Migratory destinations of humpback whales wintering in the Mexican Pacific

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ABSTRACT

The migratory destinations of humpback whales that winter off the Pacific coast of Mexico were examined using photo-identification. Fluke photographs taken between 1983 and 1993 from the three main whale aggregations in this area (383 from the Mainland coast; 471 from Baja California Peninsula; and 450 from Revillagigedo Archipelago) were compared with collections from all known summering grounds in the North Pacific (593 off California-Oregon-Washington; 48 off British Columbia; 429 off Southeastern Alaska; 141 off Prince William Sound; and 133 from the western Gulf of Alaska). The migratory movements of these whales were clearly non-random. The results of the photographic comparisons and the statistical tests show clear evidence for preferred migratory destinations of humpback whales from Mainland and Baja California to California-Oregon-Washington and British Columbia summering regions. Nevertheless, differences in whale abundance estimates between these summering and wintering aggregations indicate the presence of some unsampled summering region(s). The principal migratory destination was not detected for the Revillagigedo region, although matches were found with all the summering regions sampled. This supports the hypothesis that the humpback whales from Revillagigedo are separate from the 'American stock'. Based on the known abundance estimates, historical whaling records and genetic structure of the populations, it is proposed that historical feeding grounds off the Aleutian Islands and/or the Bering Sea are the main summer destinations of the whales from Revillagigedo.

KEYWORDS: HUMPBACK WHALE; BREEDING GROUNDS; DISTRIBUTION; MIGRATION; SITE FIDELITY; PHOTO-ID; NORTHERN HEMISPHERE; PACIFIC OCEAN

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) make long annual migrations between higher latitude, summering regions, and tropical and sub-tropical wintering areas where calving and presumably mating occur (e.g. Kellogg, 1928; Matthews, 1937; Mackintosh, 1942; Nishiwaki, 1959; Chittleborough, 1965; Dawbin, 1966).

The known summering range of humpback whales in the North Pacific extends offshore from California, along the coast of Oregon, Washington, British Columbia and Alaska, into the Bering Sea and southern Chukchi Sea, the Gulf of Alaska along the Aleutian Islands, the Sea of Okhotsk and northern Japan (Tomilin, 1957; Rice, 1978). Humpback whales appear to be divided into relatively discrete summering sub-populations, with only limited interchange among them (Baker *et al.*, 1986; Calambokidis *et al.*, 1996). Fidelity to these summering regions is determined maternally (Baker *et al.*, 1987; Clapham and Mayo, 1987). Summer humpback whale photo-identification research has been concentrated in the waters around Kodiak Island, Alaska (Waite *et al.*, 1999), Prince William Sound, Alaska (von Ziegesar, 1992), southeastern Alaska (Darling and McSweeney, 1985; Baker *et al.*, 1986; 1992; Perry *et al.*, 1990; Straley, 1990; 1994), British Columbia (Darling and McSweeney, 1985; Calambokidis *et al.*, 1996), and California (Dohl *et al.*, 1983; Calambokidis *et al.*, 1989; 1996). Comparisons between these photographic datasets suggest that there may be more interchange among the summering aggregations from northern British Columbia up the coast to Prince William Sound than with the California summering aggregation (Calambokidis *et al.*, 1996; Waite *et al.*, 1999).

In the winter, North Pacific humpback whales migrate to three distinct regions: the western North Pacific around the Ogasawara (Bonin), Ryukyu and Mariana Islands (Townsend, 1935; Nishiwaki, 1959; Darling, 1991; Darling and Mori, 1993); the central North Pacific around the main Hawaiian Islands (Herman and Antinoja, 1977; Herman, 1979; Baker and Herman, 1981); and the eastern North Pacific near the offshore Revillagigedo Islands, in the southern part of Baja California Peninsula, and off mainland Mexico to as far south as Costa Rica (Rice, 1978; Urbán and Aguayo, 1987; Steiger *et al.*, 1991; Acevedo and Smultea, 1995).

Photo-identification studies have documented matches between Mexico and Hawaii (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986; Calambokidis *et al.*, 2000), and between Hawaii and the Ogasawara Islands (Darling and Cerchio, 1993; Salden

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et al., 1999; Calambokidis *et al.*, In press), but the rate of this interchange is unknown (Baker *et al.*, 1998). To date, no matches had been found between Japan and Mexico.

Early observers of this species believed that the eastern and western North Pacific stocks moved up and down their respective coastlines, between winter and summer regions (Scammon, 1874; Kellog, 1928; Tomilin, 1957). The failure of these authors to consider the Hawaiian wintering region may mean that either they were unaware of its existence or that it was not colonised by humpbacks at that time (Herman, 1979).

The first direct evidence of connections between summer and winter regions in the North Pacific came from eight humpback whales tagged with 'Discovery' tags. These tags were shot into the whales and later recovered when the whales were killed and processed (e.g. Brown, 1977). The data from the tags show that these marked animals moved between the eastern Aleutians and the Ryukyu Islands (Omura and Ohsumi, 1964; Nishiwaki, 1966; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975; NMFS, 1991). More recently, studies based upon the photographic identification of individuals have revealed a more complex pattern of migratory movements: between Alaska and Hawaii (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1985; 1986; Perry *et al.*, 1988; Straley, 1994); British Columbia and Hawaii (Darling and McSweeney, 1985); British Columbia and Japan (Darling *et al.*, 1996); California and Hawaii (Calambokidis *et al.*, 1989; 1993); and California and Costa Rica (Steiger *et al.*, 1991).

With regard to the Mexican wintering regions, evidence of a migratory destination was reported by Baker *et al.* (1986) and Perry *et al.* (1988). They found three resightings from 36 photographically identified whales in Mexican waters: one off California; one off southeastern Alaska; and one in the western Gulf of Alaska region. Urbán *et al.* (1987) found that approximately 10% of the whales matched between a comparison of about 100 whales from coastal Mexico and a similar number off central California.

These studies indicate strong fidelity to specific summer feeding areas and consistent migratory returns to winter breeding and calving regions. Baker *et al.* (1994) concluded that humpback whales in the eastern North Pacific could be divided into at least two groups or 'stocks' based on genetic evidence: a central stock that feeds in Alaskan waters and migrates predominantly to Hawaii, and an 'American' stock that feeds along the coast of California and winters off Mexico.

This paper reports on the migratory destinations of humpback whales that winter in the Mexican Pacific. Results are presented from a comparison of three catalogues of individually identified humpback whales photographed from the mainland coast of Mexico, Baja California Peninsula and Revillagigedo Archipelago, to collections from five summering regions in the North Pacific: the western Gulf of Alaska; Prince William Sound; southeastern Alaska; British Columbia; and the California-Oregon-Washington region.

METHODS

Photographic methods

Humpback whales were individually identified from photographs of the black and white pigment patterns and other natural marks on the ventral surface of the flukes (Katona *et al.*, 1979; IWC, 1990). Photographs were taken using 35mm cameras with 200-300mm lenses. The type of film used varied from project to project.

Black and white prints of whale flukes were compared visually by personnel of the Marine Mammal Laboratory of the Universidad Autónoma de Baja California Sur (UABCS) (all collections), and the Mexican and California-Oregon-Washington collections also by Cascadia Research Collective (CRC).

Study locations and periods

Research effort was concentrated in eight regions of the North Pacific (Table 1, Fig. 1). Three of these regions were winter breeding regions in Mexico and five were summer feeding regions.

Table 1

Sample sizes and sample periods of humpback whales identified in Mexican wintering regions and the North Pacific summering regions.

Regions	Years	No. individuals
Mexican wintering regions		
(1) Mainland coast	1983-92	383
(2) Baja California Peninsula	1987-93	471
(3) Revillagigedo Archipelago	1986-92	450
North Pacific summering regions		
(4) California-Oregon-Washington	1981-92	593
(5) British Columbia	1975-91	48
(6) Southeastern Alaska	1987-92	429
(7) Prince William Sound	1977-91	141
(8) Western Gulf of Alaska	1992-93	133

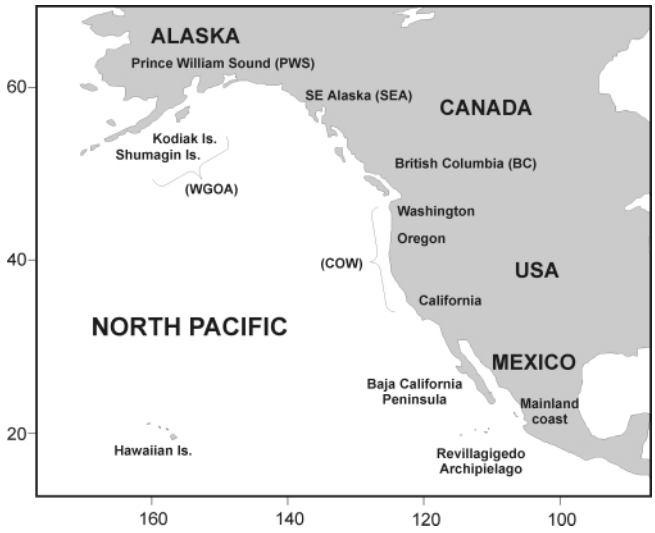

Fig. 1. Locations of photographic identification data collected for this study.

Mainland coast of Mexico (Mainland)

A total of 383 whales was identified off the mainland coast of Mexico between 1983 and 1992. Study areas in this region included Bahía de Banderas, Chacala, Isla Isabel and Islas Tres Marías. This region, as well as Baja California Peninsula and the Revillagigedo Archipelago, are described by Urbán and Aguayo (1987). Field work periods and participating institutions in the Mexican Pacific regions are shown in Table 2.

Baja California Peninsula (Baja California)

A total of 471 whales was identified between 1987 and 1993 off the southern coast of Baja California Peninsula, from Bahía Magdalena in the west coast to Bahía de la Paz in the Gulf of California.

Table 2

Study periods and data sources for each of the Mexican wintering regions. Key: UNAM, Universidad Nacional Autónoma de México; UABCS, Universidad Autónoma de Baja California Sur; CWR, Center for Whale Research.

Region/ Season	Study period	Source
Mainland coast		
1983	19 Jan. 1983 - 15 Feb. 1983	UNAM
1984	23 Oct. 1983 - 26 Feb. 1984	UNAM
1985	18 Nov. 1984 - 1 Mar. 1985	UNAM
1986	20 Dec. 1985 - 4 Mar. 1986	UNAM
1987	25 Dec. 1986 - 20 Mar. 1987	UNAM
1988	22 Jan. 1988 - 8 Feb. 1988	UNAM
1989	24 Jan. 1989 - 5 Mar. 1989	UNAM
1990	25 Nov. 1989 - 21 Mar. 1990	CWR/UABCS/UNAM
1991	28 Nov. 1990 - 26 Feb. 1991	UNAM
1992	26 Dec. 1991 - 6 Mar. 1992	UNAM
Baja California Peninsula		
1987	10 Feb. 1987 - 5 Mar. 1987	CWR/UABCS
1988	6 Feb. 1988 - 8 Mar. 1988	CWR/UABCS
1989	23 Jan. 1989 - 25 Mar. 1989	CWR/UABCS
1990	20 Feb. 1990 - 31 Mar. 1990	CWR/UABCS
1991	24 Jan. 1991 - 23 Mar. 1991	UABCS
1992	20 Jan. 1992 - 2 Apr. 1992	UABCS
1993	15 Jan. 1993 - 5 Apr. 1993	UABCS
Revillagigedo Archipelago		
1986	16 Jan. 1986 - 20 Feb. 1986	UNAM
1987	20 Jan. 1987 - 5 Mar. 1987	UNAM
1988	1 Feb. 1988 - 9 Mar. 1988	UNAM
1989	16 Jan. 1989 - 7 Mar. 1989	UNAM
1990	31 Jan. 1990 - 20 Mar. 1990	UNAM
1991	5 Jan. 1991 - 25 Apr. 1991	UNAM
1992	18 Feb. 1992 - 7 May 1992	UNAM/UABCS

Revillagigedo Archipelago (Revillagigedo)
A total of 450 whales was identified between 1986 and 1992 off Revillagigedo Archipelago, primarily at Isla Socorro.

California, Oregon and Washington (COW)
Based on the high rate of matches between Oregon and Washington with California (Calambokidis *et al.*, 1996), this region has been considered a single intermixing summering ground. This is also supported by an analysis of historical whaling data (Clapham *et al.*, 1997). A total of 593 individuals identified between 1981 and 1992 was used in the comparison with Mexican wintering regions. Photographs were taken by Cascadia Research Collective (CRC), the Center for Whale Research (CWR) and other collaborators during humpback and blue whale photo-identification studies. Research was primarily conducted between July and November in waters out to about 60km off central California between 1986 and 1990 (Calambokidis *et al.*, 1990); whales have been sampled along the entire Californian coast since 1991 (Calambokidis *et al.*, 1993). Photographs taken before 1986 were contributed by other researchers. Coverage off Oregon and Washington was less extensive than off California and consisted of only 32 days of effort. Field methods are described in Calambokidis *et al.* (1996).

British Columbia (BC)
Two collections of humpback whale photographs from British Columbia were compared with whales identified from Mexico. Both collections were primarily from La Perouse Bank, off southwestern Vancouver Island, where 48 individuals were identified between 1975 and 1990 by the West Coast Whale Foundation (WCWF) and between 1990 and 1991 by CWR.

Southeastern Alaska (SEA)
Photographs of 429 individual humpback whales from the northern portion of southeastern Alaska (Frederick Sound to Icy Strait) were taken from 1988-1993. Field methods are as described in Straley (1990).

Prince William Sound, Alaska (PWS)
A total of 141 individual humpback whales was identified in Prince William Sound from 1977-1991 by the North Gulf Oceanic Society. Photographic methods are reported in von Ziegesar (1992).

Western Gulf of Alaska (WGOA)
Humpback whales were identified off Kodiak Island (104), the Shumagin Islands (22), and the eastern Aleutian Islands (7) during July and August 1992 and 1993 by staff of the National Marine Mammal Laboratory during line-transect vessel surveys for killer whales (Dahlheim and Waite, 1993; Dahlheim, 1994; Waite *et al.*, 1999).

Additional comparisons
In addition to the above comparisons, the Mexican humpback whale catalogue was also compared with that of the eastern North Pacific compiled by Perry *et al.* (1988). This includes 464 whales that were identified in southeastern Alaska between 1979 and 1985 (Baker *et al.*, 1992) and 95 humpbacks identified in the western Gulf of Alaska, Yakutat Bay and Prince William Sound between 1977 and 1985. This catalogue is a compendium of photographs from many independent researchers. Some of these photographs from Alaska are duplicates of photographs in the regional collections described above.

North Pacific Humpback Whale Fluke Collection
Information on matches in the North Pacific Humpback Whale Fluke Collection maintained by the National Marine Mammal Laboratory in Seattle, Washington (Mizroch *et al.*, 1990) was also used.

Interchange
An index of interchange was calculated to provide a relative quantification of the amount of movement between regions:

$$Interchange\ Index = (m_{12}/(n_1 * n_2)) * 1000$$

where:

n_1 = whales identified (Marked) in sample 1;
n_2 = whales identified in sample 2;
m_{12} = marked whales matched between sample 1 and sample 2.

This index is basically the inverse of the Petersen capture-recapture index and has been used to examine rate of interchange of humpback whales among areas by several other researchers (Baker *et al.*, 1985; 1986; Calambokidis *et al.*, In press). A high value in this index occurs as a result of a small population being present or a high probability of the same individual being recaptured in both samples, while a low value reflects a low probability of recapture due to either a large population or an unlikely interchange of animals between the two samples.

Chi-squared test
Two kinds of chi-squared (χ^2) tests were performed for the three wintering areas. The first, a goodness of fit χ^2, tested the null hypothesis that the observed whale distribution does

not differ from an expected ratio, in other words, that the whales are uniformly distributed across all the summering grounds. If the null hypotheses for all three areas are rejected, it can be concluded that the whales from a particular wintering region prefer at least one summering ground over the rest (i.e. they do not distribute equally across all the summering grounds). It is then valid to raise the question of whether the three samples belong to the same population and test this as a null hypothesis under a heterogeneity χ^2 test (Zar, 1996). The second test can be applied to the three wintering areas together or in pairs. If the null hypothesis of the heterogeneity test is rejected on any of the comparisons, this can be interpreted either that the populations have different preferences on summer destinations or that one has a particular preference but the other does not. On the other hand, if the null hypothesis is not rejected with high statistical power (> 0.8), this suggests that the whales belong to a single population with similar preferences in summer destinations.

RESULTS

Migratory destinations

All Mexican regions together

A total of 153 humpback whales from the Mexican regions matched to North Pacific summering regions show an overall rate of resightings (as measured by the Interchange Index) of 0.096. The COW region had the highest number of matches (131) and Interchange Index (0.187). The WGOA region had the fewest matches (4), and the SEA region had the lowest Interchange Index (0.010-Table 3; Fig. 2).

Mainland

A total of 107 humpback whales was matched between the Mainland and all summering regions. The largest number of matches was with the COW region (97), which represent 54% of all matches found. The highest Interchange Index with the Mainland was with the COW region with a value of 0.427. The Mainland region also presented a high Interchange Index with BC (0.218-Table 3, Fig. 2 and Fig. 3).

Baja California

The Baja California region showed a similar pattern as the Mainland. A total of 58 humpback whales were matched throughout all summering regions, except PWS. The largest number of matches was found with COW, with an Interchange Index of 0.193, whilst BC had only 0.088 (Table 3; Fig. 2 and Fig. 4).

Revillagigedo

Only 12 humpback whales were matched throughout all summering regions. No main migratory destination was identified; the highest degree of interchange was with BC (0.093), followed by PWS (0.079-Table 3; Fig. 2 and Fig. 5).

Goodness of fit

The goodness of fit test conducted for each of the Mexican wintering regions showed that in the three areas, the observations significantly differed from the expectations under the null hypothesis (Table 4). Thus, for all free areas, whales have specific preferences in their migratory destinations and are not distributed equally across the tested summering grounds.

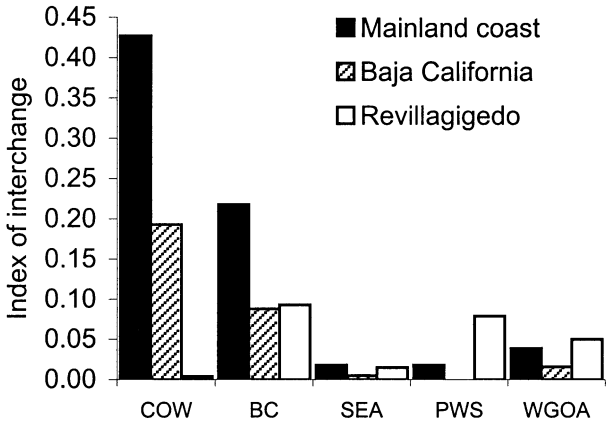

Fig. 2. Interchange Index between sampled summering areas and the three Mexican wintering regions.

Table 3

Number of matches observed and expected, and Interchange Index between Mexican wintering regions and North Pacific summering regions.

	COW (*n*=593)	BC (*n*=48)	SEA (*n*=429)	PWS (*n*=141)	WGOA (*n*=133)	All feeding regions (*n*=1,344)
All Mexican regions (*n*=1,180)						
Observed	131	7	5	6	4	153
Expected	68	5	49	16	15	153
Index	0.187	0.123	0.010	0.036	0.025	0.096
Mainland coast (*n*=383)						
Observed	97	4	3	1	2	107
Expected	47	4	34	11	11	107
Index	0.427	0.218	0.018	0.018	0.039	0.210
Baja California (*n*=471)						
Observed	54	2	1	0	1	58
Expected	26	2	18	6	6	58
Index	0.193	0.088	0.005	0	0.016	0.093
Revillagigedo (*n*=450)						
Observed	1	2	1	5	3	12
Expected	5	1	4	1	1	12
Index	0.004	0.093	0.005	0.079	0.050	0.023

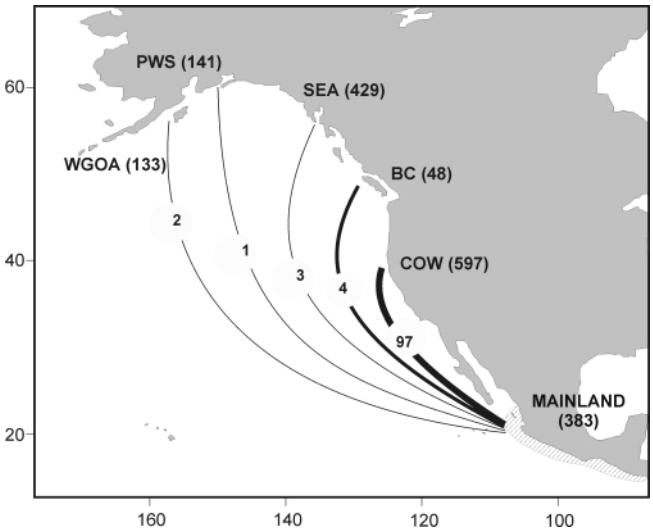

Fig. 3. Migratory destinations of the whales identified off the Mainland coast of Mexico.

The heterogeneity tests performed comparing the whales identified on each of the three wintering grounds, showed that the animals from Baja California and Mainland belong to the same population unit with similar preferences in their

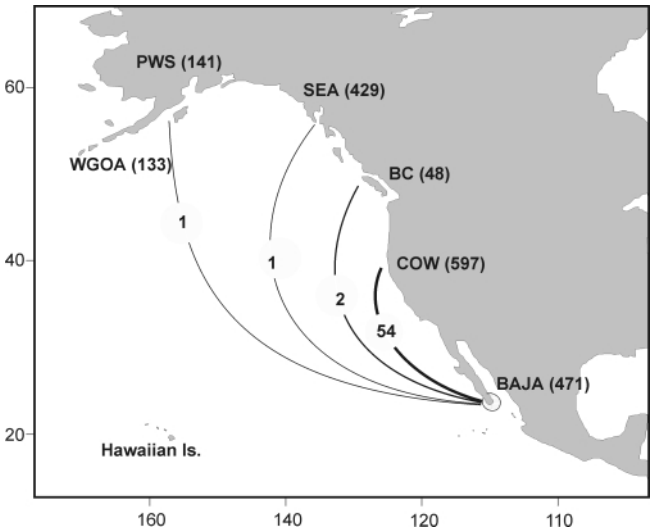

Fig. 4. Migratory destinations of the whales identified off Baja California Peninsula.

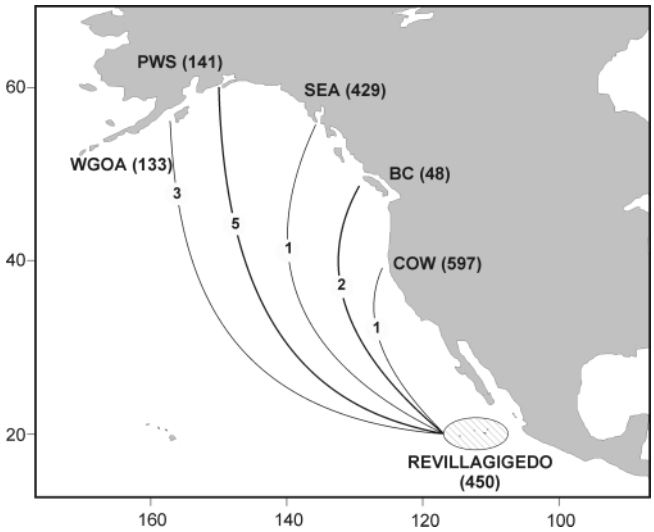

Fig. 5. Migratory destinations of the whales identified off the Revillagigedo Archipelago.

migratory destinations ($p > 0.995$). The humpback whales from Revillagigedo showed little if any similarity with the other Mexican wintering ground in their summer destinations (Table 5).

Different destinations

Humpback whales recorded in two or more Mexican wintering regions and a single summering region

A total of 23 whales photographed in both Mainland and Baja California were matched to a single summering region: 20 with COW, 1 with BC and 2 with SEA. Similarly, two whales photographed in both Mainland and Revillagigedo

Table 4

Interchange Index and Chi-Square test of the resightings between each of the Mexican wintering grounds and the summering regions.

Wintering regions	Interchange Index with all the Summering regions	Chi-Square	df	*p*
Mainland coast	0.210	97.2	4	<0.000000
Baja California	0.093	58.1	4	<0.000000
Revillagigedo	0.023	25.2	4	<0.000045

Table 5

The heterogeneity chi-squared (χ^2) tests performed comparing the whales identified on each of the three wintering grounds.

	COW	BC	SEA	PWS	WGOA	$\chi 2$	df
All wintering regions:							
Total of $\chi 2$						180.5428	12
Pool Obs.	152	8	5	6	6		
Pool Exp.	78.0959	6.3214	56.4977	18.5692	17.5156		
$\chi 2$ of Totals	69.9370	0.4457	46.9402	8.5078	7.5709	133.4018	4
					Heterogeneity $\chi 2$	47.1409	
				The homogeneity null hypothesis is rejected		$p = < 0.001$	8
Mainland + Baja California:							
Total of $\chi 2$						155.3224	8
Pool Obs.	151	6	4	1	3		
Pool Exp.	72.8013	5.8928	52.6674	17.3102	16.3281		
$\chi 2$ of Totals	83.9961	0.0019	44.9712	15.3680	10.8793	155.2166	4
					Heterogeneity $\chi 2$	0.1058	
				The homogeneity null hypothesis is accepted		$p = > 0.995$	4
Mainland + Revillagigedo:							
Total of $\chi 2$						122.4362	8
Pool Obs.	98	6	4	6	5		
Pool Exp.	52.5052	4.25	37.9843	12.4843	11.7760		
$\chi 2$ of Totals	39.4204	0.7205	30.4056	3.3679	3.8989	77.8135	4
					Heterogeneity $\chi 2$	44.6227	
				The homogeneity null hypothesis is rejected		$p = < 0.001$	4
Baja California + Revillagigedo:							
Total of $\chi 2$						83.3269	8
Pool Obs.	55	4	2	5	4		
Pool Exp.	30.8854	2.5	22.3437	7.3437	6.92708		
$\chi 2$ of Totals	18.8280	0.9	18.5227	0.7480	1.2368	40.2357	4
					Heterogeneity $\chi 2$	43.0912	
				The homogeneity null hypothesis is rejected		$p = < 0.001$	4

were matched to a single summering region; one with PWS, and the other with WGOA. Finally, a whale photographed in the three Mexican wintering regions was matched with WGOA (Table 6).

Humpback whales from one or two Mexican wintering regions matched with two summering regions

Only one whale was matched with two different summering regions. A whale photographed in Revillagigedo was matched with SEA and PWS regions (whale No. 912 UABCS and 2419 NMML catalogues).

Humpback whales matched between a summering region and more than one North Pacific wintering region

Only two whales were photographed in both a Mexican wintering region and Hawaii as well as a known summering region destination. Both whales were recorded at Revillagigedo. One was recorded in the SEA summering region and the other in the WGOA (whales No. 48 and 2255 NMML catalogue).

DISCUSSION

Mainland and Baja California

The results of the photographic comparisons and the statistical tests show clear evidence for preferred migratory destinations of humpback whales from Mainland and Baja California to COW and BC summering regions. These findings are consistent with the previous demographic evidence for population structure in the North Pacific (Baker *et al.*, 1986; Urbán *et al.*, 1987; Alvarez *et al.*, 1990; Baker *et al.*, 1998; Calambokidis *et al.*, In press).

Nevertheless, it is important to consider that the population size estimated for COW (around 900 animals, Calambokidis *et al.*, 1999), is about half of the population size of the wintering regions of Baja California and Mainland (around 1,800 animals, Urbán *et al.*, 1999). This indicates the presence of some unsampled summering region(s). This is also consistent with the early 1900s whaling data. During an eight-year period, 2,473 humpback whales were killed from three stations off California and Washington. Although this hunting depleted the whale aggregations in this summering region, such a decline was not as apparent off Mexico, where 902 humpbacks were taken in Baja California between late 1924 and 1926, at a time when the catches off California and Washington were in marked decline, because that wintering region is the migratory destination of whales from a number of summering regions (Clapham *et al.*, 1997).

It should also be pointed out that, although the proportion of matched whales is almost identical between Baja California and Mainland, the Interchange Index of Baja California with the different summering regions is just under half that of the Mainland (Table 3). This may indicate a greater importance of unsampled summering regions as migratory destinations to Baja California than to the Mainland. Calambokidis *et al.* (2000), found 11% of the whales from Baja California, 25% from Mainland Mexico and 84% from Costa Rica/Panama matched with the whales from the COW summering region. This pattern of migration suggests a series of partially overlapping migratory corridors and destinations along the coast of North America that could result in a clinal distribution of mtDNA types as suggested by Medrano-González *et al.* (1995).

If this hypothesis is true, Baja California, and to a lesser degree Mainland, could be a region of overlap for animals migrating from unsampled regions, BC and COW to primary wintering grounds in Mexico and Central America. The high genetic diversity in this region supports this idea (Baker *et al.*, 1998).

Table 6

Humpback whales matched between a summering region and more than one Mexican wintering region.

Whale No. UABCS {CRC} [NMML]	Region	Year	Mexican wintering region	Year
004 {10605}	COW	1992, 93, 94	Baja Mainland	1989 1990
054 {10131}	COW	1987, 90, 91, 92, 94	Mainland Baja	1986 1990
058 {10132}	COW	1987, 88, 89	Mainland Baja	1987 1988, 90
060 {10415}	COW	1990, 91, 92	Mainland Baja	1989 1990, 92
067 {10028}	COW	1985, 86, 87, 88, 89, 90, 92, 94	Mainland Baja	1983, 84, 89 1989
070 {10530}	COW	1991, 92, 93	Mainland Baja	1987, 90 1988
072 {10042}	COW	1986, 87, 88, 89, 90	Baja Mainland	1989 1990
092 {10338}	COW	1989, 90, 92, 93	Mainland Baja	1986 1988
134 {10068}	COW	1986, 87, 88, 89, 90, 91, 92, 93, 94	Baja Mainland	1988 1990
196 {12002}	COW	1990, 91, 93	Mainland Baja	1990, 91 1991, 92
204 {10433}	COW	1990, 92	Mainland Baja	1990, 91 1991
248 {10002}	COW	1986, 87, 88, 91, 92, 93, 94	Mainland Baja	1985, 86, 90, 92 1992
258 {10028}	COW	1985, 86, 87, 88, 89, 90, 92, 93, 94	Mainland Baja	1985, 86 1992
303 {10020}	COW	1986, 87, 88, 89, 92	Mainland Baja	1990 1992
326 {9029}	COW	1988, 91, 92, 94	Mainland Baja	1990 1992
389 {10104}	COW	1987, 88, 89, 90, 91, 92, 93, 94	Mainland Baja	1990 1992
398 {10004}	COW	1986, 87, 88, 89	Mainland Baja	1990 1993
258 {10028}	COW	1985, 86, 87, 88, 89, 90, 92, 93, 94	Mainland Baja	1985, 86 1992
1105 {9018}	COW	1988, 90, 91, 92, 94	Mainland Baja	1985, 89, 91 1993
1124 {10150}	COW	1987, 88, 92	Mainland Baja	1986 1988
111 [2044]	BC	1989, 90	Mainland Baja	1986 1987
364 [2021] {14015}	BC	1989, 90, 94	Revillagigedo Baja	1986, 91 1992
035 [7601]	SEA	1988	Baja Mainland	1990
039 [5016]	SEA	1980, 81, 82, 86, 89, 91, 94	Baja Mainland	1988 1990
267 [5456]	SEA	1979, 80, 85, 92	Baja Revillagigedo	1992 1991
755 [2435]	PWS	1977,79, 80, 83	Mainland Revillagigedo	1978 1988, 91
926 [2070]	WGOA	1992	Mainland Revillagigedo Baja	1986 1989 1990, 93

Revillagigedo

Migration patterns for the Revillagigedo region differ from those for the other Mexican wintering grounds. Although matches were found with all the summering regions sampled, no principal migratory destination was detected.

The hypothesis that the humpback whales from Revillagigedo are separate from the 'American stock', that feeds along the coast of British Columbia, California, and winters off Baja California, mainland coast of Mexico, and Central America, has been suggested previously. This hypothesis is based on: the different degree of individual interchange of the three Mexican wintering regions (Urbán *et al.*, 1989; 1999; Alvarez *et al.*, 1990; Ladrón de Guevara P *et al.*, 1993); the significant difference in mtDNA haplotype frequencies relative to those found off Baja California and mainland coast regions (Medrano-González *et al.*, 1995; Baker *et al.*, 1998); a higher resighting rate of individuals during the season than at any other wintering region studied (50% versus 4-15%), perhaps due to the small number of islands in a relatively small area, and a low population size; and the higher number of known matches between Hawaii and Revillagigedo than between Hawaii and the other Mexican regions (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986; Perry *et al.*, 1988; 1990; Calambokidis *et al.*, In press).

Missing summering ground(s)?

Evidence from abundance estimates

As previously stated, estimates of abundance on the wintering grounds are typically considerably larger than those from known summering grounds. Abundance in the California region was estimated at 582 in 1991-92 (Calambokidis *et al.*, 1993) and 905 in 1997 (Calambokidis *et al.*, 1999); while for the Mainland and Baja California Mexican wintering grounds it was estimated at 1,813 (918-2,505) in 1992, and 914 (590-1,193) for Revillagigedo in 1991 (Urbán *et al.*, 1999). In the central stock, abundance in southeastern Alaska was estimated to be 504-590 in 1986 (Baker *et al.*, 1992) and 350-458 for the period 1985-92 (Straley *et al.*, 1995), while in Hawaii it was estimated to be 1,400-2,000 in 1981-84 (Darling and Morowitz, 1986; Baker and Herman, 1987), and close to 4,000 in 1993 (Cerchio, 1998).

Results of an ocean-basin-wide mark-recapture study of North Atlantic humpback whales show that both the genotypic and photographic estimates using only feeding-area data were significantly lower than those using only breeding-area data (Smith *et al.*, 1999). The authors concluded that the apparent downward bias of the estimate could be due to (1) the existence of a still-unknown feeding area that was not sampled; (2) spatial heterogeneity in the probability of animals being sampled in known feeding areas; or (3) heterogeneity in the probability of being sampled that was related to other individual animal characteristics (Smith *et al.*, 1999).

It seems likely that the differences in estimates of abundance between summering and wintering grounds in the North Pacific can at least partially result from uncertain reliability and representativeness because of limitations in both sampling methodology and spatial coverage, and reflect bias due to the different causes of heterogeneity in the probability of animals being sampled (Hammond, 1986). However, taking into account the large differences in the abundance estimates, it seems probable that there is also a lack of data from one or more summering regions used by humpback whales in the North Pacific.

Evidence from historical distribution

Information on the pre-exploitation summering range of humpback whales points to some probable locations for one or more of these missing stock components. The waters along the continental shelf of the central Aleutian Islands were once considered the centre of the North Pacific humpback whale population (Nishiwaki, 1966; NMFS, 1991). A comparison of a map of distribution of humpback whales during the period of feeding with the scheme of currents in the Northeast Pacific, reveals that the most dense aggregations of whales were observed in the regions of cyclonic circular currents to the south of the Fox, Shumagin and Kodiak islands, in the northwestern part of Bristol Bay and partly in the northwestern part of the Gulf of Alaska (Doroshenko, 2000).

Whaling records indicate that 1,510 humpback whales were caught mainly in Unimak Pass and the Bering Sea, between 1926 and 1939 by American whalers based at Akutan and Port Hobron, Alaska (Reeves *et al.*, 1985). Russian and Japanese fleets harvested whales intensively throughout the Aleutian Islands from 1905-1929 and again from 1960-1965. During these periods, more than 4,700 humpbacks were killed in this region (Rice, 1978).

Recent information documenting the 'real' Soviet catches of humpback whales in the North Pacific shows that close to 7,000 whales were caught between 1961 and 1971 (compared to 4,254 originally reported to the International Whaling Commission). In 1963 alone, the catch of humpback whales was 2,625, whereas in the late 1960s the catches dropped to zero. For several more seasons, Soviet whaling fleets searched the Gulf of Alaska and Bristol Bay for humpback whales, but neither whalers nor scouting ships could find them (Doroshenko, 2000).

Humpback whales were also known to summer along the Asian coast, particularly around the Kamchatka Peninsula and the Sea of Okhotsk (Tomilin, 1957), but there are few data on their distribution south of the Sea of Okhotsk (NMFS, 1991). According to Doroshenko (2000), in recent years, many whales have been observed in the northwestern part of the Bering Sea in the Gulf of Anadyr and in the region of the Bering Strait, as well as in the southern part of the Chukchi Sea.

The current status of humpback whales along the Aleutians is largely unknown, although aerial surveys report substantial numbers around Kodiak Island (Brueggeman *et al.*, 1989). Recently, Waite *et al.* (1999) suggest that the Kodiak Island region supports a separate summering aggregation of humpback whales in the North Pacific, which could be large, based on the low number of resights between years.

Evidence from genetic structure

Regarding the genetic structure of humpback whales in the North Pacific, Baker *et al.* (1990; 1994; 1998) describe that the greatest differences in mtDNA haplotype frequencies were found among three summering grounds. The California summering ground was dominated by *E* and *F* types while southeastern Alaska and Prince William Sound were all *A*- and *A*+ types. There is no genetic information about the whales from the Aleutian or Kodiak Islands. Differences among the wintering grounds were less marked; *E*, *F* and *A*+ types dominated the Mexican wintering grounds but the *A*- type was also present. The Ogasawara Islands, in Japan, showed a surprising similarity to Mexican wintering grounds. Only Hawaii differed significantly from all the other wintering grounds, being dominated by *A*+ and *A*- types although types *E* and *F* were also represented.

Conclusion

Considering the information presented above, we hypothesise that there is at least one unsampled summering ground of more than 2,000 whales dominated by *E* and *F* types. These whales could occupy their historical distribution off the Aleutian Islands and/or the Bering Sea. This summering ground(s) would be the main summer destination of the whales from Revillagigedo and the summering area for the 'missing' whales from Baja California, Mainland, Japan and Hawaii.

Population structure

Despite the site fidelity of humpback whales to specific areas, migrations between summering areas and wintering regions have not generally followed a sufficiently simple pattern to allow the definition of an integrated wintering/summering region population structure. The present findings (see Figs 3-5) show a preference of the Baja California and Mainland humpback whales to COW and BC, but also the presence of humpback whales from all the sampled summering regions in each of the Mexican wintering regions (except between PWS and Baja California).

No systematic comparison has been conducted between the Mexican humpback whale catalogues and those of the wintering regions of Hawaii and Japan. Nevertheless, there are some matches published based on comparisons of limited samples (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986; Perry *et al.*, 1988; 1990; Calambokidis *et al.*, 2000), and others from the North Pacific Humpback Whale Collection (unpublished data). There are no matches known with Japanese wintering regions. A total of 31 matches between Hawaii and Mexican wintering regions are known, none of which were to the mainland region: 2 whales were seen in both the Revillagigedo and Baja California regions, 6 only in Baja California and 21 only in Revillagigedo. One of these 21 matches was for 5 February 1986 at Isla Clarión, Revillagigedo Archipelago and 28 March 1986 at Kauai, Hawaii, some 4,700km away (North Pacific Humpback Whale Collection, unpublished data; Helweg *et al.*, 1990; Darling and Cerchio, 1993).

Some management strategies recognise, explicitly or implicitly, reproductive isolation as a requirement for defining population sub-divisions (e.g. the International Whaling Commission, Donovan, 1991; and the US Endangered Species Act, Waples, 1991). According to Baker *et al.* (1998) the finding of significant differences between a central (Alaska-Hawaii) and eastern (California-Mexico) stock of humpback whales in both mitochondrial and nuclear DNA loci fulfils the criterion of reproductive isolation.

Defining population structure based on whale distribution on the wintering grounds appears less ambiguous than using data from the summering regions because whales breed in the former, are separated geographically by large distances, and most regions have been sampled using photo-identification methods and genetic analyses. Based on this, Calambokidis *et al.* (In press) conclude that there are at least three sub-populations of humpback whales in the North Pacific (those wintering off Hawaii, Japan and Mexico-Central America). Our data from the sub-regions of Mexico support the conclusion that a link between the known BC-COW areas and the Baja California-Mainland-Central America region is evidence of a distinct sub-population (Calambokidis *et al.*, 2000). The results also indicate that this coastal sub-population is relatively distinct from that of Revillagigedo. However, the preferred summer destination for this sub-population remains unknown.

ACKNOWLEDGEMENTS

This project would not have been possible without the collaboration of many researchers who generously agreed to provide their data. Organisations supporting these researchers include: Universidad Autonoma de Baja California Sur; Universidad Nacional Autonoma de Mexico; Cascadia Research Collective; Center for Whale Research; J. Straley Investigations; North Gulf Oceanic Society; National Marine Mammal Laboratory; University of Hawaii and the University of Auckland. In addition to the authors, a number of people had key roles in the collecting or cataloguing of photographs used in this study. They include: Juan C. Salinas, of the Universidad Autónoma de Baja California Sur; Prentice Bloedel, at the Center for Whale Research; and Craig Matkin with the Gulf Coast Oceanic Society. Many other people and organisations assisted in the funding and collection of data in the individual studies, including at Revillagigedo: the Secretaría de Marina (Sector Naval, Isla Socorro), Whale and Dolphin Conservation Society, W. Rossiter and the Cetacean Society International, E. Connors, M. Cannava, C. Olivera, L. Sarti, M. Rivas and M. Arias; off Mainland Mexico: the Consejo Nacional de Ciencia y Tecnología (CONACyT), Amy Camacho from Africam Safari, Cetacean Society International, Cet-Mar No. 6, Staff of the Marine Mammal Laboratory and Fishermen from Punta Mita; off Baja California: Consejo Nacional de Ciencia y Tecnología (CONACyT), Instituto Nacional de Ecología (INE-SEMARNAP), Consejo Nacional para la Biodiversidad (CONABIO), Earthwatch (1990), A. Jaramillo, S. Chávez, J.C. Salinas, E. Vázquez and Luis Enriquez Alejandro Gómez-Gallardo; off Kodiak and the western Gulf of Alaska: K. Balcomb-Bartok, B. Caruso, T. Chandler, K. Chumbley, D. Ellifrit, J. Evenson, C. Hutchinson, J. Jacobsen, J. Lerczak. B. Mathews, B. Miller, R. Osborne, R. Ream, J. Sease, F. Sharpe, J. Stern, M. Strick, J. Swenson and R. Towell; off California: Pacific Cetacean Group, Moss Landing Marine Laboratory, Southwest Fisheries Science Center, Oceanic Society Expeditions and Shearwater Journeys; also, N. Black, T. Chandler, K. Flynn, Z. Thomas, P. Rudolph, A. Reitsch, D. Meister, J. Quan, L. Randolph, Z. Schwartz, A. Rebollo, A. Randle, T. Kieckhefer, P. Howorth, R. Smith, E. Martin and others. P. Clapham, G. Donovan and two anonymous reviewers critically read the manuscript, made valuable suggestions and corrected the English.

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