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Distribution and migratory destinations of humpback whales off the Pacific coast of Central America during the boreal winters of 1996–2003

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ABSTRACT

Here, we examine the distribution, habitat use, and migratory destinations of North Pacific humpback whales wintering off Central America. Coastal boat surveys were conducted off Costa Rica and Panama between 1996 and 2003. In 1999, a broader survey was conducted along most of Central America. Over 23,000 km were surveyed, with the greatest effort off southern Costa Rica. We made 191 sightings of 320 individual humpback whales. Whales were seen between 14°N and 8°N, making this the most southerly of the North Pacific wintering areas. Encounters included singles, adult pairs, singers, and mother/calf pairs. Mother/calf pairs accounted for 27% of all groups sighted, which is one of the highest sighting rates reported among North Pacific wintering areas. Sixty percent of sightings occurred in depths <50 m. Average sea surface temperature was 28.6°C (±1.0 SD). Ninety percent of the 77 unique whales photo-identified were also seen in the California–Oregon–Washington feeding aggregation. The 1999 survey showed that humpback whales were widely distributed along the Central American coast at relatively low densities. The extensive distribution of animals, the higher proportion of calves, and the almost exclusive migration to a single feeding area contrast with observations in other regions.

Key words: humpback whale, *Megaptera novaeangliae*, Central America, migration, breeding area, regional fidelity.

During winter, humpback whales worldwide use warm, shallow waters, often near island groups or offshore reefs (Dawbin 1966, Whitehead and Moore 1982, Clapham

and Mead 1999). The presence of small calves is typical in these areas, as are behaviors associated with mating, such as competitive groups (Tyack and Whitehead 1983, Baker and Herman 1984, Clapham *et al.* 1992) and song production (Payne and McVay 1971, Winn and Winn 1978). Wintering areas are often low in productivity; consequently whales generally do not feed at this time.

In the North Pacific, the number and ranges of humpback whale breeding grounds are currently being debated and refined. Movement and genetic research suggest more divisions than the previous long-held division of three areas: off Japan, Hawaii, and Mexico (Rice 1978). Humpback whales were killed off Central America during 19th century whaling (Townsend 1935), but it was not until the late 1980s that photo-identification revealed humpback whales occurred in this area and they were part of the California–Oregon–Washington feeding aggregation (Steiger *et al*. 1991, Acevedo and Smultea 1995, Flórez-González *et al*. 1998, Calambokidis *et al.* 2000, May-Collado *et al.* 2005, Rasmussen 2006). The waters off Central America are now considered as a distinct North Pacific breeding region (Calambokidis *et al*. 2000; Barlow *et al*., in press). Interestingly, this area is also inhabited by breeding humpback whales in the austral winter; it is the only known whale-breeding habitat that is shared by whales from two different hemispheres (Rasmussen *et al*. 2007).

Here, we examine the distribution, habitat use, and migratory destinations of humpback whales in this wintering area off Central America during the boreal winter between 1996 and 2003. We compare these to other humpback whale wintering areas in the North Pacific basin.

Methods

Boat Surveys

Our primary area of effort was off the northwest side of the Osa Peninsula, off southwestern Costa Rica (Fig. 1). Surveys were conducted for 1–3 wk annually in January and March between 1996 and 2003. Two small boats (5–7 m in length) covering different areas were used each survey day. Other small-boat surveys were conducted in the Gulf of Chiriqui in Panama (2001–2003) and northern Costa Rica (1999–2003). One additional survey was conducted in 1999 along Guatemala, El Salvador, Nicaragua, and northern Costa Rica from a 17 m sailboat with a deployable 4 m inflatable boat and an observation platform 7.6 m above the water's surface. All surveys were conducted over the continental shelf in water depths less than 1,000 m. During small-boat surveys, between two and eight observers were on board with at least one standing at the bow of the boat. Our primary goal was photo-identification; therefore, survey coverage was not systematic. Areas where humpback whales were previously sighted were targeted to increase sighting chances and as much additional area as possible was surveyed to examine distribution.

Data Collection

Time, latitude and longitude, weather, sighting conditions, group size, group composition, and behaviors were recorded every 30 min, and whenever marine mammals were encountered. Group composition was defined as single, pair, more than two adults, mother/calf, mother/calf and another adult (called an escort, Herman and Antinoja 1977), mother/calf with more than one escort. Behaviors included slow travel, fast travel, milling, stationary, singing, competitive behavior, and

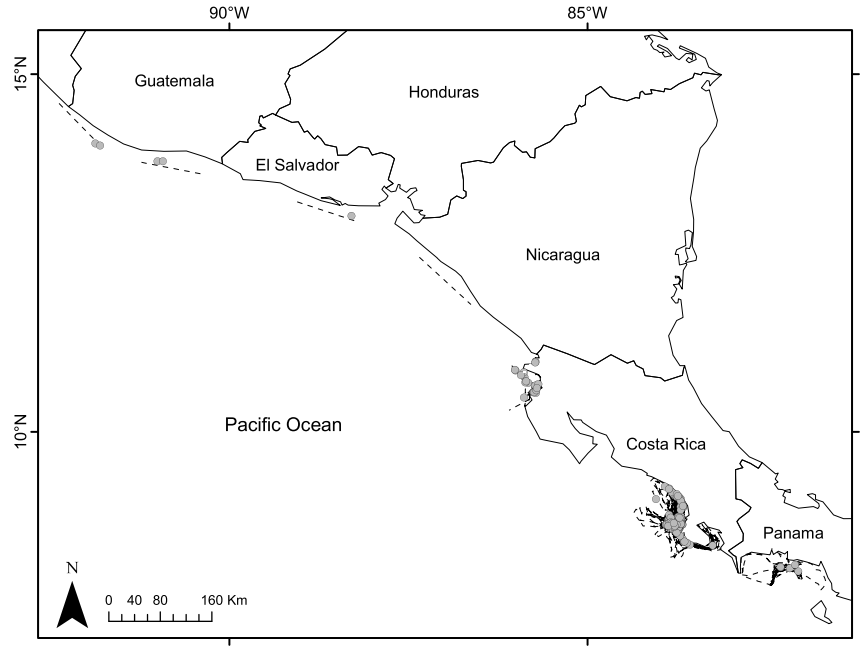

Figure 1. Survey effort and humpback whale sightings off Central America during the boreal winter 1996–2003. Dashed lines show survey tracklines, circles represent sightings.

classifications of any acrobatic behaviors such as breaching, pectoral slapping, and tail lobbing. Multiple behaviors could be recorded in one sighting. Singing was defined as a whale vocalizing continuously for >10 min repeating phrases and themes (Payne and McVay 1971). Competitive groups were defined as groups of greater than three adults exhibiting aggressive behaviors toward each other. These groups typically contain one female and multiple males competing to mate with the female, although calves may be present (Tyack and Whitehead 1983). The underside of tail flukes was photographed when possible to identify individual whales (Katona and Whitehead 1981). Prior to 2002, 35 mm cameras equipped with a motor drive, 300 mm telephoto lenses, and high-speed black and white Ilford HP5+ film were used. Since 2002, digital SLR cameras were used with various telephoto lenses. Additionally, 17 identification photographs were submitted by collaborators and naturalists working in the area.

Photographs of individual whales (identification photographs) were compared with Cascadia Research Collective's (CRC) catalog of whales identified off California, Oregon, and Washington between 1986 and 2003 ($n = 1{,}437$) (Calambokidis and Barlow 2004).

Acoustic monitoring for humpback whale song was conducted every half hour with a deployed hydrophone to locate whales, and when whales were sighted to detect if any were singers. Between 1996 and 2000, a hydrophone designed by Offshore Acoustics with a sensitivity of −154 dBV/uPa ± 4 dB at 100 Hz, and frequency response from 6 Hz to 14 kHz of ± 3 dB was used. Starting in 2001, hydrophones designed by Cetacean Research Technology with a sensitivity of −180 dBV/uPa ± 4 dB,

and a frequency response from 0.02 kHz to 60 kHz, and from 100 kHz to 250 kHz also were used. Some singing whales could be heard through the hull of the boat without the aid of the hydrophone. Due to the relatively low density of animals in our study area, it was not difficult to identify which individual was singing.

Data Analysis

Yearly encounter rates (whales seen per kilometer surveyed per year) were calculated for the three primary subregions surveyed (northern Costa Rica, southern Costa Rica, and Panama) to give an index of relative density and adjust for bias in areas of higher effort.

All survey effort and sightings were mapped using ArcGIS version 9.2 (ESRI 2006). Water depths at each sighting were obtained from the SRTM30_PLUS global topography product version 3.0 (18 December 2007). The product has a grid resolution of 30 arc seconds (~1 km), and is available on line from the Institute of Geophysics and Planetary Physics at the Scripps Institution of Oceanography (http://topex.ucsd.edu/). Seafloor data were based on the Smith and Sandwell (1997) bathymetry, version 9.1 (1 arc minute resolution). To account for the relatively low spatial resolution of the data, analyses on depth were done by grouping sightings into 10 m depth bins.

Satellite-derived sea surface temperatures (SST) for each of the three main regions where humpback sightings occurred (northern Costa Rica, southern Costa Rica, and Panama), were obtained from the NOAA/NASA AVHRR Oceans Pathfinder program (http://poet.jpl.nasa.gov/). The product used is the 8 d, 4 km resolution data (ascending pass and descending passes were combined to increase coverage). A single SST value was computed for each area and survey period from the 8 d averages.

All statistical analyses were conducted using Systat v. 10. Tests for equal variances were performed on the residuals using Cochran's test, and normal distribution of data was tested using the Kolmogorov–Smirnov test (Zar 1999).

RESULTS

Sightings

A total of 191 sightings were made of 320 individual humpback whales between 1996 and 2003. Group size ranged from 1 to 5, with a mean group size of 1.69 (±0.80 SD). The proportion of sightings of single whales, pairs, singers, and groups with calves were similar, all between 23% and 27% (Table 1). Singers were always singles. Virtually absent from our sample were sightings of competitive groups; only two sightings occurred, in 1996 and 2002, and none of these were more than five individuals. Groups greater than two animals that did not include calves also were rare.

Behaviors ($n = 276$) were recorded for 201 sightings. Of these, the most common were slow travel (35%), milling (18%), acrobatic activities, such as breaching, pectoral slaps, and tail lobbing (19%), fast travel (9%), and stationary (7%). On one occasion, in February 2003 off northern Costa Rica, a mother with a small calf nearby was seen feeding on unidentified small schooling fish. It was seen on its side with its mouth open and throat pleats extended.

Table 1. Group composition of humpback whale sightings in the study area off Central America, 1996–2003 including total sightings (number) and overall percentage (%) for each category. Groups were only counted one time in this analysis, that is, lone singers were not counted as singles.

	Total	
Group composition	Number	Percent (%)
Lone singers	45	24
Singles	43	23
Adult pairs	44	23
Mother/calf	31	16
Mother/calf/escort	21	11
Groups larger than two no calf	3	1.6
Competitive groups	2	1
Undetermined	2	1
Total groups with calf	52	27
Total	191	

Whales were observed throughout the study area with the highest encounter rates off northern Costa Rica and the lowest off Panama (Table 2, Fig. 2). Distribution of whales in the primary study area off southern Costa Rica was associated with bathymetry and distance from shore (Fig. 3). Whales seen between the mainland and Canos Island were roughly within the 50 m depth contour. North of this area, whales were primarily seen near shore in depths less than 50 m. Along the Osa Peninsula, whales were seen along the southwestern edge where the slope is shallow, but no sightings occurred where the slope was steeper (Fig. 3).

Seventy-five percent of all sightings occurred in depths <50 m. The mean depth of all sightings was 42 m (SD $\pm$ 20, $n = 191$). The mean depth for sightings containing a calf was 36 m (SD $\pm$ 20, $n = 51$) and for singers was 42 m (SD $\pm$ 19, $n = 35$). Calves accounted for the highest number of sightings in depth bins <30 m, and singers accounted for the most between 30 and 50 m (Fig. 4). Groups containing a calf were more frequently encountered in 10 m depth than were groups without calves ($\chi^2 = 201.81$, df $= 10$, $P < 0.0001$). There were no significant differences found between the depths of sightings of singers and all other sightings ($\chi^2 = 10.31$, df $= 10$, $P = 0.41$).

Average sea surface temperature in all regions surveyed during all years was 28.6°C (SD $\pm$ 1.0).

Photo-Identification

Identification photographs were taken on 151 occasions of 77 unique individual humpback whales (Table 3). Of the 77 individuals, 44 (76%) were seen in 1 yr only, nine (16%) were seen in two separate years, four (7%) during 3 yr, and one (2%) individual was seen in 4 yr. The mean number of days an individual was seen in 1 yr was 1.4 (SD $\pm$ 0.9) and the greatest number of days was five. The longest duration a whale was seen (time between first and last sighting) was 17 d.

A within-year movement between subregions was documented once. Whale (CRC ID number 10411) was seen off southern Costa Rica on 6 and 7 February 2002. This whale was also photo-identified by biologist Carolina Garcia Imhof 10 d later, off

Table 2. Survey effort, including dates, total kilometers surveyed, and humpback whale sightings, including total sightings and number of whales seen, number of calves seen, and encounter rates off Central America 1996–2003.

		Survey effort			Humpback whale sightings				
Year	Region	Start date	End date	km	Sightings	Whales	Calves	Whales/km	Calves/km
2001	Panama	14 February	17 February	493	2	4	1	0.008	0.002
2002	Panama	22 February	27 February	626	1	1	0	0.002	0.000
2003	Panama	25 February	28 February	695	1	2	1	0.003	0.001
1996	S Costa Rica	26 January	16 February	2,927	15	19	0	0.006	0.000
1997	S Costa Rica	31 January	14 February	2,231	27	45	3	0.020	0.001
1998	S Costa Rica	24 January	18 February	3,211	18	25	2	0.008	0.001
1999	S Costa Rica	27 January	7 February	2,313	32	60	19	0.026	0.008
2000	S Costa Rica	25 January	13 February	3,219	29	46	6	0.014	0.002
2001	S Costa Rica	24 January	11 February	3,685	28	59	13	0.016	0.004
2002	S Costa Rica	6 February	14 March	1,556	11	21	3	0.013	0.002
2003	S Costa Rica	29 January	7 February	1,145	6	8	1	0.007	0.001
1999	N Costa Rica*	2 March	10 March	67	8	12	2	0.180	0.030
2000	N Costa Rica	23 January	24 January	57	1	1	0	0.017	0.000
2001	N Costa Rica	19 January	21 January	219	3	4	0	0.018	0.000
2002	N Costa Rica	8 March	10 March	248	2	3	1	0.012	0.004
2003	N Costa Rica	11 March	14 March	241	2	3	1	0.012	0.004
1999	Nicaragua*	1 March	1 March	107	0	0	0	0.000	0.000
1999	El Salvador*	28 February	28 February	100	1	2	0	0.020	0.000
1999	Guatemala*	26 February	27 February	191	4	5	0	0.026	0.000
			Total	23,330	191	320	53	0.014	0.002

*Surveys in 1999 were done from an 18 m sailboat, so observation methods differed.

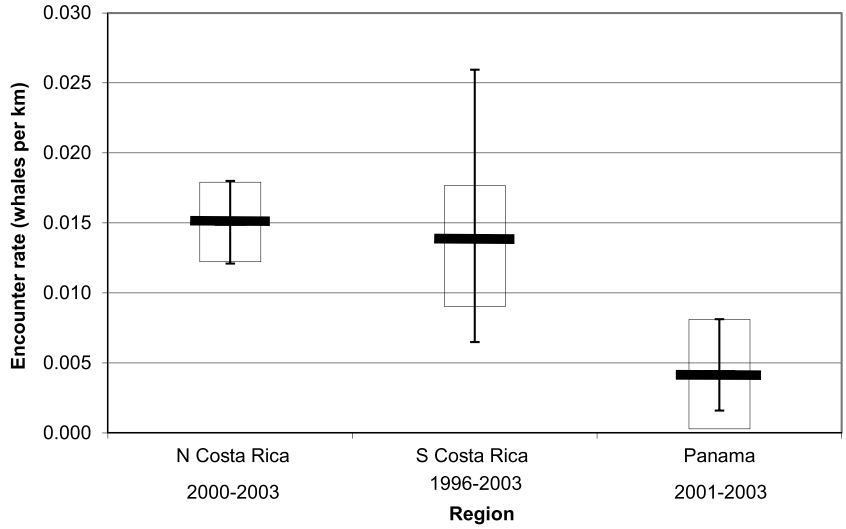

Figure 2. Mean annual encounter rates by region. Boxes represent the 95% confidence intervals, vertical bars represent the minimum and maximum encounter rates, and solid horizontal lines represent the means.

Bahia Honda, Panama.[1] This is a minimum distance of 288 km. This whale was seen with another adult whale in both sightings.

Of the 77 individuals seen off Central America, 69 whales (or 90%) had also been photo-identified off California–Oregon–Washington (Table 3). Fifty individuals were seen off Costa Rica and California–Oregon–Washington in consecutive seasons at least once, some of them in multiple years. One whale (CRC ID 11408) was seen for two consecutive years off Costa Rica, and following each of those years off California.

The shortest time interval between when an individual was seen off California and off Costa Rica was 56 d. Whale CRC ID 9031 was seen off northern California on 1 December 1995, then again on 26 January 1996 off Costa Rica. The migration time was likely shorter assuming the whale had not been photographed on the day it left California and when it arrived in Costa Rica. The distance between these two points is 5,200 km, therefore a minimum migration rate of 93 km/d, or at least 3.9 km/h. Previous migration rates have been documented by Gabriele *et al.* (1996) between Alaska and Hawaii at 4.74 km/h. The farthest documented distance we observed was a whale that traveled, in one season, 5,427 km between Pt. St. George, northern California (seen on 6 October 1998), and Costa Rica (seen on 6 February 1999).

Of the 77 whales identified off Central America, sex was determined for 28, either from sightings off Central America or sightings and genetic information off California–Oregon–Washington. Ten individuals were identified as females because they were seen with calves, eight of these off California and two off Central America. Eighteen individuals were males, 15 were heard singing off Central America, which

[1]Personal communication from Carolina García Imhof, Fundación MarViva, Calle 98 #8–19 Interior 102, Bogotá, Colombia, June 2002.

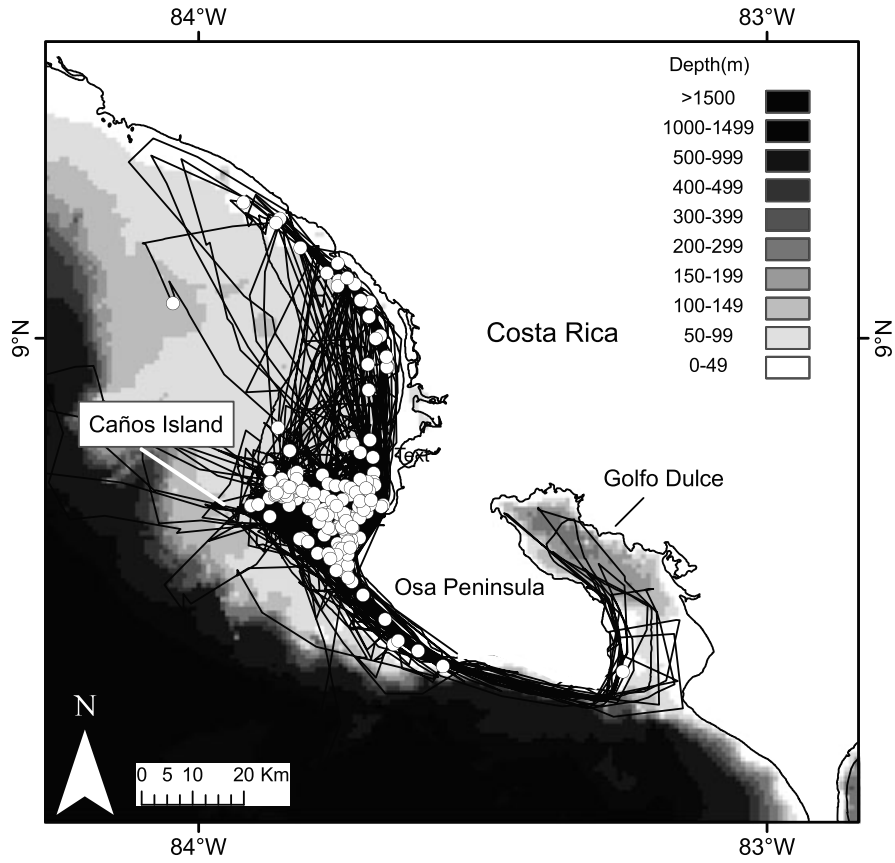

Figure 3. Humpback whale sightings (indicated by circles) and small-boat survey effort (indicated by black lines) over bathymetry off southern Costa Rica.

is a behavior known only for males (Winn and Winn 1978, Glockner 1983), and three were determined as males using genetic samples collected off California (Baker *et al.* 1991).

Discussion

Humpback whales were distributed throughout the survey area off Central America, although encounter rates varied between regions. In general, the encounter rates during boat surveys indicated that humpback whales were not particularly abundant but were, however, broadly distributed along almost the entire Central American Pacific coast.

This study reports one of the highest percentage of groups with calves (27%, other studies ranged from 8% to 28%; Mobley and Herman 1985, Mattila and Clapham 1989, Mattila *et al.* 1989, Garrigue *et al.* 2001, Hauser *et al.* 2000, Zerbini *et al.* 2004, Felix and Botero-Acosta 2011). While it is possible that our results are

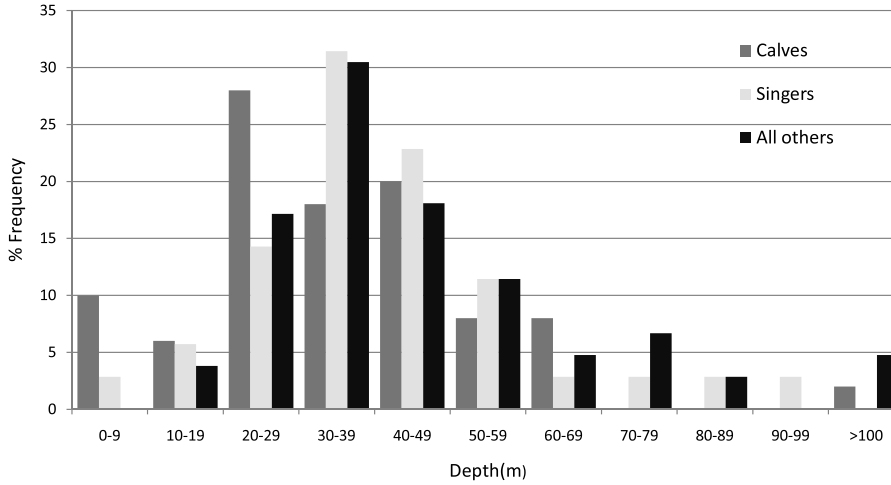

Figure 4. The depth distribution of all humpback whale sightings shown by using the total percentage of sightings in 10 m depth bin categories which included calves, singers, and all other group types ($n = 191$ sightings).

biased by the limited geographic range and nearshore emphasis of our surveys, the prevalence of mothers with calves in this region makes evident the importance of this habitat to reproductive females. A high reproductive rate is probably not the reason for our findings, based on trends in abundance and reproductive rates for this population compared to others in the North Pacific (Steiger and Calambokidis 2000). Segregation by age class may occur in this region as humpback whale mothers and calves have been found to favor particular regions off Hawaii (Craig and Herman 2000).

Table 3. Results of photographic identification research of humpback whales off Central America 1996–2003. ID's is the total number of identification photographs taken each year including resightings of individuals, unique whales is the number of unique individual whales of the total identifications, new whales are whales that had not been identified in previous years, no. matching the California Oregon Washington feeding area (CA/OR/WA) are total number that have also been identified off CA/OR/WA, % matching CA/OR/WA is the percentage of whales identified that year that have also been seen off this feeding area.

Year	ID's	Unique whales	New whales	No. Matching CA/OR/WA	% Matching CA/OR/WA
Pre-1996	5	5	5	4	80%
1996	16	13	12	10	83%
1997	19	11	10	8	80%
1998	12	7	4	3	75%
1999	28	21	20	20	100%
2000	26	12	7	7	100%
2001	25	16	11	9	82%
2002	11	7	6	6	100%
2003	9	8	2	2	100%
All years	151	77		69	90%

The high proportion (90%) of whales identified off Central America that had also been identified off California–Oregon–Washington suggests that whales from this breeding area almost exclusively inhabiting a single feeding area. This high proportion of matching is higher than the percentage of matches found between years within this feeding aggregation.[2] If whales were migrating to Central America from other feeding areas, we would likely not see such a high match rate to California–Oregon–Washington. All other areas, North Pacific wintering areas, are comprised of whales from several different feeding areas. Whales off Japan were seen off British Colombia and Kodiak Island (Calambokidis *et al.* 2001). Whales off Hawaii have been seen off northern British Colombia, southeast Alaska, Prince William Sound, Kodiak Island, and Shumagin Island (Calambokidis *et al.* 2001). Whales off Mexico have been seen in areas used for feeding off California–Oregon–Washington, British Columbia, southeast Alaska, Prince William Sound, and the western Gulf of Alaska (Urbán *et al.* 2000; Calambokidis *et al.* 2001).

Whales identified off Central America are mostly migrating from the southern range of the California–Oregon–Washington feeding area. When compared to whales from both Mexico and Central America that were known to migrate to feeding areas off California–Oregon–Washington, whales from Central America were three times more likely to be seen in Southern California than those migrating from Mexico, while they were less than half as likely to been seen in northern waters than those sighted off Mexico (Calambokidis *et al.* 2000).

The mean sea surface temperature of 28.6°C for the Central America region is higher than the overall average for all humpback whale wintering areas worldwide (24.6°C ± 1.9 SD), and higher than the other wintering areas in the North Pacific (21.60°C–24.32°C) (Rasmussen *et al*. 2007). At the basin scale, Rasmussen *et al*. (2007) demonstrated a direct correlation between water temperature and location of humpback whale wintering areas, suggesting that warmer waters are an important factor driving humpback whale migration. However, other factors might influence their distribution on a finer scale, including depth (Felix and Haase 1997, Ersts and Rosenbaum 2003), availability of suitable reproductive habitat, and intrinsic population parameters.

In addition to having warmer water temperatures, Central America is also the southernmost humpback whale wintering area in the North Pacific. The majority of our sightings took place around 9°N (all sightings ranged between 8°N and 14°N), whereas the mean latitude for wintering areas off both Mexico and Hawaii are at 20°N, and Japan is at 26°N.

Humpback whales were sighted in habitat similar to what has been described at other wintering areas. The majority of sightings were in depths of <50 m, which has been documented elsewhere (Winn *et al*. 1975, Herman and Antinoja 1977, Whitehead and Moore 1982). Singers were found in deeper depths, with higher frequencies of sightings at 30–50 m. Frankel *et al.* (1995) found that singers off Hawaii were not necessarily limited to the shallower waters, possibly due to acoustic conditions or social factors. Groups with a calf were largely found in shallower waters, which is consistent with other studies (Whitehead and Moore 1982, Smultea 1994,

[2]Calambokidis J., E. Falcone, A.B. Douglas, L. Schlender, and J. Huggins. 2009. Photographic identification of humpback and blue whales off the U.S. West Coast: Results and updated abundance estimates from 2008 field season. Final Report for Contract AB133F08SE2786 from Southwest Fisheries Science Center (unpublished). 18 pp. Available at http://www.cascadiaresearch.org.

Felix and Haase 1997, Craig and Herman 2000, Martins *et al.* 2001, Ersts and Rosenbaum 2003, Felix and Botero-Acosta 2011).

While there are similarities to other wintering areas, there are several aspects that make this wintering area interesting. The waters are farther south and warmer than any other wintering area in the North Pacific. Whales seen here are all migrating from the California–Oregon–Washington feeding area, which is in contrast to other wintering areas, where whales from different feeding areas intermix. This same area is also inhabited by humpback whales from the austral population during the opposite winter season, resulting in spatial overlap between Northern and Southern Hemisphere populations not seen anywhere else in the world (Rasmussen *et al*. 2007). Considering the current debate by marine mammalogists about the reason for why humpback whales migrate (*e.g*., Corkeron and Connor 1999, Clapham 2001), the characteristics of this region may provide future insights into the behavioral ecology of humpback whales.

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