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MOVEMENTS AND POPULATION STRUCTURE OF HUMPBACK WHALES IN THE NORTH PACIFIC

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ABSTRACT

Despite the extensive use of photographic identification methods to investigate humpback whales in the North Pacific, few quantitative analyses have been conducted. We report on a comprehensive analysis of interchange in the North Pacific among three wintering regions (Mexico, Hawaii, and Japan) each with two to three subareas, and feeding areas that extended from southern California to the Aleutian Islands. Of the 6,413 identification photographs of humpback whales obtained by 16 independent research groups between 1990 and 1993 and examined for this study, 3,650 photographs were determined to be of suitable quality. A total of 1,241 matches was found by two independent matching teams, identifying 2,712 unique whales in the sample (seen one to five times). Site fidelity was greatest at feeding areas where there was a high rate of resightings in the same area in different years and a low rate of interchange among different areas. Migrations between winter regions and feeding areas did not follow a simple pattern, although highest match rates were found for whales that moved between Hawaii and southeastern Alaska, and between mainland and Baja Mexico and California. Interchange among subareas of the three primary wintering regions was extensive for Hawaii, variable (depending on subareas) for Mexico, and low for Japan and reflected the relative distances among subareas. Interchange among these primary wintering regions was rare. This study provides the first quantitative assessment of the migratory structure of humpback whales in the entire North Pacific basin.

Key words: humpback whale, *Megaptera novaeangliae,* population structure, movements, North Pacific, photo-identification, interchange, migration.

The geographic structure of humpback whale populations in the North Pacific has been derived from: (1) accounts from commercial catches (Kellogg 1928, Tomilin 1957, Berzin and Rovnin 1966) and movements based on Discovery tag recoveries (Nishiwaki 1966, Omura and Ohsumi 1964, Ohsumi and Masaki 1975, Ivashin and Rovnin 1967), (2) movements determined from photographically identified humpback whales (Darling and Jurasz 1983; Darling and McSweeney 1985; Baker *et al.* 1986; Darling and Mori 1993; Calambokidis *et al.* 1996, 2000; Steiger *et al.* 1991; Darling and Cerchio 1993; Darling *et al.* 1996; Waite *et al.* 1999; Urbán *et al.* 2000), (3) geographic differences in genetic patterns of humpback whales based either on mtDNA (Baker *et al.* 1990, 1994; Medrano-González *et al.* 1995) or nuclear DNA (Baker *et al.* 1993, 1998; Palumbi and Baker 1994), (4) geographic differences in the songs (Helweg *et al.* 1990, Payne and Guinee 1983), and (5) differences in the proportion of whales with different fluke coloration patterns (Baker *et al.* 1985, 1986; Allen *et al.* 1994; Pike 1953; Rosenbaum *et al.* 1995).

Despite these studies, no clear consensus exists on the structure of humpback whale populations in the North Pacific. The International Whaling Commission considers humpback whales in the North Pacific as one "stock" for management purposes (Donovan 1991). Evidence of at least some intermixing among wintering regions has led some researchers to suggest these constitute one or at most two "stocks" (Darling and McSweeney 1985, Darling and Cerchio 1993, Darling *et al.* 1996). 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

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Alaskan waters and migrates predominantly to Hawaii, and an "American" stock that feeds along the coast of California and winters off Mexico. Barlow (1994) and Barlow *et al.* (1997) concluded that, based on the need to define conservative population units, humpback whales in the North Pacific should be divided into four migratory populations. They described these separate migratory populations as the coastal California/Oregon/Washington-Mexico stock, the Mexico offshore (Revillagigedos) stock (feeding destination unknown), the central North Pacific stock (Hawaii-Alaska), and the western North Pacific stock (Japan-feeding destination unknown).

Photographic identification of individual humpback whales has proved to be valuable in describing movements of animals among wintering or feeding areas, as well as in describing the dynamics of movements within areas. Unfortunately, these studies often have been limited to a few sites and have not provided a quantitative assessment of the rates of interchange.

Here we describe the population structure and movements of humpback whales in the North Pacific based on a large collaborative effort among 16 research groups that collected identification photographs throughout the North Pacific from 1990 to 1993. The years and collections used were designed to provide a broadly distributed sample across the entire North Pacific Ocean. These data are integral to the calculation and interpretation of a geographically stratified mark-recapture abundance estimate of humpback whales in the North Pacific basin which will be published separately.

Methods

Selection of Photographs

This project encompassed all locations in the North Pacific where photo-identification research has been conducted (Fig. 1, Table 1). These included three wintering regions (Mexico, Hawaii, and Japan), each with two or three subareas, and feeding areas that extended from southern California to the Aleutian Islands. The years 1991–1993 were selected because samples throughout the entire North Pacific were the largest and the most complete during this period. The sample from Mexico also included 174 suitable identification photographs from 1990 taken off mainland Mexico and Baja (Table 1) to obtain a more representative sample from this region. In all of the studies the natural marks on the ventral side of the flukes were photographed. Field methods of many of these studies have been described (*e.g.,* Calambokidis *et al.* 1990, 1996; Cerchio 1998; Cerchio *et al.* 1998; Waite *et al.* 1999; Darling and Mori 1993; Uchida *et al.* 1993; von Ziegesar *et al.* 1994).

Photographs of each individual whale identified were provided as black-and-white prints or negatives, or color slides. Custom black-and-white prints (6.4 × 8.9 cm) were made for all the negatives. Within-year duplicates in each collection were removed. We received and screened a sample of 6,414 identification photographs (Table 1).

Each photograph was graded from highest quality (1) to lowest quality (5)

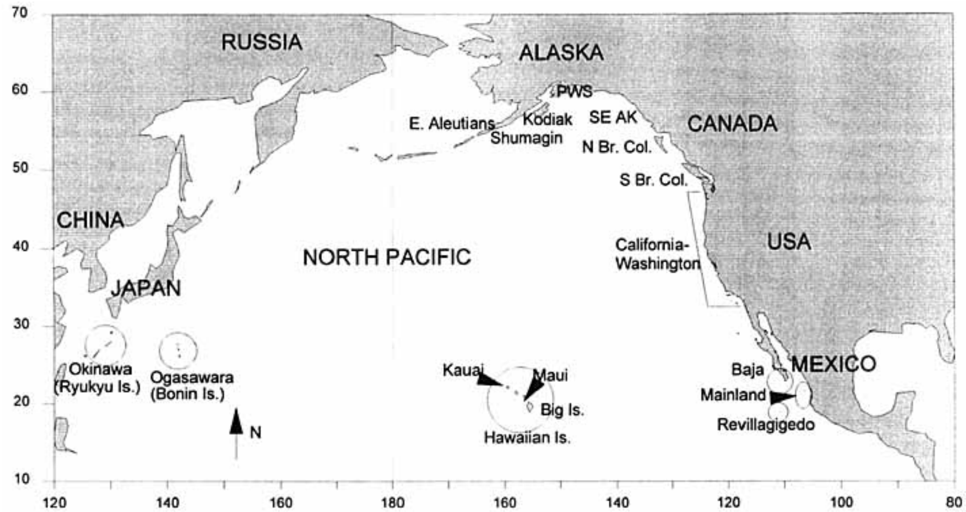

Figure 1. Locations where photographic identification data were collected that were used in this study.

using a uniform set of criteria to select the sample of photographs used for the comparison. Quality was judged on each of six variables: the proportion of the fluke that was visible, fluke angle (*i.e.,* how perpendicular it was to the water), the lateral angle of the photographer, the sharpness and grain, fluke size on print, and the photographic quality (lighting, exposure, and contrast). Because some of these measures were clearly subjective, photograph archetypes for the different codes were used during the scoring process. Photographs that were graded a 4 or 5 in any category or that received a 3 in three or more categories were rejected. Selected and rejected photographs were then checked visually and recoded in certain cases where photographs appeared to have been scored incorrectly. Before the comparison began, all photographs from each collection were divided into five subcategories based on the proportion of light and dark coloration of the flukes. Photographs of calf flukes were excluded because markings have the potential to change in the first year (Carlson *et al.* 1990). Of the 6,414 identification photographs obtained, 3,650 were selected for comparison (Table 1).

Comparison of Photographs

Two matching teams made independent comparisons of the entire collection. Photographs were compared based on the coloration, trailing edge, scars and other markings on the flukes. At least one member of each team compared each photograph to all other photographs. Another redundancy built into the process was that photographs, once compared, were returned to the sample. Therefore, there were two opportunities for each team to match two photographs (except for the 1990 Mexico photographs which were added later in the process). Matches were recorded independently and were not discussed

Table 1. Summary of photographs received and used by region in this comparison.

Region code	Location	Collector	Photos submit-ted	Photos selected	Unique IDs	Year* 1990***	1991	1992	1993
1	Revillagigedo	Jacobsen, UNAM, UABCS	250	168	159		158	10	0
2	Mainland Mexico	UNAM	193	139	138	131	4	4	0
3	Baja	UABCS	408	255	233	43	56	100	56
4	Hawaii-Big Is.	KBMML	1,184**	433	401		175	74	184
5	Hawaii-Maui	HWRF	744	393	368		117	114	162
6	Hawali-Kauai	S. Cerchio	929**	386	375		101	137	148
7	Ogasawara	OMC	576	360	257		110	136	114
8	Okinawa	OEA, WWF	129	88	63		30	23	35
9	California & Washington	CRC	917	694	454		190	316	188
10	Southern British Columbia	CWR, CRC	17	13	14		11	0	2
11	Northern British Columbia	G. Ellis	76	64	59		2	23	39
12	Southeast Alaska	GBNP, J. Straley	670	421	287		148	158	115
13	Prince William Sound	NGOS	180	135	87		45	64	26
14	Kodiak Island	NMML, NGOS	116	79	76		1	43	35
15	Shumagin Islands	NMML	18	15	15		0	4	11
16	Eastern Aleutian Islands	NMML	7	7	7		0	7	0
	Total		6,414	3,650	2,993	174	1,148	1,213	1,115

* Year code reflects 1990–1993 except for some SEAK early winter sightings kept with their respective field season.
** Includes several hundred within-year duplicates.
*** 1990 Mexico photogaphs included to increase sample size.

among the team members. When the comparison was complete, all matches found by only one team were verified by the second team. Where a match suggested unusual or undocumented movements between locations, the photographs were checked a second time. The success rate of finding matches was calculated based on comparison of the matches found between the two independent teams, as well as their success in finding matches known by the contributing teams (but to which the matchers were blind).

Match Index

A match index was calculated to provide a relative measure of the amount of movement between regions. We used the match index for various combinations of years. This index (previously termed "Interchange Index") is basically the inverse of the Petersen capture-recapture index and has been previously used to examine the rate of interchange of humpback whales among areas (*e.g.,* Baker *et al.* 1986; Urbán *et al.* 1999, 2000). Let

a_i = number of marked releases at time 1 in region i, $i = 1, \ldots, R$,

n_j = number examined for marks at time 2 in region j,

$m_{i \to j}$ = marked recaptures in region j originally marked in region i,

p_j = probability of capture in region j,

$\theta_{i \to j}$ = probability that a marked release from region i moves to region j,

N_j = population abundance in region j.

The match index can be written

$$I_{i \to j} = [m_{i \to j}/(a_i n_j)] \times 1{,}000. \quad (1)$$

The expected value of this index can be found in a straightforward manner. First, the expected value of the number of marked recaptures is $E(m_{i \to j}) = a_i \theta_{i \to j} p_j$, because the expected number of marked recaptures is the number originally marked in region i that move to region j and that are captured there. If a simple random sample is taken at time 2, then the probability of capture is $p_j = n_j/N_j$. By combining these relationships, the expected value of the index is

$$E(I_{i \to j}) = \theta_{i \to j}/N_j \times 1{,}000, \quad (2)$$

which shows that the expected value of the index is directly proportional to the movement probability and inversely proportional to abundance. A high value of this index occurs as a result of a small population being present or a small movement probability, while a low value occurs due to either a large population or an unlikely interchange of animals. Note that if $i = j$, then the movement probability is the probability of remaining in the same region, and the index is a relative measure of return.

Means of multiple match indices are accompanied with the standard error for the estimates (based on the variation in the observed values without a calculation of their inherent variance).

Results

Evaluation of Matching Success

Of our sample of 3,650 photographs, there were 1,220 pairs of matches found by one or both teams. Each team found 93%–94% (1,141 and 1,149) of the matches. A Peterson capture-recapture calculation (using total matches found by each team as n_1 and n_2 and the number of these found in common by both teams as m_{12}) yielded an estimate that 99.6% of the matches would have been found by at least one team. This estimate, however, is biased upwards because matches found by each team were not truly independent events; some whales were easier or harder to match than others for both teams. We also measured our success in finding matches that were known by the contributors but to which our teams were blind. These were generally interyear matches within their collections that they had a high degree of success finding because of their familiarity with their smaller collections. Of the 620 matches provided to us by the contributors (involving whales in our comparison), 599 (97%) were found by one or both teams. This is a more unbiased assessment of our matching success rate. The 21 matches missed by our teams were included in our analyses (total of 1,241 matches) but no other correction was made for the low rate of missed matches.

Total Matches and Unique Whales

Based on matches found, our sample of 3,650 photographs represented 2,712 unique whales, 2,003 seen only once and 709 whales seen two to five times (Table 2). Of the 1,241 pairs of matches, those involving whales seen within the same region were more common than those between regions and accounted for 808 (65%) of the matches. Because catalogs from each area had been already internally compared and duplicate photographs eliminated, most of these matches were of whales seen in different years in the same area. A disproportionate number of resightings was made in feeding areas (550) compared to wintering regions (258). The rate of resightings within a region or area (as measured by the match index, Table 3) varied, with highest resighting rates at the two subareas off Japan and at most feeding areas (Prince William Sound, southeastern Alaska, British Columbia, and California-Washington). Whales identified off Kodiak and in the western Gulf of Alaska were the only feeding-area samples with low resighting rates. Rates of among-year resightings within regions reflect the size of the overall population being sampled and the degree of site fidelity.

Table 2. Number of individual whales seen multiple times in the same region or in more than one region. Number of acceptable quality photographs used (Photo) and unique identifications (IDs) are shown.

Region	Abrev.	Photo	IDs	Rev.	Mnl.	Baja	Big Is	Maui	Kuai	Ogas.	Okin.	A-WA	SBC	NBC	Seak	PWS	Kodi-ak	Shum.	Aleut.
Revillagigedo	Rev.	168	159	9															
Mainland Mexico	Mnl.	139	138	0	1														
Baja	Baja	255	233	9	12	19													
Hawaii-Big Island	Big ls	433	401	1	0	2	31												
Hawaii-Maui	Maui	393	368	0	0	0	40	24											
Hawaii-Kauai	Kuai	386	375	2	0	0	19	32	10										
Ogasawara	Ogas.	360	257	0	0	0	3	1	0	82									
Okinawa	Okin.	88	63	0	0	0	0	0	0	7	22								
California-Washington	CA-WA	694	454	1	32	19	1	2	0	0	0	197							
S British Columbia	SBC	15	13	0	0	1	0	0	0	1	0	0	2						
N British Columbia	NBC	62	60	0	0	1	6	4	0	1	0	0	0	2					
Southeast Alaska	SEAK	421	287	0	0	0	25	23	18	0	0	0	0	0	97				
Prince William Sound	PWS	135	87	0	1	0	6	5	3	0	0	0	0	0	2	37			
Kodiak	Kodiak	79	76	0	0	1	3	5	3	1	0	0	0	0	1	1	3		
Shumagin Is.	Shum.	15	15	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Eastern Aleutians	Aleut.	7	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		3,650	2,993																
Total unique			2,712																

Table 3. Match index among years for each location sampled. British Columbia and W. Gulf of Alaska pooled due to sample size.

Code	Location	*n* (yr)	Index	SE
1	Revillagigedo	1	1.32	
2	Mainland Mexico	2	0.95	0.95
3	Baja	6	1.00	0.24
4	Hawaii-Big Island	3	0.27	0.02
5	Hawaii-Maui	3	0.39	0.09
6	Hawaii-Kauai	3	0.25	0.05
7	Ogasawara	3	2.89	0.10
8	Okinawa	3	11.64	3.09
9	California & Washington	3	1.82	0.04
10 & 11	British Columbia	3	2.12	0.66
12	Southeast Alaska	3	2.80	0.20
13	Prince William Sound	3	10.72	1.05
14	Kodiak	3	0.66	0.66
15 & 16	Shum./Aleut.	1	0.00	

Interchange Among and Within Wintering Regions

Within-region movements—Movements and interchange among the three Hawaii subareas was extensive (Table 2, 4). The same whales were seen in multiple subareas both in the same year and in different years. The mean match index for whales at the same subarea in different years (0.306) was only slightly higher than that between subareas in different years (0.264). This indicates that whales were equally likely to return to a different subarea as they were

Table 4. Match indices for different combinations of years and regions for three subareas in Hawaii 1991–1993. Same area in different year values were averaged for three combinations of years (1991–1992, 1991–1993, 1992–1993) at each subarea. Different areas in same year values were averaged for pairs of subareas for three sample years (1991, 1992, 1993). Different areas in different year values were pooled for each pair of subareas in combinations of different years.

Samples	*n*	Mean	SE
Same area in different years	**9**	**0.306**	**0.038**
Big Island	3	0.271	0.024
Maui area	3	0.395	0.089
Kauai	3	0.253	0.054
Different areas in same year	**9**	**0.138**	**0.042**
Big Island-Maui	3	0.254	0.057
Maui-Kauai	3	0.108	0.078
Big Island-Kauai	3	0.053	0.036
Different areas and years	**18**	**0.264**	**0.043**
Big Island-Maui	6	0.306	0.102
Maui-Kauai	6	0.276	0.062
Big Island-Kauai	6	0.211	0.062
All	**36**	**0.243**	**0.027**

Table 5. Match indices for different combinations of years and regions for three subareas in Mexico 1990–1993 (see Table 4 for explanation). Small samples only used for within-area calculations.

Samples	*n*	Mean	SE
Same area in different years	9	**0.950**	**0.225**
Mainland	2	0.954	0.954
Revillagigedos	1	1.324	
Baja	6	0.997	0.240
Different areas in same year	2	**0.298**	**0.057**
Mnld-Baja	1	0.355	
Rev-Baja	1	0.241	
Different areas and years	7	**0.258**	**0.063**
Mnld-Baja	3	0.380	0.088
Rev-Baja	3	0.221	0.034
Rev-Mnld	1	0.000	
All	18	**0.608**	0.139

to return to the same subarea in successive years. Only the among-subarea match index in the same year was lower (0.138), indicating whales were not as likely to travel to multiple subareas in the same year as they were to return to the same or a different subarea in a different year.

Interchange among the Mexico subareas was less extensive and showed some clear preferred directions of interchange, although sampling among subareas and years was incomplete (Table 5). The highest index values were obtained for whales returning to the same subarea in different years (0.95). No interchange was seen between the mainland Mexico and Revillagigedo subareas, although large samples (more than 100 individuals) were available only for 1991 from the Revillagigedos and 1993 from mainland Mexico. Interchange among subareas was most common between mainland and Baja, both for the same year and among years (match indices of 0.355 and 0.380, respectively). Interchange between the Revillagigedos and Baja was only slightly lower (0.221 and 0.241). This suggests that Baja may be primarily a migratory corridor where whales from both the Revillagigedos and mainland overlap. Thus, the Baja subarea was more representative of the Mexico wintering region as a whole than either of the other two subareas. The sample from Baja was larger and included four years (1990–1993) compared to only the single-year large samples from the other two subareas.

Off Japan the match index for different years in the same subarea was much higher than that within Mexico and Hawaii, indicating a high rate of return of a small population (Table 6). This was especially true off Okinawa where the index was four times higher than off Ogasawara (11.6 *vs.* 2.9). Although movement between these two subareas was documented in both the same year and in different years, the match index was more than an order of magnitude lower than that for return to the same subarea in different years.

Interchange between regions—Interchange between wintering regions was seen, but occurred infrequently. The match indices between any two wintering re-

Table 6. Match indices for different combinations of years and locations for 2 subareas in Japan 1991–1993 (see Table 4 for explanation).

Samples	*n*	Mean	SE
Same area in different years	6	7.265	2.395
Okinawa	3	11.636	3.093
Ogasawara	3	2.893	0.096
Different areas in same year			
Okin.-Ogas.	3	0.167	0.167
Different areas and years			
Okin.-Ogas.	6	0.244	0.084
All	15	3.037	1.293

gions were one to two orders of magnitude lower than the among-year rate for the same region (Table 7). Six transits of five individual whales were documented between Mexico and Hawaii: three of these whales traveled between the Revillagigedos and Hawaii and two between Baja and Hawaii. Four transits of three whales were found between Hawaii and Japan (Fig. 2). One whale made multiple transits between Hawaii and Japan (Maui in 1991, Ogasawara in 1992, and off the Big Island of Hawaii in 1993). None of these whales were seen in more than one wintering region in the same year. No exchange was found between Mexico and Japan.

Interchange Among Feeding Areas

There was little interchange among different feeding areas. At five of the eight feeding areas, no between-area matches were found. Only four whales were found to have traveled to different feeding areas. Of the 287 whales photographed in southeastern Alaska, two were seen in Prince William Sound (87) and one was seen off Kodiak (69). Additionally, a single whale was seen

Table 7. Match indices for different combinations of years and pooled wintering regions (see Table 4 for explanation).

Samples	*n*	Mean	SE
Same region in different years			
Mexico	6	0.518	0.103
Hawaii	3	0.257	0.032
Japan	3	2.365	0.090
Different regions in same year			
Mexico-Hawaii	3	0.000	0.000
Hawaii-Japan	3	0.000	0.000
Mexico-Japan	3	0.000	0.000
Different regions and years			
Mexico-Hawaii	9	0.015	0.007
Hawaii-Japan	6	0.010	0.005
Mexico-Japan	9	0.000	0.000

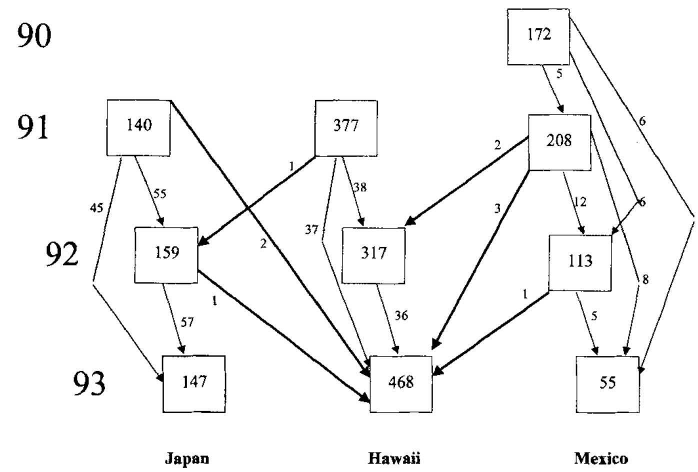

Figure 2. Interyear and interregion matches between the wintering regions off Japan, Hawaii, and Mexico. Numbers in boxes show number of individuals; numbers next to lines show number of whales that matched between years or regions.

both off Kodiak and in Prince William Sound. In all but one case these matches were of whales seen in different years. The exception was one animal that moved between Prince William Sound and southeastern Alaska in the same year (July and November 1992).

Migratory Movements

Whales from each of the three wintering regions were found at multiple feeding areas in the North Pacific (Fig. 3–5, Table 8). Additionally there were

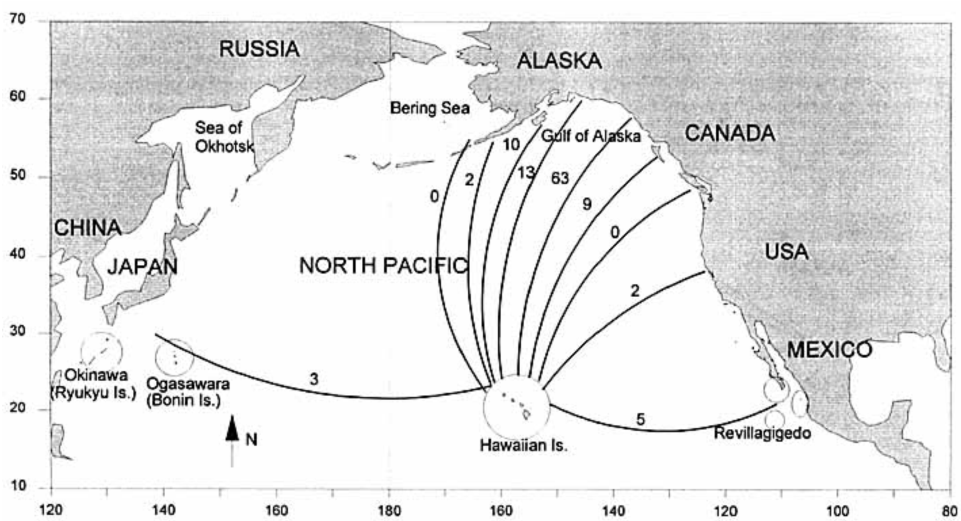

Figure 3. Number of whales seen in Hawaii (n = 1,056) that were also identified at other locations.

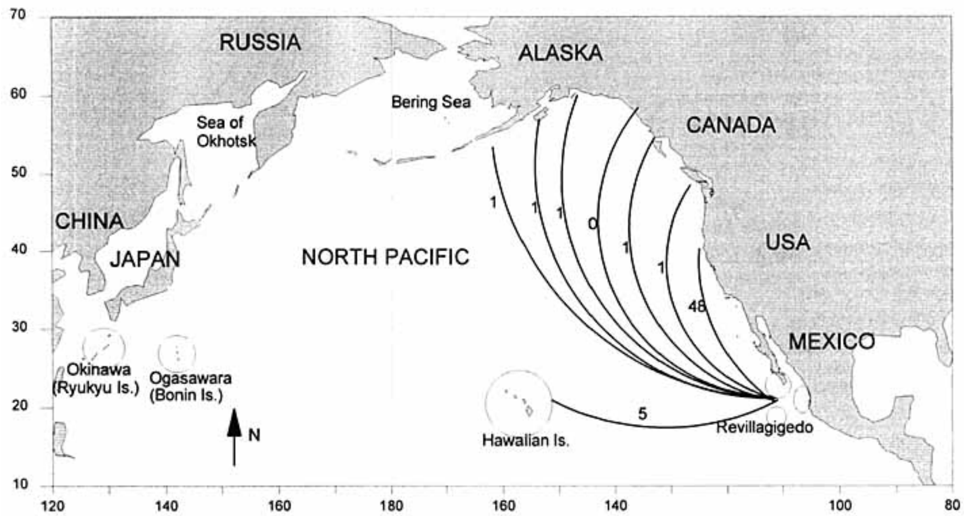

Figure 4. Number of whales seen off Mexico (n = 509) that were also identified at other locations.

differences among subareas in the migratory destinations of whales wintering in Mexico and Japan.

Overall, whales photographed off Mexico were most likely to be resighted off California (match index = 0.208), although they were also seen off northern and southern British Columbia, Prince William Sound, Kodiak and the Aleutian Islands (Fig. 4). Differences among subareas of Mexico were substantial, however (Table 8). Whales identified off mainland Mexico had a very high match index with California, those identified off Baja had an intermediate index with four different feeding areas, and those identified off the Revilla-

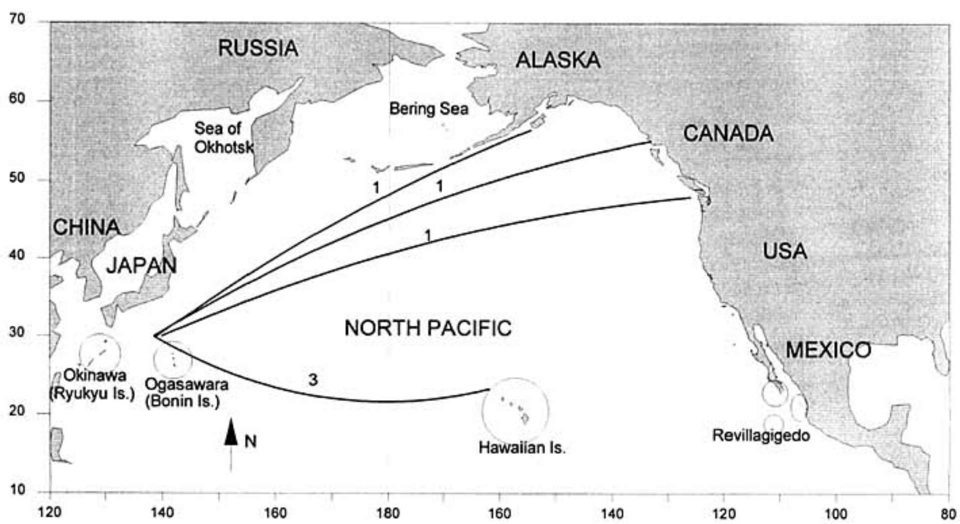

Figure 5. Number of whales seen off Japan (n = 313) that were also identified at other locations.

Table 8. Match indices among sampled feeding areas and wintering regions.

		Wintering region										
Feeding area	*n*	Revillagi-gedos 159	Mainland Mexico 138	Baja 233	All Mexico 509	Big Is 401	Maui 368	Kauai 375	All Hawaii 1,056	Ogasawara 257	Okina-wa 63	All Japan 313
Ca-Wa	454	0.01	0.51	0.18	**0.21**	0.01	0.01	0	**0.00**	0	0	**0**
BC	73	0	0	0.12	**0.05**	0.20	0.15	0	**0.12**	0.11	0	**0.09**
SEAK	287	0	0	0	**0**	0.22	0.22	0.17	**0.21**	0	0	**0**
PWS	87	0	0.08	0	**0.02**	0.17	0.16	0.09	**0.14**	0	0	**0**
Kodiak	76	0	0	0.06	**0.03**	0.10	0.18	0.11	**0.12**	0.05	0	**0.04**
Shum./Aleut.	22	0	0	0.20	**0.09**	0.23	0	0	**0.09**	0	0	**0**

gigedos had a low match index with all sampled feeding grounds. Of the 159 individuals photographed off the Revillagigedo Archipelago, only one was seen at any feeding area (off California).

Whales identified in all three subareas of Hawaii were seen in multiple feeding areas with the highest overall match index to southeastern Alaska (0.208, Fig. 3, Table 8). Whales identified off Hawaii were also observed off California, northern British Columbia, Prince William Sound, Kodiak Islands, and the Aleutian Islands (Fig. 3). There were no large differences in the match indices by subarea of Hawaii to the different Alaskan feeding areas. Of the 11 whales that were found to move between Hawaii and the easternmost feeding areas from California to British Columbia, none were from Kauai. This is significantly different than would be expected ($\chi^2 = 6.4$, df = 2, $P < 0.05$) if whales from each Hawaii subarea had an equal tendency to migrate to these feeding areas and may indicate that whales seen in the westernmost subarea of the Hawaiian Island chain are less likely to migrate to the easternmost feeding areas.

Only three whales were documented moving between the Japan wintering regions and feeding areas; these consisted of single matches to southern British Columbia, northern British Columbia, and Kodiak Island (Fig. 5, Table 8). All three of these whales were identified off Ogasawara; we found no matches for whales that had been seen off Okinawa.

Whales identified in a specific feeding area sometimes showed a clear preference for a wintering region (Table 8). Whales identified in southeastern Alaska showed a high match index with Hawaii and were not identified in any other wintering region (match index of 0). Whales identified off California, Oregon, and Washington were almost exclusively identified in Mexico, with only a few matches with Hawaii. For most other feeding areas, however, migrations were documented to multiple wintering regions. Whales identified off British Columbia, for example, showed a similar match index with Mexico, Hawaii, and Japan.

Discussion

Movements of humpback whales between some regions have been examined by previous studies using a variety of methods. This study describes some movements that were unknown previously and also confirms many documented findings. Our primary contribution, however, is the use of a broad geographic scope and comparison of quantitative exchange rates among all wintering areas and all studied feeding areas for humpback whales in the North Pacific. This has shown that while the structure of humpback whale populations in the North Pacific is complex there are some clear, interpretable patterns.

Site Fidelity and Interchange Among Wintering Regions

While interchange of animals between wintering regions was documented, it occurred at a much lower rate compared to animals returning to the same wintering region. Movement between wintering regions has been reported previously between Hawaii and Japan (Darling and Cerchio 1993) and Mexico and Hawaii (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990). While we also found these movements, we demonstrate that the rate of exchange among wintering regions is low, indicating fidelity to these regions.

The wide variations in interchange among subareas for the three primary wintering regions were consistent with the distances among them. Interchange was most extensive among Hawaii subareas where the distances were smallest (less than 500 km between all subareas), intermediate among Mexico subareas (500–800 km apart), and most limited among the Japan subareas (1,500 km apart). The high degree of interchange among subareas of the Hawaiian Islands found in this study and reported previously between some subareas (Baker and Herman 1981, Darling and Morowitz 1986, Darling and McSweeney 1985, Cerchio *et al.* 1998) supports the conclusion that the waters surrounding the Hawaiian Islands constitute one wintering region. For Mexico, movements among subareas were more stratified. Samples from this study were consistent with the larger sample analyzed by Urbán *et al.* (1999, 2000) that showed only a low rate of interchange between whales wintering along the mainland and those around the offshore Revillagigedo Islands. The Baja Peninsula, however, may serve as a migratory corridor for animals from both these subareas (Urbán *et al.* 2000). Interchange among the two subareas sampled off Japan, reported previously in a small sample (Darling and Mori 1993, Uchida *et al.* 1993) and found in this study, occurred at a lower rate than expected if whales mixed randomly.

Humpback whales are probably also inhabiting regions that are unknown or unsampled. Humpback whales were hunted during the winter months at numerous other locations in the western North Pacific, even though whale occurrence off Taiwan, the Mariana Islands and the Marshall Islands is currently uncommon or unknown (Darling and Mori 1993). Humpback whales also winter at scattered locations along the Mexican mainland south of the subareas that have been sampled (Urbán and Aguayo 1987). One known wintering region not included in our sample is the coastal waters of Central America, especially Costa Rica and Panama (Steiger *et al.* 1991, Calambokidis *et al.* 2000). This is a region where humpback whales from the North Pacific mate and give birth to calves, although no photographs were available from 1991 to 1993 for this analysis. This region appears to be used by humpback whales that migrate almost exclusively from feeding areas off California, with limited evidence of interchange with whales wintering off mainland Mexico (Calambokidis *et al.* 2000).

Site Fidelity and Interchange among Feeding Areas

Site fidelity was strongest at the feeding areas. Resighting rates among years at most feeding areas were high and only limited between-area movements were seen. The low rate of among-year resightings for a few feeding areas such as off Kodiak and in the western Gulf of Alaska probably reflects a combination of low effort and large number of whales, of which relatively few have been sampled. Brueggeman *et al.* (1988) reported a minimum estimate of 1,247 humpback whales based on ship surveys in the Shumagin-Kodiak Island area of the western Gulf of Alaska, an area from which we had only 91 identifications. Many of the areas in the North Pacific where whales feed are remote and have not been sampled.

Interchange between feeding areas in the North Pacific found in this study has been previously documented among some of the areas we examined: interchange between California and British Columbia (Calambokidis *et al.* 1996), British Columbia and southeastern Alaska (Darling and McSweeney 1985), southeastern Alaska and the western Gulf of Alaska including Prince William Sound (Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990, von Ziegesar *et al.* 1994, Waite *et al.* 1999), and among areas in the western Gulf of Alaska (Waite *et al.* 1999). Consistent with this study, such interchanges occur at low rates involving just a few whales. A relatively distinct feeding aggregation of humpback whales has been documented along the coast of California, Oregon, and Washington with little interchange with feeding areas farther north (Calambokidis *et al.* 1996). Although there was a steep drop in interchange at the Washington-British Columbia border, interchange rates also declined with distance within the feeding groups that range off California, Oregon, and Washington (Calambokidis *et al.* 1996). Humpback whales in the North Atlantic also show strong site fidelity to feeding areas with only limited interchange among these areas (Katona and Beard 1990, Clapham *et al.* 1993*a*).

Currently, it is not possible to evaluate the total number and nature of the divisions among most of the North Pacific feeding areas. Samples used in this study are centered at locations where field effort has been conducted and do not necessarily represent centers of distinct feeding areas. Examination of larger samples collected from a more complete sampling of all feeding areas will be required to assess whether there are specific boundaries or a more continuous distribution with interchange decreasing with distance. Also, habitat use may change as abundance increases.

Migratory Movements of Whales

Despite the site fidelity of humpback whales to specific areas, sightings between feeding areas and wintering regions have not generally followed a simple pattern to allow definition of an integrated wintering/feeding area population structure. Results of photo-identification studies conducted in the North Pacific over the past 20 yr provide additional insight into migratory destinations of these whales.

The findings of this study, combined with those from others, confirm the dichotomy in the migratory destinations of whales wintering in the different subareas of Mexico. Humpback whales from the Revillagigedos, for which our limited sample uncovered only one match to a feeding area (California), migrate to feeding areas off California, British Columbia, southeastern Alaska, Prince William Sound, and the Kodiak Island area (Gabriele *et al.* 1996, Calambokidis *et al.* 2000, Urbán *et al.* 2000). Consistent with this study, the rate at which whales from the Revillagigedos were seen at these feeding areas was extremely low. These results suggest that other feeding areas that have not been well sampled, such as the offshore waters of the Gulf of Alaska and the Aleutian Islands, are likely the primary destinations of these whales. Conversely, whales wintering off mainland and Baja Mexico have a high rate of movement to feeding areas such as California to Washington, where over 100 matches have been documented, and at lower rates to British Columbia, southeastern Alaska, Prince William Sound, and the western Gulf of Alaska (this study, Baker *et al.* 1986, Perry *et al.* 1990, Urbán *et al.* 2000).

We found that humpback whales migrate at varied rates between Hawaii and most of the feeding areas in the eastern and central North Pacific. The high match rate between whales feeding in southeastern Alaska and those wintering in Hawaii is consistent with several past studies (Darling and McSweeney 1985; Baker *et al.* 1985, 1986). A migration time of as short as 39 d has been recorded between these two areas (Gabriele *et al.* 1996). Several of the migratory transits between Hawaii and Alaska documented in this study were also very short, including an animal seen in southeastern Alaska through late January 1993 and then in Kauai 36 d later.

Some of the migratory destinations of humpback whales wintering in the western North Pacific have not previously been documented. Our finding of movement of a whale between Japan and Kodiak Island is consistent with Discovery tag recaptures that indicated whale movement 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 (Nishiwaki 1966, Omura and Ohsumi 1964, Ohsumi and Masaki 1975). One whale tagged off Ogasawara in March was killed in June of the same year northwest of Japan, possibly indicating movement north towards the Kuril Islands (Nishiwaki 1966). Given these patterns, whale movements to feeding areas near Kodiak Island and northern British Columbia found in this study are not surprising. Similarly, the one whale that we found to move between Ogasawara, Japan, and a feeding area off southern British Columbia is the same individual (0–112) as that reported by Darling *et al.* (1996, same transit). This study revealed a second whale that moved between Ogasawara and British Columbia, although this time to northern British Columbia.

Population Structure

An understanding of population structure of humpback whales in the North Pacific is crucial to estimating abundance. The population structure of humpback whales in the North Pacific is complex and problematic for applying capture-recapture models. It is clear from our study that the limited movements among many areas make it inappropriate to treat the North Pacific as a single population.

There are measurable differences in genetic patterns (both mtDNA and nuclear DNA) among whales inhabiting different feeding areas, as well as less dramatic, but still significant differences among wintering regions. Significant differences in mtDNA haplotypes were found between 38 humpback whales biopsied in southeastern Alaska and 20 from central California, suggesting a long-term migration rate of less than one female per generation (Baker *et al.* 1990, 1994). However, differences in nuclear DNA were not found between humpback whales off California and southeastern Alaska (Baker *et al.* 1993, Palumbi and Baker 1994), suggesting some reproductive interchange, recent or historical. A larger analysis of samples from 205 humpback whales from an expanded number of areas in the North Pacific confirmed highly significant differences in mtDNA among both feeding and wintering areas and weaker, although still significant differences in nuclear actin, intron, and microsatellite alleles (Baker *et al.* 1998). The differences in alleles were significant when tested based on two presumed "stocks" which compared the wintering and feeding areas of the eastern North Pacific (Mexico and California) against those from the central North Pacific (Hawaii and Alaska). Medrano-González *et al.* (1995) reported weak but significant differences in mtDNA haplotypes between humpback whales wintering off the Revillagigedos and those off the Mexican coast.

The occurrence of distinct feeding aggregations, as indicated by photographic identification and mtDNA, does not necessarily indicate an absence of some interbreeding among whales from these different groups. Because mtDNA is maternally transmitted, mtDNA differences among feeding grounds may only indicate that offspring return to their mothers' feeding area. Mattila *et al.* (1989) and Clapham *et al.* (1993b) have reported that breeding groups in the West Indies have included males and females from different feeding areas. Similarly, since humpback whales from feeding areas in both Alaska and California migrate to both Hawaii and Mexico (although with very different frequencies, Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990, Calambokidis *et al.* 2000, Urbán *et al.* 2000), the opportunity does exist for whales to interbreed. Although the frequencies of mtDNA haplotypes on Mexican and Hawaiian wintering regions are significantly different, they are not as marked as between California and Alaska (Baker *et al.* 1994). This may reflect the mixing of whales from different feeding areas on the wintering regions or migration from as yet unsampled feeding areas (Medrano-González *et al.* 1995).

These genetic and demographic patterns of population structure appear to be quite different from those in the North Atlantic. Current evidence suggests that humpback whales from the feeding areas interbreed at a single wintering ground in the West Indies to form a single panmictic population (Mattila *et al.* 1989, 1994; Clapham *et al.* 1993*b*; Larsen *et al.* 1996; Palsbøll *et al.* 1997; Smith *et al.* 1999).

Humpback whales appear to show a strong degree of site fidelity at feeding areas; movements among these areas are often limited and genetic differences are most pronounced. Although the boundaries of one distinct feeding ground in the North Pacific have been defined off California, Oregon, and Washington (Calambokidis *et al.* 1996), they may not be as easily defined in other areas. The nearly continuous distribution of humpback whales along their feeding range around the North Pacific may make setting exact borders for feeding aggregations impossible, even though animals might show a high degree of site fidelity. The pattern of decreasing interchange with distance seen among the sampled subareas along the coast of California, Oregon, and Washington (Calambokidis *et al.* 1996) may be a typical pattern all along the feeding range. Genetic and photographic identification research has been conducted in very limited areas. In particular, little research has been conducted in the Gulf of Alaska and along the Aleutian Islands.

The complexity of defining the population structure of humpback whales results from the difficulty in integrating the wintering and feeding areas into a single cohesive model. This is problematic currently because of the varied and sometimes unusual pattern of migratory destinations and the lack of information from many feeding areas. Although defining population structure based on wintering regions is currently traditional, it is important for management considerations not to lose sight of the strong site fidelity to specific feeding grounds. Commercial whaling off California and Washington in the early 1900s provided a demonstration of the management implications of such fidelity. During an eight-year period 2,473 humpback whales were killed from three stations off California and Washington (Clapham *et al.* 1997). Although this hunting depleted the whale aggregations in this feeding area (as evidenced by a dramatic decline in catch rates), such a decline was not as apparent off Mexico because that wintering region includes whales from a number of feeding areas (Clapham *et al.* 1997).

Defining population structure based on whale distribution on the wintering grounds is more feasible currently than that based upon feeding areas because whales breed in the former, are more separated geographically by large distances, and most areas have been sampled using photo-identification methods and genetic analyses. Our results of relatively rare movements between wintering regions are consistent with the significant differences in mtDNA that have been found between whales off Hawaii and Mexico. We conclude that, while there is clear evidence for at least three subpopulations of humpback whales in the North Pacific (those that winter off Hawaii, Japan, and Mexico), a precautionary management approach should consider the evidence for up to six subpopulations (with subdivisions in Mexico and Japan, plus Central America). Our data from subareas of Mexico, though limited, indicate whales in the Revillagigedo Archipelago should be considered a separate subpopulation from the whales using mainland Mexico, as suggested by Barlow *et al.* (1997) and Urbán *et al.* (2000). This conclusion is based on evidence of limited interchange with mainland Mexico, evidence that these animals migrate to different feeding areas, and the weak mtDNA differences between this area and coastal Mexico (Medrano-González *et al.* 1995, Urbán *et al.* 2000). Similarly, the low rate of interchange between the two subareas of Japan and the limited evidence of potential differences in migratory destinations indicate these two wintering grounds may need to be considered as separate subpopulations. Finally, it is unclear if humpback whale use of Central American waters (Steiger *et al.* 1991, Calambokidis *et al.* 2000) represents a distinct wintering region or an extension of the Mexican mainland region.

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