z.[4], Jeff K. Jacobsen[5], C. Scott Baker[6,], Louis M. Herman[6], Salvatore Cerchio[7,***], James D. Darling[8]**

[1]Cascadia Research Collective, Waterstreet Building, 218½ West Fourth Avenue, Olympia, Washington 98501, USA
[2]Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Apt. Post 19-B, B.C.S. 23081, Mexico
[3]Center for Whale Research, 1359 Smuggler's Cove Road, Friday Harbor, Washington 98250, USA
[4]Laboratorio de Mamiferos Marinos, Universidad Nacional Autónoma de México, Apt. Post 70-572, México City, D.F. 04510, Mexico
[5]PO Box 4492, Arcata, California 95521, USA
[6]Kewalo Basin Marine Mammal Laboratory, University of Hawaii, 1129 Ala Moana Blvd., Honolulu, Hawaii 96814, USA
[7]Moss Landing Marine Laboratories, PO Box 450, Moss Landing, California 95039, USA

ABSTRACT: The migratory destinations of humpback whales that feed off California, Oregon and Washington were determined using photo-identification. Fluke photographs of 594 individuals were taken between 1981 and 1992 and compared to collections from 9 wintering regions in the North Pacific: Ogasawara (162) and Okinawa (17) islands of Japan; the Big Island and Maui (634 for both) and Kauai (384) of Hawaii; the Revillagigedo Archipelago (450), the mainland coast (383) and Baja Peninsula (471) of Mexico; and Central America (31). A total of 160 matches were found to 6 central and eastern North Pacific wintering regions, with most from Central America, Baja, and mainland Mexico. Of whales identified off Central America, 84% were resighted off California-Washington; this high rate of interchange suggests that whales in these tropical waters appear to be comprised entirely of animals from the California-Washington feeding aggregation. Humpback whales seen off Central America were resighted disproportionately off southern California while those from mainland Mexico tended to be seen off northern California-Washington. From 157 same-season migratory transits documented, the shortest were 29 d to Baja and 56 d to Costa Rica and the longest distance was 5322 km. Of the California-Washington whales with known sex, the proportion of males identified at a wintering region was significantly higher than females (2.2:1, $p < 0.05$).

KEY WORDS: Humpback whales · Migration · Photo-identification · North Pacific

INTRODUCTION

Humpback whales *Megaptera novaeangliae* undergo the longest migration documented for any mammal (Stone et al. 1990). Their movement patterns between summer feeding areas at high latitudes and winter mating and calving areas at low latitudes have been

*E-mail: calambokidis@cascadiaresearch.org
Present addresses:
**School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand
***Univ. of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA

the subject of research in a number of regions. In the North Atlantic, defining these migratory movements and the resulting stock structure has been relatively straightforward due to the existence of a single primary wintering area (Palsboll et al. 1997, Smith et al. 1999). Defining the stock structure of humpback whales in the North Pacific has proven to be more complicated due to the existence of both multiple summer feeding and winter breeding areas. At least 4 wintering areas have been described: (1) the waters off Mexico (mainland Mexico, Baja California and the Revillagigedo Archipelago) (Urbán & Aguayo 1987, Alvarez et al. 1990), (2) Costa Rica (Steiger et al. 1991, Acevado & Smultea 1995, Rasmussen et al. 1995), (3) the Hawaiian Islands (Herman & Antinoja 1977) and (4) islands of Japan (Nishiwaki 1959, Darling & Mori 1993, Uchida et al. 1993).

Although the number and boundaries of the feeding grounds for humpback whales in the North Pacific have not been fully described, the range of one major feeding aggregation off California, Oregon and Washington has been well defined. Whales in this region were first thought to be en route to feeding grounds off Alaska (Kellogg 1929, Tomilin 1957), but more recently photo-identification studies (Calambokidis et al. 1996) and mtDNA studies (Baker et al. 1990, 1998) suggest that whales from this area constitute a separate feeding aggregation. This feeding ground ranges between 32 and 48° N, with the main concentration inhabiting Californian waters between 32 and 39° N (Calambokidis et al. 1996). The abundance of this subpopulation in the early 1990s was estimated at about 600 whales and appears to be increasing (Barlow 1994, 1995, Calambokidis & Steiger 1995).

While migratory destinations of humpback whales that feed off Alaska and British Columbia have been reported (Darling & Jurasz 1983, Darling & McSweeney 1985, Baker et al. 1986, Darling & Cerchio 1993, Darling et al. 1996, Gabrielle et al. 1996), very little information has been published on the migratory destinations of the humpback whales that feed off California, Oregon and Washington. Baker et al. (1986) reported resightings of a single whale between California and mainland Mexico and a second whale between California and Hawaii, but this was based on a sample of only 18 whales from California. Preliminary results of movements between California and Mexico from a small sub-sample (about 100 identifications) of the sample used in this study were reported by Urbán et al. (1987). Steiger et al. (1991) reported the first documented migrations of 3 whales between California and Costa Rica.

We examine several aspects of the migratory destinations of humpback whales of this major feeding aggregation. We provide the first quantitative analysis of migratory destinations of these animals using a comprehensive collection of identified individuals and examine the evidence for stratification in these destinations related to distribution within a single feeding aggregation. We also document the fastest transit times of whales to some of these destinations and differences in migratory rates by sex.

METHODS

Collections of humpback whale fluke photographs were assembled from independent researchers working throughout the North Pacific and were compared visually at Cascadia Research Collective (CRC). Natural markings on the ventral side of the fluke were used to identify them as described previously (Katona et al. 1979). Photographs of whales taken off California, Oregon and Washington were compared with 7 independent collections from 9 wintering regions in the North Pacific (Fig. 1). Sample sizes shown are photographs judged to be of suitable quality for comparison.

California, Oregon and Washington. Because this sample was collected predominantly off California, it will be referred to as the 'California' sample. A sample of 594 individuals identified between 1981 and 1992 was used in the comparison to the wintering regions. A larger sample was used (897 unique whales identified through 1997, inclusive of the first sample used here) in the comparison of whales identified off Central America and to examine transit times (see below).

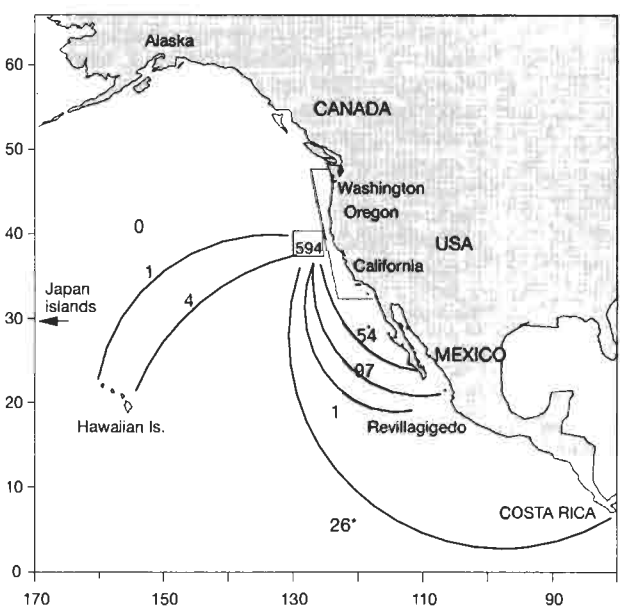

Fig. 1. Migratory destinations of humpback whales seen off California between 1981 and 1992. *Includes data through 1997 for Costa Rica

Photographs were taken by CRC, the Center for Whale Research (CWR), Friday Harbor, Washington, and other collaborators during humpback and blue whale photo-identification studies (Table 1; Calambokidis et al. 1990, 1996). Research was conducted in waters out to about 60 km off central California between 1986 and 1990 and was expanded to include surveys along the entire California coast beginning in 1991. Whales identified along the Washington/British Columbia border were not included in this analysis, because they appear to be from a separate feeding aggregation that extends northward and is largely distinct from the aggregation feeding off California, Oregon and Washington (Calambokidis et al. 1996).

The vessels included 4 to 6 m inflatable boats. Photographs were taken with Nikon motor-advance 35 mm SLR cameras with 300 mm f4.5 lenses with Ilford HP-5 or Kodak Tri-X black-and-white negative film. Shutter speeds were usually 1/1000 s or faster. Film was exposed at ISO 1200 and development times were adjusted accordingly.

Mainland Mexico. Photographs were taken in the waters of Bahía de Banderas and the areas near Islas Tres Marías and Isabel. This collection was maintained by the Universidad Nacional Autónoma de México (UNAM) (Ladrón de Guevara P. 1995). This region is described by Urbán & Aguayo (1987).

Baja California, Mexico. Whales were identified off the southern coast of Baja California. Data were collected by the Universidad Autónoma de Baja California Sur (UABCS) and CWR.

Revillagigedo Archipelago. This sample was collected in a collaborative effort. This archipelago is about 450 km southwest of Cabo San Lucas and includes Islas Socorro, San Benedicto and Clarion (Urbán & Aguayo 1987). Most survey effort was made at Isla Socorro.

Costa Rica/Panama. Most of the photo-identification data from Costa Rica has come from surveys since 1996. Because of the small sample from the period addressed here, we have included a more recent comparison of 31 humpback whales photographed off Costa Rica between 1988 and 1998. To make the comparison contemporaneous, we used whales identified off California through 1997 (965). Most of these surveys were conducted off southwestern Costa Rica along the Osa Peninsula by CRC in January and February (Calambokidis 1997). A photograph of a single whale from the Gulf of Panama on 5 January 1996 was provided by Jack Swenson.

Big Island and Maui, Hawaii. A catalog of whales identified in Hawaiian waters was provided by the Kewalo Basin Marine Mammal Laboratory at the University of Hawaii (Baker et al. 1986, Perry et al. 1988, 1990) and published as a catalog by Perry et al. (1988). Photographs were primarily taken off the leeward coasts of the Big Island and west Maui.

Kauai, Hawaii. The study region encompassed the south and west coasts from Makahuena Point and Makaha Point (Cerchio 1998).

Japan. A catalog of humpback whales was used of whales off Ogasawara and Okinawa (Darling & Mori 1993) that was published by Darling (1991).

Analysis. Migratory transit times between wintering regions and feeding areas in one season were examined. All sightings of the same individual whale off California and in a wintering region within a 1 yr period were compiled to evaluate minimum transit intervals. Because of the incomplete sampling effort, these times are not necessarily representative of the true transit times. Distances between locations where whales were sighted were calculated based on Great Circle routes without adjustment for possible deviations to avoid landmasses or follow likely migration routes. They therefore represent minimum distances.

We examined the migration destinations of whales for which sex was known. To avoid biases, we only included whales that were sexed based on evidence (i.e. molecular or behavioral) from the feeding ground from 1987 to 1992 (Baker et al. 1991, 1998).

Our sample was stratified by sub-area to examine differences in migratory destinations within the feeding ground. The occurrence of whales in 3 sub-areas was determined: (1) southern California, from the

Table 1. Summary of effort made to photo-identify humpback whales off California, Oregon and Washington. The 594 unique whales photographed from 1981 to 1992 were used in the comparison to all wintering regions except Costa Rica, for which the 1981 to 1997 sample of 897 whales was used

Year	Dates	No. of surveys	No. of whales identified
1981–1985	4 May–30 Nov	[a]	20
1986	23 Jul–15 Sep	71	91
1987	17 Aug–17 Oct	58	150
1988	19 Aug–2 Nov	66	213
1989	8 Sep–26 Oct	15	110
1990	4 Sep–13 Nov	29	208
1991	16 Jul–15 Nov	53	269
1992	24 May–16 Nov	73	398
1993	28 Jul–22 Oct	48	254
1994	15 Jun–10 Oct	51	260
1995	10 Jun–3 Dec	60	363
1996	21 Apr–12 Nov	129	364
1997	21 Feb–5 Nov	150	286
Total		803	2986
Unique whales, 1981–1992			594
Unique whales, 1981–1997			897

[a]Opportunistic surveys; photos were contributed by other researchers

Table 2. Summary of the matches found among humpback whales identified off California, Oregon and Washington between 1981 and 1992 (1997 for Costa Rica) and those photographed at the North Pacific breeding grounds. UNAM: Universidad Nacional autónoma de México; UABCS: Universidad Autónoma de Baja California Sur; CWR: Center for Whale Research; CRC: Cascadia Research Collective

Region	Primary data source	Years	No. of individuals	Matches with CA/OR/WA Number	%
Mexico					
Revillagigedos Archipelago	UNAM & Jacobsen	1986–1992	450	1	0.2
Baja California	UABCS & CWR	1987–1993	471	54	11
Mainland Mexico	UNAM	1983–1992	383	97	25
Total for Mexico			1190	130	11
Central America					
Costa Rica/Panama	CRC	1988–1998[a]	31	26	84
Hawaii					
Big Island/Maui	Perly et al. (1988)[b]	1977–1985	634	4	0.6
Kauai	S. Cerchio	1989–1991	384	1[d]	0.34
Japan					
Ogasawara	Darling (1991)[c]	1987–1990	162	0	0
Okinawa	Darling (1991)[c]	1989–1990	18	0	0

[a]This comparison included 897 whales identified off California, Oregon and Washington between 1981 and 1997
[b]Catalog published by Kewalo Basin Marine Manual Laboratory
[c]Catalog published by West Coast Whale Research Foundation
[d]Same whale also seen off Big Island/Maui

Mexican border (32° 35′ N) to Point Sur (36° 20′ N), (2) central California, from Point Sur (36° 20′ N) to Point Arena (39° 00′ N), encompassing the 2 primary areas in which effort was made, the Farallon Is./Cordell Bank region and Monterey Bay, and (3) northern waters, including northern California, Oregon and Washington (39° 00′ to 48° 00′ N). The proportion of whales and the number of years individuals were seen in these 3 sub-areas were averaged and then compared among the individuals with known winter migratory destinations and those for which the destinations were unknown.

RESULTS

Migratory destinations

A total of 160 humpback whales were matched between California and a wintering region (Table 2). The proportion of whales identified in different wintering regions that had also been seen off California varied significantly by location ($\chi^2 = 538$, $p < 0.001$). The largest number of matches (and highest proportion of whales) from California were found on the wintering grounds of Central America, mainland Mexico and Baja California (Table 2). The largest number of matches was to mainland Mexico and Baja. Of the whales photographed off mainland Mexico, 25% were from California, just over twice that found off Baja (11%). Although the number of matches was lower (due to sample size), the percentage of humpback whales identified off Central America in winter that were also sighted off California (84%) was higher than any other region.

Movement of whales between California and other wintering regions was rare (<1%, Table 2). In our sample, 4 whales were documented to have migrated between California and Hawaii at least once (Table 3). One of these (CRC 10144) was determined to be a mature female when it was accompanied by a calf off California in 1988. CRC 10093 was photographed by Marc Webber off California in 1981, and was then also sighted off Hawaii in 1982 and Kauai in 1989. This whale has not been resighted off California since 1981. Only 1 whale (CRC 10010) moved between California and the Revillagigedo Archipelago (Table 3). No interchange was observed between whales off California and those photographed off Japan.

Migratory transits

We documented 157 migratory transits (same season) of whales between California and several wintering regions (Table 4). Because longer transit intervals could be an artifact of sampling effort, we focused on the shortest intervals documented. The shortest transit time was to southern Baja California in 29 d (1900 km, CRC 9508); the fastest time to mainland Mexico was 39 d (2589 km, CRC 10020) and to Costa Rica was 56 d (5097 km, CRC 9031). The fastest record of swimming

Table 3. Records of individual humpback whales from California with unusual migratory destinations through 1992. Identification numbers of the contributing organizations and catalogs are given

Year	Region
CRC 9021/KBMML 1000	
1982	Hawaii
1988	Califomia-Pt San Luis
1991	Califomia-Pt San Luis
1992	Califomia-Santa Barbara
CRC 10093/KBMML 1103/SC-012[a]	
1981	Califomia-Gulf of Farallones[b]
1982	Hawaii
1989	Hawaii-Kauai
CRC 10130/KBMML 1084	
1982	Hawaii
1987	Califomia-Gulf of the Farallones
1988	Califomia-Gulf of the Farallones
1989	Califomia-Gulf of the Farallones
1990	Califomia-Gulf of the Farallones
1992	Califomia-Pt Arena and Fort Bragg
CRC 10144/KBMML 231	
1980	Hawaii
1987	Califomia-Gulf of the Farallones
1988	Califomia-Gulf of the Farallones[c]
1992	Califomia-Gulf of the Farallones/Pt Arena
CRC 10010/UNAM 2A 191R053 UABC5 589/JJ004	
1986	Califomia-Gulf of the Farallones
1990	Califomia-Gulf of the Farallones
1991	Revillagigedos Archipelago
1991	Califomia-Pt St George
1992	Califomia-Santa Barbara Channel

[a]Reported by Baker et al. (1986)
[b]Photographed by Marc Webber
[c]Seen with a calf

speed was 3.8 km h^{-1} between California and Costa Rica (assuming the whale was swimming on a direct route 24 h d^{-1}). Fastest speeds to both Baja California and mainland Mexico were 2.7 km h^{-1}. These maximal distances and speeds are minimums because whales probably moved more extensively or in shorter periods than we documented. The farthest straight-line distance traveled was 5322 km (northern California to Costa Rica, CRC 10583).

Feeding area occupancy and annual return by wintering region

The number of years and times per year individual whales were sighted off California did not vary greatly and were not significantly different among the whales with different known migratory destinations (Table 5). Whales known to migrate to Hawaii and the Revillagigedos Archipelago had somewhat outlying values, although sample sizes were too small to test statistically. The average number of years that whales were sighted off California did not vary significantly between those known to migrate to Hawaii, mainland Mexico, Baja California, and Central America (ANOVA, $F = 1.07$, $p > 0.05$). These values were slightly higher, however, than for whales for which winter migratory destinations were not known (Table 5).

Migratory destinations by sub-area

Whales from some wintering regions were more likely than others to be sighted in 1 of 3 sub-areas within the feeding ground (Table 5). Of whales with the known migratory destinations of Central America, mainland Mexico, and Baja California, there were significant differences in the proportion that were seen off southern California ($\chi^2 = 20.4$, $p < 0.01$) and northern waters ($\chi^2 = 4.9$ $p < 0.05$). Whales known to migrate to Central America were 3 times more likely to be seen in southern California (63 vs 21%) and less than half as likely to be seen in northern waters (22 vs 46%) than those from mainland Mexico. Whales that had been seen off Baja California had a resighting rate in the feeding sub-areas that was intermediate to those for mainland Mexico and Central America. A similar pattern was apparent in the mean number of years whales were seen in these sub-areas when divided among their known wintering regions (Table 5). Whales known to winter off mainland Mexico were seen significantly more years in northern waters (ANOVA, $F = 11.6$, $p < 0.001$) and significantly fewer years off southern California (ANOVA, $F = 4.4$, $p < 0.05$) than whales with unknown wintering destinations (Table 5).

Migratory destinations by sex

Of 69 whales for which the sex was identified off California through 1992, 23 were also sighted on a wintering ground. Known males from California were 2.2 times more likely to have also been identified on a wintering ground than known females ($\chi^2 = 5.5$, $p < 0.05$). Of 23 whales determined to be males off California, 12 (52%) were identified on a winter ground; of 46 females, only 11 (24%) were identified.

DISCUSSION

The comparison of more than 2500 identification photographs from all known wintering grounds in the North Pacific provides strong evidence for preferred

Table 4. Transit times of humpback whales between California and wintering regions

Direction	No. of transits	Shortest transit interval							Longest interval (no. of days)
		No. of days	CRC ID	CA location	Dates seen		No. of km	Speed (km h^{-1})	
Baja California									
N	33	29	9508	Pt Sur	10 Mar 1990	8 Apr 1990	1900	2.73	313
S	22	100	10563	Monterey Bay	15 Nov 1991	23 Feb 1992	1913	0.80	234
All	55								
Mainland Mexico									
N	51	137	12002	Heceta Bank	8 Feb 1990	25 Jun 1990	3152	0.96	315
S	27	39	10020	Cordell Bank	2 Dec 1990	10 Jan 1990	2589	2.77	317
All	78								
Revillagigedo Archipelago									
N	1	219	10010	Bodega Bay	23 Jan 1991	30 Aug 1991	2459	0.47	219
S	1	71	10010	Cordell Bank	13 Nov 1990	23 Jan 1991	2491	1.46	71
All	2								
Costa Rica									
N	10	69	10731	Half Moon Bay	12 Feb 1996	21 Apr 1996	5045	3.05	254
S	10	56	9031	Gulf of the Farallones	1 Dec 1995	26 Jan 1996	5097	3.79	233
All	20								
Panama									
S	1	144	10593	San Luis	14 Aug 1995	5 Jan 1996	5208	1.51	144
Hawaii									
S	1	153	10093	Gulf of the Farallones	30 Jun 1981	1982	3700		153

migratory destinations of humpback whales from the California feeding ground, with the majority of whales traveling to mainland Mexico, Baja California and Central America. These findings are consistent with and extend the previous demographic evidence for stock structure in the North Pacific including the initial reports of the first matches of humpbacks from California to those in wintering areas in Hawaii, Mexico and Costa Rica (Baker et al. 1986, Urbán et al. 1987, Steiger et al. 1991).

Among the 3 regions of Mexico, there were dramatic differences in the proportion of whales that were also seen in the California feeding ground; rates were high for both mainland Mexico and Baja California but quite low for the offshore Revillagigedo Archipelago; the proportion of whales that were also seen in the California feeding area was lower here than for the Hawaiian Islands. This is consistent with the few limited matches reported in the past between California and Mexico that only involved whales from mainland Mexico (Baker et al. 1986, Urbán et al. 1987).

In spite of the strong tendencies described here, it is clear that the migratory routes of North Pacific humpbacks do not follow the simple pattern whereby all whales of a feeding aggregation travel to a single wintering area. Similar to our findings off California, humpback whales from other North Pacific feeding grounds have been documented traveling to multiple wintering areas: whales from Prince William Sound have been seen off mainland Mexico, the Revillagigedos Archipelago and Hawaii (Baker et al. 1985, 1986, Darling & McSweeney 1985), and those off British Columbia have been sighted off all Mexican wintering grounds, Hawaii, and Japan (Darling & McSweeney 1985, Darling et al. 1996).

Our results are consistent with findings from genetics studies. Such studies have demonstrated highly significant differences in mtDNA haplotypes (Baker et al. 1990, 1994, 1998) and weak but still significant differences in alleles of nuclear microsatellites and the actin intron (Baker et al. 1998) among feeding areas, including California. Additionally, the strong migratory connections between some feeding areas and wintering regions were also reflected in similarities in mtDNA haplotypes between California and Mexico as well as some Alaskan feeding grounds and Hawaii. The mtDNA patterns were not identical between these wintering and feeding grounds, which reflects the presence of whales from several feeding areas on a wintering area. Based on our findings, however, an identical mtDNA pattern would be expected between whales off California and Central America, an area that has not yet been sampled for genetic analyses. The genetic and demographic patterns of population structure in the North Pacific appear to be different from the North Atlantic. Current evidence suggests that the majority of humpback whales from almost every feeding area in the North Atlantic gather and

Table 5. Frequency whales were seen off California, Oregon, and Washington (by sub-area); the whales are grouped by their known migratory destinations. Twenty-two whales seen in both Baja California and mainland Mexico are included twice

	No. of whales identified	Years [mean (SD)] each individual was seen in each sub-area				% of matches seen in each sub-area		
		California-Washington	Southern California	Central California	Northern waters	Southern California	Central California	Northern waters
Matched to a wintering area								
Central America	26	3.3 (1.9)	1.0 (1.0)	2.7 (1.9)	0.35 (0.7)	65	96	23
Mainland Mexico	97	4.2 (2.4)	0.51 (1.2)	3.9 (2.9)	0.81 (1.0)	21	90	46
Baja California	54	3.9 (2.5)	0.91 (1.5)	3.7 (2.8)	0.54 (0.8)	41	91	37
Revillagigedos Archipelago	1	5	2	4	1			
Hawaii	4	3.5 (1.9)	1.0 (2.0)	2.5 (1.9)	0.25 (0.5)			
All areas	160	4.0 (2.3)	0.75 (1.3)	3.6 (2.7)	0.64 (0.9)			
Not matched to a wintering area								
Seen off California through 1992	442	3.8 (2.1)	0.81 (1.3)	2.7 (2.2)	0.49 (0.8)	37	85	33
Seen off California through 1997	737	2.9 (2.1)	0.61 (1.1)	2.1 (2.0)	0.35 (0.7)			

interbreed on a single wintering ground in the West Indies, resulting in a single panmictic population (Mattila et al. 1989, 1994, Clapham et al. 1993, Larsen et al. 1996, Palsboll et al. 1997).

The use of a wintering region only by whales from a single feeding area has not been documented previously for humpback whales. The proportion of whales identified off Central America that were also sighted off California (84 %) was similar to the inter-year match rate (88 %) within California (the percentage of whales identified each year off California that matched any other year; Calambokidis et al. 1996). While humpback whales from California travel to (or through) several wintering regions, those from Central America appear to have only come from California. While it is clear that whales off Costa Rica use this region to breed and give birth to calves (Rasmussen et al. 1995), the number of whales that inhabit these waters in winter is fairly small, about 100 (Calambokidis 1997). This region is also unique because it is used by southern hemisphere whales during the austral winter (Acevedo & Smultea 1995, Flórez-González et al. 1998) and is potentially an avenue for gene flow between hemispheres (Baker et al. 1990).

It is not surprising that the whales that travel to Central America, the southernmost wintering region in the North Pacific (8° N), tend to feed off southern California, the southernmost part of a feeding area that is quite extensive (32 to 48° N). Whales from mainland Mexico and Baja California (20° N) were found more often in the northern waters (northern California to Washington). This pattern of migration suggests a series of partially overlapping migratory corridors and destinations along the coast of North America. Such a pattern could result in a clinal distribution of mtDNA types as suggested by Medrano-González et al. (1995).

Proximity of seasonal habitats, however, does not appear to be a fundamental constraint to migration. Migratory distances of whales for which we have documented transits ranged from 1900 to 5322 km (straight line, minimum). In the North Pacific, a humpback was observed to travel at least 7900 km between Japan and British Columbia (Darling et al. 1996). Records of long migratory routes have also been reported in the North Atlantic (7800 km, Palsboll et al. 1997, Stevick et al. 1998) and South Pacific (8334 km, Stone et al. 1990). Our data show that it is possible for a humpback whale to move from wintering ground to feeding ground in less than a month. The 29 d migratory transit between central California and southern Baja California is the fastest recorded (in number of days) for a humpback whale in the North Pacific. A faster speed was reported by Gabriele et al. (1996) for a whale that traveled 4400 km between southeastern Alaska and Hawaii in 39 d at 4.74 km h^{-1}.

Of the California whales for which the sex was known, the percentage of males re-sighted at wintering regions was more than twice as high as that for females (2.2 males:1 female). Similarly, studies off Hawaii have shown that more males than females were identified photographically (Craig & Herman 1997). Certain whale behaviors on the wintering grounds could affect the sex ratio of whales photographed, which would bias samples taken using this method. Males and females exhibit different affiliations and arrival and departure times (Gabriele 1992). Surface-active groups are often easier to spot and identify photographically, and tend to be composed of mostly males (Clapham et al. 1992, Medrano et al. 1994, Brown & Corkeron 1995); females with calves tend to raise their flukes less often (Craig & Herman 1997). Studies using biopsy sampling, however, also suggest that males are, in fact, over-represented on the wintering regions. Whales (n = 180) migrating to wintering regions off Australia revealed a ratio of 2.4 males:1 female, and this ratio suggests that some females do not always complete the migration to tropical waters (Brown et al. 1995). In the North Atlantic, genetic tagging used to determine sex-specific estimates of abundance on the breeding grounds showed that there were 40% fewer females than males (Palsboll et al. 1997). Samples of whales at North Pacific wintering areas showed a 2.8:1 ratio of males to females (n = 96), with males outnumbering females in all 5 samples (Baker et al. 1998). It remains to be determined whether this reflects differential habitat use, different migratory timing, or non-migration by some females, or a combination of the three.

Although previous studies have examined the movement of humpback whales among many regions in the North Pacific, few large-scale comparisons have been reported that allow a quantitative evaluation of the different rates of migratory movement from a feeding area as reported here. Expansion of this approach and the inclusion of data from all known wintering and feeding grounds in the North Pacific in a quantitative comparison would yield a more complete picture of the population structure of humpback whales and the complexities of their migrations.

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