

INTERCHANGE AND ISOLATION OF HUMPBACK WHALES OFF CALIFORNIA AND OTHER NORTH PACIFIC FEEDING GROUNDS

JOHN CALAMBOKIDIS, GRETCHEN H. STEIGER, JOSEPH R. EVENSON,
KIRSTEN R. FLYNN¹

Cascadia Research, 218½ West Fourth Avenue, Olympia, Washington 98501, U.S.A.

KENNETH C. BALCOMB, DIANE E. CLARIDGE, PRENTICE BLOEDEL
Center for Whale Research, 1359 Smugglers Cove Road,
Friday Harbor, Washington 98250, U.S.A.

JANICE M. STRALEY
P.O. Box 273, Sitka, Alaska 99835, U.S.A.

C. SCOTT BAKER
School of Biological Sciences, University of Auckland, Private Bag 92019,
Auckland, New Zealand

OLGA VON ZIEGESAR
North Gulf Oceanic Society, P. O. Box 15244, Homer, Alaska 99603, U.S.A.

MARILYN E. DAHLHEIM, JANICE M. WAITE
National Marine Mammal Laboratory, NOAA, 7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.

JAMES D. DARLING
West Coast Whale Research Foundation, 1200-925 West Georgia Street,
Vancouver, B.C., Canada V6C 3L2

GRAEME ELLIS
Department of Fisheries and Oceans, Pacific Biological Station,
Nanaimo, B.C., Canada V9R 5K6

GREGORY A. GREEN²
Ebasco Environmental, 10900 NE 8th, Suite 500,
Bellevue, Washington 98004, U.S.A.

¹ Current address: R. R. 1, Box 202, Readsboro, Vermont 05350, U.S.A.

² Current address: Parametrix, 5808 Lake Washington Blvd NE, Kirkland, Washington 98033, U.S.A.

ABSTRACT

Humpback whales feed in several high-latitude areas of the North Pacific. We examined the interchange of humpback whales between one of these areas, off California, and those in other feeding grounds in the eastern North Pacific. Fluke photographs of 597 humpback whales identified off California between 1986 and 1992 were compared with those off Oregon and Washington (29); British Columbia (81); southeastern Alaska (343); Prince William Sound, Alaska (141); Kodiak Island, Alaska (104); Shumagin Islands, Alaska (22); and in the Bering Sea (7). A high degree of interchange, both inter- and intrayear, was found among humpback whales seen off California, Oregon, and Washington. A low rate of interchange was found between British Columbia and California: two whales seen near the British Columbia/Washington border were photographed off California in a different year. No interchange was found between California and the three feeding areas in Alaska. Humpback whales off California, Oregon, and Washington form a single intermixing feeding aggregation with only limited interchange with areas farther north. These findings are consistent with photographic identification studies in the North Atlantic and with genetic studies in both the North Atlantic and North Pacific.

Key words: humpback whale, *Megaptera novaeangliae*, photoidentification, interchange, feeding grounds, North Pacific.

Humpback whales (*Megaptera novaeangliae*) alternate between low-latitude winter breeding grounds and high-latitude summer feeding areas (Nishiwaki 1966, Rice 1974). Katona and Beard (1990) reported that humpback whales in the North Atlantic form discrete feeding aggregations with relatively little interchange among them. The extent to which humpback whales use distinct feeding grounds in the North Pacific, and the number and range of such subpopulations, have not been determined.

The areas where humpback whales feed in the North Pacific include the waters off Alaska (Darling and Jurasz 1983; Darling and McSweeney 1985; Baker *et al.* 1986, 1992; Brueggeman *et al.* 1987; Rice and Wolman 1982; von Ziegesar 1992), British Columbia (Darling and McSweeney 1985), and California (Dohl *et al.* 1983; Baker *et al.* 1986; Calambokidis *et al.* 1990, 1993). Only limited information on interchange among these feeding areas has been published (Darling and McSweeney 1985, Baker *et al.* 1986). While historical accounts reported that humpback whales off California were migrants en route to and from Alaska (Kellogg 1928, Tomilin 1957), recent research has shown that humpback whales feed off California through the summer and fall (Dohl *et al.* 1983, Calambokidis *et al.* 1989). Baker *et al.* (1986) were the first to report a comparison of individually identified whales photographed in southeastern Alaska (326 individuals) and off California (20 individuals); there were no matches between these two areas. A low rate of long-term interchange was also suggested by the distribution of mitochondrial (mt) DNA haplotypes in the central and eastern North Pacific. Baker *et al.* (1990, 1994) found complete segregation of maternal lineages, as reflected in mtDNA haplotypes, between central California and southeastern Alaska.

Humpback whale populations were depleted by whaling that continued off

the California coast until 1965 (Rice 1963, 1974). Efforts are currently underway to estimate the numbers of humpback whales in this region using capture-recapture statistics based on photoidentification (Calambokidis *et al.* 1993) and line-transect methods from ship surveys (Barlow 1994, 1995).

Here we examine the relationship between humpback whales photographically identified on feeding grounds off California and those identified off Alaska, British Columbia, Washington, and Oregon. This information on population substructure or stock identity is required to ensure appropriate use of capture-recapture models and for reliable interpretation of population size estimates for this species.

METHODS

Humpback whales were identified photographically by natural marks on the ventral side of their flukes, as described previously (*e.g.*, Katona *et al.* 1979). Black-and-white prints of whales were compared visually by Cascadia Research Collective (CRC). Photographs from California, Oregon, and Washington (607 unique whales) were compared with collections of various sizes from British Columbia, southeastern Alaska, Prince William Sound, the waters around Kodiak Island and the Shumagin Islands, and the southeastern Bering Sea (Fig. 1). Details of each collection are given below.

California—A total of 597 individual whales were identified off California between 1986 and 1992. These photographs were taken by CRC, the Center for Whale Research (CWR), and other collaborators during humpback and blue whale photoidentification studies. Research was conducted primarily between July and November (with some effort from April to December) in waters out to about 60 km off central California between 1986 and 1990 (Calambokidis *et al.* 1990); the entire California coast was covered in 1991 and 1992 (Calambokidis *et al.* 1993). The research vessels included 4- to 6-m inflatable boats, a 14-m motor sailer, and 6-m fiberglass motor boats. Surveys targeted areas where whales were concentrated. Photographs of the ventral side of the flukes were taken by one or two photographers at 35–100 m behind the animals. Photographs were taken with *Nikon* motor-advance 35-mm SLR cameras with 300-mm f4.5 lenses and *Ilford* HP-5 or *Kodak* Tri-X black-and-white negative film. Shutter speeds were 1/1000 sec or faster when lighting conditions permitted. The film was exposed for ISO rating 1200 and development times were adjusted accordingly.

Oregon and Washington—Twenty-nine unique humpback whales were identified off Oregon and seven off Washington between 1990 and 1992. Photographic surveys in this area were limited: two surveys were conducted by CWR for Ebasco Environmental at Heceta Bank, Oregon, in June 1990 and off the mouth of the Columbia River in September 1990 (Green *et al.* 1992). Another survey was conducted off Tillamook Head, Oregon, by CRC in May 1992. Two humpback whales were identified in Puget Sound, Washington, during three surveys in June and July 1988 (Calambokidis and Steiger 1990).

British Columbia—Three collections of humpback whale photographs from

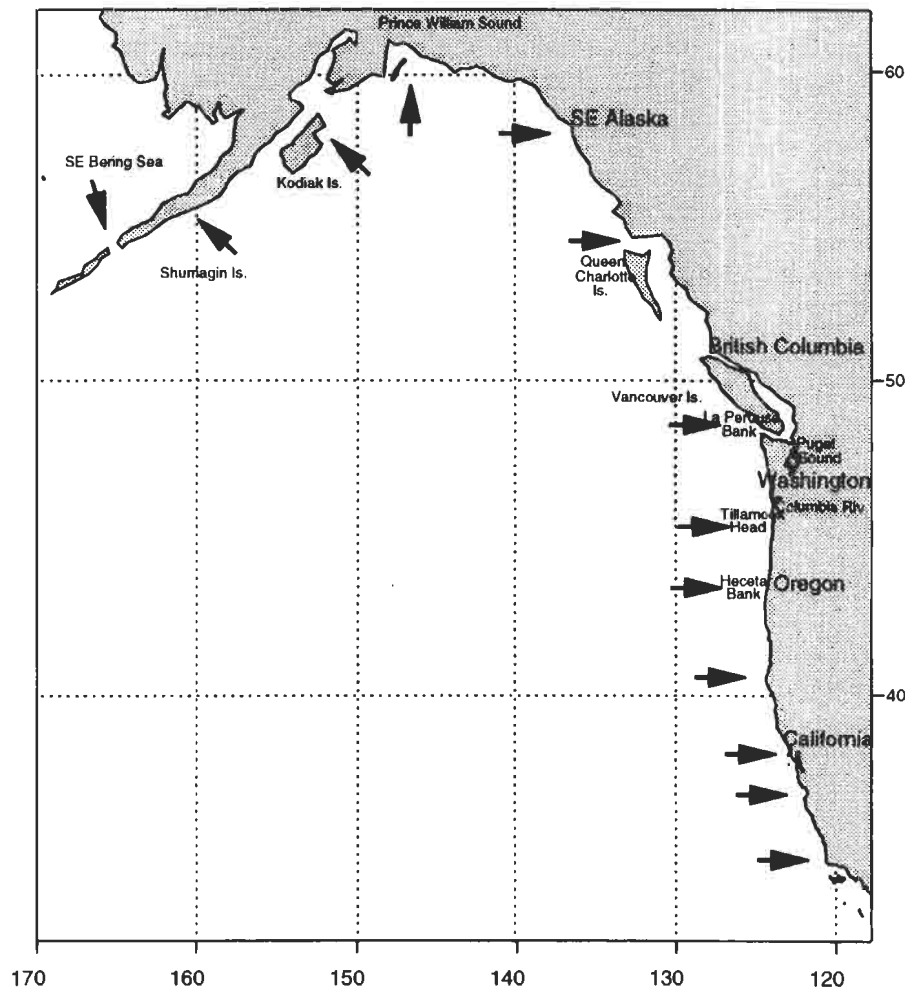


Figure 1. Principal locations where whales were identified.

British Columbia, representing 81 unique individuals, were compared to whales from California. Two collections were primarily from La Perouse Bank, off southwestern Vancouver Island near the Washington border, where 48 individuals have been identified by the West Coast Whale Foundation (WCWF) (1975–1990) and CWR (1990–1991). The third collection of photographs of 34 individuals (compiled by Graeme Ellis), including one duplicate with the WCWF catalog, were collected during 1989–1992 primarily from northern British Columbia, including off the Queen Charlotte Islands and northern Vancouver Island. Four whales in this collection were photographed on La Perouse Bank.

Southeastern Alaska—Photographs of 343 individual humpback whales from the northern portion of southeastern Alaska (Frederick Sound to Icy Strait) were taken from 1987 and 1991. Field methods were as described by Straley (1990).

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

Kodiak Island, Shumagin Islands, and the Bering Sea—Humpback whales were identified off Kodiak Island (104), the Shumagin Islands (22), and the southeastern Bering Sea (7) during July and August 1992 and 1993 by staff of the National Marine Mammal Laboratory. Photographic identification of humpback whales was conducted incidentally during line-transect vessel surveys to obtain population estimates of killer whales in Alaska (Dahlheim and Waite 1993, Dahlheim 1994).

Additional comparisons to Alaska—In addition to the above comparisons, we also compared 225 whales identified off California between 1986 and 1988 by CRC and CWR (included in the larger sample used in comparisons reported above) with the catalog of humpback whales from the eastern North Pacific compiled by Perry *et al.* (1988) with the Kewalo Basin Marine Laboratory, University of Hawaii. This includes 464 whales that were identified in southeastern Alaska between 1979 and 1985 (Baker *et al.* 1992) and 95 humpback whales identified in the western Gulf of Alaska, Yakutat Bay, and Prince William Sound between 1977 and 1985. This catalog is a compendium of photographs from many independent researchers. Some of these photographs from Alaska are duplicates of photographs in the collections described by region above.

RESULTS

The rate of matches between whales identified off both California and either Oregon or Washington was similar to the interyear match rate within California (Table 1). Seventy-one percent of the whales identified off California were seen in more than one year (424 of 597), and, from 1986 to 1992, an average of 88% (71%–97%, SD = 8.9%) of the whales identified each year were seen at least one other year.

Of 29 humpback whales identified off Oregon in 1990 and 1992, 22 (76%) were also seen off California; of these, 10 were observed in the same year (Table 2). In all but one of the intrayear matches, animals were photographed in May or June off Oregon and observed between September and October in California. The exception was a whale photographed in May off California and then in June off Oregon. Matches to California included whales that were seen in all three of the areas off Oregon that we sampled (Table 2).

Similarly, four of seven humpbacks identified off Washington were also observed off California, two in the same year (Table 1). Three of these matches were also whales that had been identified off Oregon, including one that was seen in 1990 off Oregon in June, Washington in September, and California in November (Table 2). Two of the whales from Washington were photographed in Puget Sound, an area where humpback whales are rarely observed (Calambokidis and Steiger 1990); neither was found in the California sample.

Interchange between California and British Columbia was considerably lower

Table 1. Sample sizes and number of matches found between humpback whales identified off California and other feeding areas in the North Pacific.

Region	Years	# of individuals	# of matches with California	% of whales that match with California
California	1986–1992	597	—	88*
Oregon	1990–1992	29	22	76
Washington	1988–1992	7	4	57
British Columbia	1975–1991	81	2	2.5
SE Alaska	1987–1991	343	0	0
Pr. Wm. Sound	1977–1991	141	0	0
Kodiak Is.	1992–1993	104	0	0
Shumagin Is.	1992–1993	22	0	0
SE Bering Sea	1992–1993	7	0	0

* The average of the percentage of whales identified each year that matched any other year.

than among California/Oregon/Washington (Table 1). Only two whales were matched between these areas, neither of them in the same year (Table 2). Both whales were photographed off British Columbia on La Perouse Bank. These whales had been seen in only one or two years off California (Table 2).

No matches were found with the humpback whales identified north of southern British Columbia. The feeding areas examined for these comparisons included central Vancouver Island to the Queen Charlotte Islands off British Columbia and five areas in Alaska.

DISCUSSION

The feeding area we describe ranges between approximately 32°N and 48°N (over 1,800 km), with the main concentration of whales inhabiting the waters between 36°N and 39°N. This is farther south than other feeding areas for humpback whales in the Northern Hemisphere. Humpback whales in the western North Atlantic primarily use five feeding areas from 42°N to 78°N (Katona and Beard 1991) and in the western North Pacific they feed north of 40°N (Darling and Mori 1993).

Our finding of a distinct humpback whale feeding range along the California, Oregon, and Washington coasts contradicts the beliefs of Kellogg (1928) and Tomilin (1957) who concluded that humpback whales off California were migrants en route to and from feeding areas north of Washington. They reported that humpback whales traveled north in March and April and continued north past Vancouver Island in May and June and reached Alaska by late summer; they appeared again off California on their southbound migration in October and November. Our results show that the feeding ground off the U.S. west coast is separate from feeding grounds off Alaska. Although some humpback whales migrate between Mexico and Alaska (Baker *et al.* 1986) and must

Table 2. Matches found between California and other feeding areas.

ID #	Sighting outside CA		Years in CA	Regions seen in CA*
	Date	Location		
California–Oregon				
10001	6/25/90	Heceta Bank	86–92	51, 53
10045	10/10/92	S. Oregon	86	53
10048	6/25/90	Heceta Bank	86, 87, 91	53, 63
10055	10/10/92	S. Oregon	86–88, 91	53, 63
10126	6/25/90	Heceta Bank	87, 91, 92	53, 63
10148	6/25/90	Heceta Bank	87, 90	51, 53
10149	6/25/90	Heceta Bank	87–89	53, 62
10151	6/25/90	Heceta Bank	86–88, 93	53
10163	6/25/90	Heceta Bank	86–88, 91, 93	53, 54, 63
10167	6/25/90	Heceta Bank	86, 87, 89–93	53, 54, 63
10177	5/24/92	N. Oregon	87, 92	53, 61
10226	5/24/92	N. Oregon	88, 90	53
10308	5/24/92	N. Oregon	89, 90, 92	52, 53
10319	6/25/90	Heceta Bank	89–92**	53, 63
10319	5/24/92	N. Oregon		
10338	6/25/90	Heceta Bank	89, 90, 92, 93	53, 63
11011	6/25/90	Heceta Bank	88	62
12001	6/25/90	Heceta Bank	90, 92	53, 61
12002	6/25/90	Heceta Bank	90, 91, 93	52, 62, 63
12003	6/25/90	Heceta Bank	92	53, 61
12004	6/25/90	Heceta Bank	92, 93	63
12011	6/25/90	Heceta Bank	91–93	52, 53, 61, 63
12013	6/25/90	Heceta Bank	91, 92	63
California–Washington				
10126	9/28/90	N. Astoria Canyon	87, 91, 92	53, 63
12002	9/28/90	N. Astoria Canyon	90, 91, 93	52, 62, 63
12004	8/18/90	Grays Canyon	92, 93	63
13004	9/28/90	N. Astoria Canyon	90, 91	53, 63
California–British Columbia				
14014	9/06/90	La Perouse Bank	91, 92	53, 63
14025	8/24/91	La Perouse Bank	92	63

* Regions in CA: 51—Monterey Bay; 52—Half-Moon Bay; 53—Gulf of Farallones/Cordell Bank; 54—Bodega Bay to Pt. Arena; 61—Ft. Bragg—Cape Mendocino; 62—Humboldt Bay area; and 63—Point St. George.

** Found dead off California in 1993.

therefore pass California, most must either migrate well offshore (more than 65 km) or pass earlier or later in the season than our sampling effort (April to December). Humpback whales have been seen from aerial surveys off California from February to early April and could represent animals migrating to more northern feeding areas (Forney *et al.* 1995). Six of 10 humpback whales identified early in the season (March to 8 April) in our catalog, however, were seen later in the season off California.

Our results are consistent with recent findings in genetics research in the North Pacific. 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.* 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.

No obvious geographic boundary separates humpback whales that feed off California from those farther north. However, the dramatic drop in the resighting rate that occurs between whales off Washington and those off British Columbia suggests the existence of a demographic boundary between feeding grounds in this vicinity. Additional comparisons of humpback whales off Washington and British Columbia are needed to clarify the affiliation of whales in this region.

Although the number and boundaries of other feeding grounds in the North Pacific are not defined, interchange among some regions has been documented. A few matches have been found between British Columbia and southeastern Alaska (Darling and McSweeney 1985; G. Ellis and J. Straley, unpublished data). Six matches have been made between southeastern Alaska and Prince William Sound, both well-studied areas, between 1977 and 1993 (Baker *et al.* 1986; von Ziegesar and Matkin 1989; Perry *et al.* 1990; J. Straley, unpublished data). Baker *et al.* (1992) reported no interchange between whales identified in southeastern Alaska in 1986 and other areas in the western Gulf of Alaska. Waite and Dahlheim (in preparation, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115) found that of 104 whales identified off Kodiak Island, two had been seen in Prince William Sound and three in southeastern Alaska. No matches were found among whales off Kodiak Island, the Shumagin Islands, and the southeastern Bering Sea, although the sample size from the latter two areas was small. Nishiwaki (1966) reported a Discovery-tagged whale that moved from the Gulf of Alaska to the eastern Aleutian Islands.

There is also evidence of distinct feeding grounds for humpback whales in the North Atlantic. Katona (1986) and Katona and Beard (1990) report on the existence of four to five separate feeding substocks for humpback whales in the western North Atlantic with little interchange among them. Although genetic differences (mtDNA) between the western continental feeding grounds (Gulf of Maine and Newfoundland) have not been found (Baker *et al.* 1994, Palsbøll *et al.* 1995), recent studies have revealed significant differences in mtDNA patterns between feeding areas in the western North Atlantic and those in the eastern North Atlantic (Palsbøll *et al.* 1995).

The occurrence of distinct feeding herds does not necessarily indicate an absence of some interbreeding among these subpopulations. Because mtDNA is maternally transmitted, mtDNA differences among feeding grounds may only indicate that offspring return to their mother's feeding ground. Mattila *et al.* (1989) and Clapham *et al.* (1993) have reported that breeding groups in the West Indies have included males and females from different feeding grounds and they suggest that the western North Atlantic comprises a single panmictic unit. Humpback whales from feeding areas in 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, Urbán *et al.* 1987, Calambokidis *et al.* 1989) hence the opportunity for whales to interbreed exists. Humpback whales from different feeding areas in Alaskan waters have been observed together on the breeding grounds in Hawaii (Darling and McSweeney 1985). A few individuals have also been observed on both Hawaiian and Mexican wintering grounds (Darling and Jurasz 1983, Darling and McSweeney 1985, Baker *et al.* 1986, Perry *et al.* 1990). Although the frequencies of mtDNA haplotypes on Mexican and Hawaiian wintering grounds 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 grounds or migration from as yet unsampled feeding grounds (Medrano *et al.* 1995).

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