COMPARISON OF TWO DISTINCT HUMPBACK WHALE POPULATIONS (*MEGAPTERA NOVAEANGLIAE*) OFF PACIFIC CENTRAL AMERICAN WATERS

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Comparison of two distinct humpback whale (*Megaptera novaeangliae*) populations off Pacific Central America

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Humpback whales make long annual migrations between high-latitude areas used for feeding during summer, and low-latitude areas used for breeding during winter. Humpback whales from two distinct populations use an area off the Pacific coast of Central America during their winter. Surveys were conducted off Central America between 1996 and 2004 during the boreal winter, and between 2001 and 2004 during the austral winter. Comparisons of sightings from both seasons indicated that spatial overlap occurred between 11.05°N and 8.05°N. Mean encounter rates (whales seen per kilometer surveyed) were greater for the austral season. Photo-identification results indicated that whales during the boreal winter were migrating from feeding areas off California, and whales during the austral season were migrating from feeding areas off Antarctica. A review of sea surface temperatures of areas used by humpback whales during winter indicated that humpback whales sought waters greater than 24°C.

DEDICATION

Dedicated to the memory of Peggy Rasmussen King (1957-2005)
and to Larry, Megan, Crockett and Leonard for their courage and grace

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CHAPTER ONE

Distribution and migratory destinations of humpback whales off Central America during the boreal winters of 1996-2004

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INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is found in all the major ocean basins, and makes annual migrations between summertime areas in productive waters of high latitudes used for feeding and wintertime areas of low latitudes where they mate and calve. Historical whaling records provided information on worldwide distribution of humpback whales (Townsend 1935), whereas discovery tags used during whaling contributed to knowledge of their migratory destinations (Chittleborough 1965). Modern research techniques have added to this information, including photo-identification (Katona and Whitehead 1981), satellite tagging (Mate *et al*. 1998), and genetics (Baker *et al*. 1994, Baker and Medrano-Gonzalez 2002).

Humpback whale populations were decimated during the whaling era until a worldwide moratorium was established in 1966. Since then, most populations have slowly increased. Rice (1978) crudely estimated the North Pacific population of humpback whales before whaling as 15,000 individuals, and the post whaling population was roughly 1,000 individuals. The most recent population estimate for the North Pacific is between 6,000 and 10,000 whales (Calambokidis *et al.* 1997).

During winter, humpback whales 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). Areas used during winter typically are low in productivity, consequently whales generally do not feed at this time.

In the North Pacific, there are three major areas used during winter: several island groups in Asia south of Japan (Nishwaki 1959, Darling and Mori 1993, Uchida *et al.* 1993); Hawaii (Herman and Antinoja 1977); and Mexico (Urban and Aguayo 1987, Alvarez *et al.* 1990). Areas used for feeding occur along the coast of the North American continent, from the Southern California Bight northward to the Aleutian Island chain and west to Russia. Within this range, feeding occurs off California to Washington with minimal interchange with other feeding groups to the north, (Baker *et al*. 1990, Calambokidis *et al*. 1996, Baker *et al*. 1998). Other areas of feeding occur off British Columbia (Darling and McSweeney 1985), southeast Alaska, Prince William Sound, Kodiak Island, and along the Aleutian Island chain (Darling and McSweeney 1985, Perry *et al*. 1990, Baker *et al*. 1994, Calambokidis *et al*. 1996, Darling *et al*. 1996, Barlow and Clapham 1997). It remains unclear how these areas can be divided into separate feeding populations and how much interchange occurs amongst them (Calambokidis *et al*. 2001).

Whales usually migrate between a specific area used for feeding and a specific area used during winter. There is little interchange between areas used for feeding as indicated by interchange of photographically-identified individuals and genetic analysis among feeding areas (Baker *et al.* 1990, 1994, Calambokidis *et al*. 2001). Although humpback whales have greater site fidelity for areas used for feeding than areas used during winter, there is a small degree of interchange between areas used during winter (Baker *et al.* 1986, Darling and Jurasz 1983, Darling and McSweeney 1985, Darling and Cerchio 1993, Perry *et al.* 1990, Calambokidis *et al.* 2001).

An additional area used during winter in the North Pacific exists off Central America (Steiger *et al*. 1991, Rasmussen *et al*. 1995, Calambokidis *et al.* 2000). Whaling records indicated humpback whales were seen off Central America during the austral winter (Townsend 1935). More recently, humpback whales have been reported off Costa Rica (Steiger *et al*. 1991, Acevedo and Smultea 1995, May-Collado *et al.* 2005) and off Panama (Flórez-González 1998) during the boreal winter, indicating that this area was potentially shared by populations from two different hemispheres at different times of year. Few studies have been conducted off Central America to assess its use during winter by humpback whales from either the northern or southern hemispheres.

The goals of this study were to determine the distribution and migratory destinations of humpback whales seen off Central America during the boreal winter (December-April), and determine if this was a typical breeding area in terms of habitat and behavior. Our hypotheses were; (1) whales seen off Central America during the boreal winter were migrating from areas used for feeding in the North Pacific, likely California, and (2) Central America was a typical wintering area as indicated by behaviors, habitat use, and presence of small calves.

METHODS

This study was conducted off the Pacific coast of the Central American Isthmus, in the eastern tropical Pacific (Fig. 1). This region is characterized by a complex series of currents and upwellings, and is bordered by two of the largest upwelling systems in the world; the California Current to the north, and the Humboldt Current to the south. The coastal area has three localized coastal upwelling plumes that occur in winter; the Gulf of Tehuantepac, the Gulf of Papagayo, and the Gulf of Panama. These upwelling plumes are a result of winds formed by geostrophic flow through mountain passes associated with high pressure systems in the Gulf of Mexico (McCreary *et al.* 1989); these localized systems can significantly decrease sea surface temperatures by 10°C and increase primary productivity (Roden 1961, Gonzalez *et al.* 2004). In general, the surface waters off the Pacific coast of Central America are classified as Tropical Surface Waters, with relatively lesser salinities (<34 psu), greater temperatures (>27° C), and lesser variation in seasonal temperature (Fiedler 1992).

The continental shelf off Central America is relatively narrow with a steep slope. The shelf is virtually absent off southern Mexico until the Gulf of Tehuantepac. Between the Gulf of Tehuantepac and the Gulf of Papagayo the shelf is narrower than 100 km. South of Papagayo it narrows again to widths less than 50 km until the Gulf of Panama. The Middle American Trench is what delineates the continental shelf, thus deep water can be found relatively near the coastline (Bakun *et al.* 1999).

Our primary area of effort was off the northwest side of the Osa Peninsula, off southwestern Costa Rica (Fig. 1). Surveys were conducted from 1996 to 2004 in small boats (5-7 meters in length), many of these in collaboration with Oceanic Society Expeditions and Elderhostel. Two boats were used every day for these surveys, and each boat covered a different area. Other small boat surveys were conducted in the Gulf of Chiriquí in Panama (2001-2003), northern Costa Rica (1999-2004), Nicaragua (2004), El Salvador (2004), and Guatemala (2004; Fig. 1). All surveys in 2004 were part of the SPLASH (Structure of Populations, Levels of Abundance and Status of Humpbacks) project, a North Pacific basin-wide project on humpback whales. One additional survey was conducted in 1999 along Guatemala, El Salvador, Nicaragua, and northern Costa Rica from a 17-meter sailboat with a deployable 4-meter inflatable boat. Observations from this survey occurred from two crow's nests 7.6 meters off the water's surface. All surveys were conducted over the continental shelf in water depths less than 1000 meters. During surveys, between two and eight observers were on board, and at least one was standing at the bow of the boat. Our primary goal was photo-identification; therefore, survey coverage was not systematic. Due to visibility limitations of small boats, areas where humpback whales were previously sighted were targeted to increase sighting chances. However, we also surveyed as much area as logistically possible to effectively determine distribution.

Data were collected every 30 minutes, and whenever marine mammals were encountered. Data collected included: time, latitude and longitude using a handheld Global Positioning System, weather and sighting conditions, group size, group composition, and behaviors. Group composition was defined as single, pair, more than two adults, mother/calf, mother/calf and another adult (called an escort), mother/calf with more than one escort. Behaviors included slow travel, fast travel, milling, stationary, singing, competitive behavior, and classifications of any aerial 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 greater than 10 minutes. Competitive groups were defined as groups of greater than three adults exhibiting aggressive behaviors towards each other. These groups typically contain one female and multiple males competing to mate with the female. Calves may be present in these competitive groups (Tyack and Whitehead 1983). We photographed the underside of tail flukes when possible to identify individual whales (Katona and Whitehead 1981). We used *Nikon* 35mm cameras equipped with a motor drive, 300mm telephoto lenses, and a high speed black and white film *Ilford* HP5+. Since 2002, *Nikon* D100 digital SLR cameras were used with telephoto lenses. Seventeen identification photographs also were submitted by contributors.

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

Acoustic monitoring of humpback whale songs was conducted every half hour. Between 1996 and 2000 a hydrophone designed by Offshore Acoustics was used. This hydrophone had a sensitivity of -154 dBV/uPa ± 4 dB at 100 Hz, and frequency response from 6 Hz to 14 kHz of ± 3 dB. Starting in 2001, hydrophones designed by Cetacean Research Technology also were used, with a sensitivity of -180 dBV/uPa ± 4 dB, and a frequency response from 0.02 kHz to 60 kHz, and 100 kHz to 250 kHz. When a song was heard, we recorded at least 30 minutes of song onto a Digital Audio Tape (DAT) using a Sony TCD-D7 or D8 DAT recorder (frequency response 20-14,000 Hz, 32 Hz sampling rate). We photographed the singer when possible.

We conducted four aerial surveys in February and March 2002 covering the entire Pacific coast of Costa Rica, and the western Pacific coast of Panama (Fig. 2). Surveys were conducted in collaboration with Lighthawk, a volunteer-based aviation organization based in Lander, Wyoming. Surveys were conducted using a single engine Cessna Turbo 206, at an altitude of 305 meters, and a speed of 100 knots. An observer was placed on either side of the plane, and a data recorder in the co-pilot seat observed when possible. When a sighting of a marine mammal occurred, we recorded time, location using a handheld GPS, group size, behaviors, and horizontal angle to the sighting using a Suunto clinometer.

Yearly encounter rates (whales seen per kilometer surveyed per year) were calculated for the three primary sub-regions surveyed [northern Costa Rica, southern Costa Rica (in this study 9°30'N divides northern and southern Costa Rica), and Panama] to indicate sightings per unit effort, adjust for bias of areas of greater effort, and to give an index of relative density. A single factor model I ANOVA (Zar 1999) was conducted on these mean yearly encounter rates amongst the three regions, and mean yearly encounter rates of singers and calves respectively amongst the three regions.

Water depths at each sighting were obtained using Global Digital Elevation Models from ETOPO2 (USDC 2001). These data provide gridded (2 minute by 2 minute) bathymetry derived from the National Geophysical Data Center Marine Geology and Geophysics dataset (ETOPO2) and University of California, San Diego, Seafloor Topography. Depth values for each sighting were grouped into 50-meter classes using ArcGIS version 9 (ESRI 2004), and all analyses were conducted on these groups to account for the relatively low resolution of the data. All values were compared with nautical charts and personal knowledge of the area to determine whether the values were reasonable. Chi-square analyses were conducted on types of whale groups in each 50 meter water depth bin (Zar 1999).

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 eight-day, 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 eight-day averages.

Regression analyses were conducted on SST and yearly encounter rates for southern Costa Rica to test the effect of SST on encounter rates (Zar 1999). ANCOVA analyses were conducted to test the relationship between encounter rates, SST, and region for the common years surveyed in all regions (2001-2003) (Systat v.10).

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

We had 229 sightings of 378 humpback whales. Whales were sighted throughout the study area with some variation in encounter rates among regions. The greatest encounter rates occurred off northern Costa Rica, decreasing southward with the least encounter rates off Panama (Table 1, Fig. 3). Differences in mean encounter rates among the three most surveyed regions (northern Costa Rica, southern Costa Rica, and Panama) were not significant (ANOVA, F=2.993, P=0.08).

Group size ranged from 1 to 7, with a mean group size of 1.68 (±0.80 SD). The proportion of sightings of single whales, pairs, singers, and groups with calves were similar, all between 21% and 28% (Table 2). Virtually absent from our sample were sightings of competitive groups. Only three sightings of competitive groups occurred, in 1996, 2002, and 2004, and none of these were more than 5 individuals. Groups greater than 2 animals that did not include calves also were rare. There were no significant differences among regions in encounter rate of calves (ANOVA, F = 0.698, P=0.52) or encounter rate of singers (ANOVA, F= 1.352 P=0.29).

Behaviors (n=322) were recorded for 229 sightings. Of these, the most common were slow travel (34%), milling (18%), and acrobatic activities, such as breaching, pectoral slaps, and tail lobbing (18%). Friendly behaviors, such as close approaches to the boat, were recorded 4% of the time. Fast travel and stationary animals were observed 8% of the time. On one occasion, in February 2003 off Playas del Coco in northern Costa Rica, a whale was seen feeding on unidentified small schooling fish. The whale was seen on its side with its mouth open and throat pleats extended, which is indicative of feeding. This was a cow, with a small calf nearby.

Average sea surface temperature in all regions surveyed during all years was 28.3° C (±1.0 SD). The maximum mean yearly temperature (30.1°C ± 0.1 SD) in any region was off southern Costa Rica in 1998 (an El Niño year). The minimum temperature (26.3°C ± 0.6 SD) was off northern Costa Rica in 2000, a La Niña year (Table 1). Regression analysis indicated there was no significant relationship between encounter rates and sea surface temperatures off southern Costa Rica (r^2=0.313, P=0.15). There also was no significant interaction between sea surface temperature and year for the common years (2001-2003) surveyed in all three regions (ANCOVA, F=0.215, P=0.82), and no effect of year on encounter rate (ANOVA, F=0.211, P=0.82)

The majority of sightings occurred at locations where water depths were ≤ 50 meters, and most effort was in this depth category (Fig. 4). This sighting trend was similar for groups containing calves, and for singers. For sightings that occurred between 51 and 100 meters depth, singers were more common than all other groups, and calves were more common in the 0-50 meter depth category than elsewhere. These differences were significant for calves (x^2= 12.09, df=5, P=0.03) and highly significant for singers (x^2 = 134.448, df=5, P<0.0001) when group types within each 50 meter category were compared with each other (Fig. 4).

Distribution of whales off southern Costa Rica (area of greatest effort) was associated with bathymetry and distance from shore (Fig. 5). Whales seen between the mainland and Caños Island were roughly within the 50-meter depth contour, which forms a triangle from the mainland with the point being Caños Island. North of Caños Island, whales were primarily seen near shore. 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. 5).

Four sightings of five humpback whales occurred during aerial surveys. All sightings were off northern and central Costa Rica (Fig. 2). Three sightings were of single animals, and one sighting was a pair of adults.

Photo-Identification

Identification photographs were taken on 174 occasions of 92 unique individual humpback whales (Table 3). Of the 92 individuals, 18 were seen multiple years; 74 (80%) were seen in one year only, 11 (12%) were seen in two separate years, 6 (7%) during three years, and one (1%) individual was seen in four years. The greatest number of days a whale was seen in one season was 5 days. The greatest duration a whale was seen during one season was 40 days.

Within-year movements between sub-regions were documented twice. One whale, CRC ID #10753 was seen off southern Costa Rica on 9 February and 9 March 2004. It was seen 12 days later on 21 March off northern Costa Rica, a minimum distance of 330 kilometers. Both times it was seen alone. Another whale (CRC ID #10411) was seen off southern Costa Rica on 6 and 7 February 2002. This whale was also seen by Carolina Garcia (pers. comm.) 10 days later, off Bahia Honda, Panama. This is a minimum distance of 288 kilometers. For these sightings, this whale was seen with another adult whale.

Of the eighteen whales seen in multiple years, seven whales were sighted in different sub-regions in different years. Five of these were between northern and southern Costa Rica, one between southern Costa Rica and Panama, and one between southern Costa Rica and Nicaragua.

Of the 92 individuals seen off Central America, 80 whales (or 87%) were seen off California and Oregon (Table 3). Fifty-six individuals were seen off Costa Rica and California in consecutive seasons at least once, some of them multiple years. One whale (CRC ID 11408) was seen for two consecutive years off Costa Rica, and following each of those years off California, demonstrating that it completed this round trip migration from Central America to California at least one and a half times.

The fastest migration noted between California and Costa Rica was 56 days. Whale CRC ID 9031was seen off northern California on 1 December 1995, then again on 26 January 1996 off Costa Rica. The distance between these two points is 5200 km, therefore a migration rate of 93 km per day, or 3.9 km per hour. The farthest documented distance a whale traveled in one season was 5,427 km between Pt. St. George, northern California (seen on 6 October 1998), and Costa Rica (seen on 6 February 1999).

Of the whales that have been identified off Central America and California, the majority migrated from southern and central California (Fig. 6). Whales seen off southern California were more likely observed later off Central America (12%) than off Mexico (6-8%). Whales off Monterey Bay, in central California, were equally likely to be seen off Mexico or Central America. Whales seen off northern California, Oregon, and Washington were more likely to be resighted off Mexico (John Calambokidis and Jorge Urbán, pers. comm.). No whales seen off northern Washington or British Colombia were seen off Central America.

Of the 92 whales we identified, we determined sex of 28, either from sightings off Central America or sightings and genetic information off California. Ten single adults were identified as females because they were seen with calves, 8 of these off California and two off Central America. Eighteen individuals were males, 15 due to singing, which is a behavior known only for males (Winn and Winn 1978), and three determined as males using genetic samples collected off California.

DISCUSSION

Humpback whales were distributed throughout the survey area off Central America, although our varying encounter rates indicated different relative densities among regions. The encounter rates off Panama and Costa Rica increased northward toward the areas used for feeding. Although this trend does not appear true for encounter rates north of Costa Rica, fewer surveys were conducted in this region, and these rates may not be as accurate. Further surveys in this area should help determine the trend of relative densities throughout Central America. Because estimating abundance was not a primary objective of this study, we were unable to estimate abundance with these data; however, the encounter rates during boat and aerial surveys indicated that humpback whales were not greatly abundant in the survey area.

The habitat where humpback whales were sighted was consistent with other areas used during winter. Almost 80% of our survey effort was in depths of less than 100 meters, and consequently most whales were found in water depths less than 100 meters, which is typical of other areas (Winn *et al*. 1975, Herman and Antinoja 1977, Whitehead and Moore 1982). Singers most notably varied from the distributional pattern of the other group types, with a greater proportion of them in the 50-100 meter depth category. 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 (Craig 2000, Ersts and Rosenbaum 2003, Felix and Haase 1997, Martins *et al.* 2001, Smultea *et al*. 1994, Whitehead and Moore 1982).

Most areas used during winter have sea surface temperatures between 24° and 28° C (Dawbin 1966, Herman and Antinoja 1977, Whitehead and Moore 1982). All sea surface temperatures in this study were within that range or greater. Temperatures off northern Costa Rica were the least, and temperatures increased southward towards Panama. The change in sea surface temperature did not to affect sightings and resulting annual relative densities of whales off southern Costa Rica. However, the temperature variation in this area is relatively minimal, and it is unlikely that we would detect a significant effect.

Our findings for group composition and behavior support our hypothesis that this is a relatively typical area used by humpback whales during winter. Repeated sightings of mother/calf pairs and the presence of singers strongly indicated that this area was used for mating and calving. The majority of our sightings were of single animals, pairs of adults, and singers, which is comparable with studies at other areas used during winter. Because most behaviors were milling, slow travel, and aerial behaviors, it is indicative that this area is not simply a migratory corridor where whales are passing through quickly.

There were two noticeable differences between our study and other studies at areas used during winter; we had the least percentage of competitive groups (1%, other studies ranged 2%-18%) and the greatest percentage of groups with calves (28%, other studies ranged 8%-27%; Mattila and Clapham 1989, Mattila *et al.* 1989, Mattila *et al.* 1994, Garrigue *et al.* 2001, Hauser *et al.* 2000, Zerbini *et al.* 2004). Competitive groups are formed when multiple males are vying for the opportunity to mate with a female, therefore, are an indication of mating behavior (Darling and Jurasz 1983, Tyack and Whitehead 1983, Baker and Herman 1984). Although we observed only three competitive groups, we saw a greater proportion of mother/calf/escort groups compared with these same studies. Escort behavior also is considered mating behavior, and likely is a prelude to a competitive group (Tyack and Whitehead 1983, Baker and Herman 1984). The lack of any large groups, competitive or otherwise, may be a result of the relatively lesser density of whales in this area. There may not be enough reproductively active males to form large competitive groups, which would explain greater numbers of escorts, and fewer competitive groups than typical for other areas.

Habitat partitioning by humpback whales during winter has been reported by other researchers. Cow/calf pairs are often found in shallower, near-shore waters (Whitehead and Moore 1982, Smultea 1994, Craig and Herman 2000, Martins *et al*. 2001, Felix and Haase 2001, Ersts and Rosenbaum 2003). This partitioning could occur because cow/calf pairs seek more protected waters away from the potentially dangerous competitive activity (Smultea 1994) that potentially can result in death (Pack *et al*. 1998). Costa Rica and Panama appear to be the southern limit for humpback whales from the northern hemisphere, with relative density decreasing southward. If mothers with calves sought areas of lesser densities and a decrease in potentially dangerous activity, it would make sense for them to move further south along the coast away from the potentially greater densities off Mexico. We did not find, however, any significant difference in calf distribution within the three regions off Costa Rica and Panama. Extending the study area further north into Central America and Mexico may help determine if this is mostly used as a nursery area.

Because our sample period was relatively short each year, it is difficult to make inferences about resident time for individual whales, and movements within these regions. The two movements of whales within a year between southern Costa Rica and Panama, and southern Costa Rica and northern Costa Rica, indicated there was some interchange between sub-regions. These two cases did not indicate any trend in directional movement (i.e. northerly or southerly movements).

Twenty percent of whales identified off Central America have been seen more than one year, suggesting that there is some degree of site fidelity to this area. Whales seen in multiple years in more than one sub-region however, indicated that these whales were not exhibiting site fidelity to sub-regions during winter. It is typical for humpback whales during winter to move among sub-regions when they are close together (Baker and Herman 1981, Darling and McSweeney 1985, Darling and Morowitz 1986, Cerchio *et al.* 1998, Calambokidis *et al.* 2001). Interchange among sub-regions occurs at a lesser rate when sub-regions are farther apart (Darling and Mori 1993, Uchida *et al.* 1993, Urban *et al.* 2000, Calambokidis *et al*. 2001). Further research off Mexico and Central America could help determine whether this should be considered one large area used during winter with a high degree of interchange throughout the region, or a large area comprised of smaller sub regions with a lesser degree of interchange.

The percentage of whales seen off both Central America and off California indicated that whales off Central America were likely migrating from areas where they feed off California. CRC has been conducting photo-identification studies off California since 1986. Eighty-five percent of whales photographed off California/Oregon/Washington annually have been identified in previous years. This is similar to our matching rate between California and Central America (87%). We suspect that due to population growth rate and lack of complete survey coverage, 15% of the California whales have not been identified, thus we would not expect to find 100% of whales off both California and Costa Rica.

All other areas used during winter in the North Pacific are used by 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 Colombia, Southeast Alaska, Prince William Sound, and the Western Gulf of Alaska (Urban *et al.* 2000). Because the California/Oregon/Washington area is the southernmost area used for feeding in the North Pacific, it is not surprising that these whales are migrating to the southernmost area used during winter.

Another noteworthy aspect of this migration between California and Central America is the different migratory destinations of whales. Whales off central and southern California are more likely to migrate to Central America, whereas whales further north off California are more likely to migrate to Mexico. This phenomenon of different migratory destinations due to location of feeding within a feeding aggregation has not yet been described for other areas.

Mixing of whales from several areas of feeding in the winter can be advantageous for gene flow among groups of humpback whales (Palsbøll *et al*. 1995, Baker *et al.* 1998). There probably is reduced gene flow in Central America because all whales are from California. However, because whales from California also migrate to Mexico (Calambokidis *et al*. 2000, Urban *et al.* 2000), an area used by whales from several different feeding populations, the reduced gene flow in the California populations is probably negligible.

The question remains: What drives migration to Central America? The tendency for whales from the southern portion of the foraging range migrate to the southern portion of the wintering area makes sense, although the reason why whales bypass Mexico and continue to Central America is still unclear. As discussed above, it could be due to partitioning by reproductive status, with more mothers and calves moving farther south to avoid areas with greater density. It is possible that it is density dependent, with whales simply dispersing along the Mexico/Central American coastline as density dictates. However, Medrano-Gonzalez *et al*. (1995) suggested, however, that the use of Central America during winter is a relict from the last ice age, in which the area of ocean was more restricted, and that some whales simply continue to migrate there. It is difficult to know the conditions that existed when these migrations developed, and whether or not there are current forces acting on them, or if it is simply a relict behavior.

The observation of a mother humpback whale feeding off northern Costa Rica indicates another possible factor that may be driving some whales to go further south than Mexico. The female with calf was seen feeding in the Gulf of Papagayo, an area that experiences intense localized wind driven upwelling between December and April and increased productivity (Mueller-Karger and Fuentes-Yaco 2000). This area off northern Costa Rica experiences some of the greatest productivity in tropical waters as a result of this upwelling and nutrient influx from nearby rivers. Mean surface chlorophyll concentrations in February off Central America are greatest off northern Costa Rica and southern Nicaragua (Palacios *et al*. 2006). It may be that by traveling to these areas of greater productivity, humpback whales are able to feed, therefore, increasing fitness. Feeding is something that rarely occurs during winter, although it has been documented before (Baraff 1991, Gendron 1993). This would be of particular importance for cows nursing calves, who undergo a great energy expenditure producing a weaned calf while they themselves are fasting (Lockyer 1981). We suggest that given the opportunity, humpback whales during winter may travel farther south to an area where food might be available. These upwelling conditions also exist in the Gulf of Tehuantepac off Mexico, and in the Gulf of Panama, although productivity appears greatest off northern Costa Rica

(Muller-Krager and Fuentes Yaco 2000, González-Silvera *et al*. 2004, Palacios *et al.* 2006).

Central America has all the characteristics of a typical area used by humpback whales during winter. Depth and sea surface temperatures were within the range used by humpback whales during winter in other parts of the world. The behaviors and group composition we observed also were similar to other areas used during winter. The presence of cow/calf pairs, escorts to these pairs, and singing males all indicated that mating and calving were occurring.

Although Central America appears typical in these respects, there are some unique aspects to this area when compared with other areas used during winter in the North Atlantic and North Pacific. In other regions humpback whales travel from many different areas used for feeding, whereas Central America appears to be used primarily by whales from one area used for feeding (California), and by whales from the southern range of that area. Additionally, whaling records (Townsend 1935) and more current sightings (Acevedo and Smultea 1995, Florez-Gonzalez *et al*. 1998, Rasmussen 2003, Tim Gerrodette, pers. comm.) indicated that humpback whales occurred off Central America during the austral winter, which would make this the only place in the world where two distinct populations of humpback whales are sharing an area at different times of the year. This would explain the genetic similarities in both populations (Baker *et al.*

1990). Whereas the overall density in this area may not rival that of Hawaii or the West Indies, this is nevertheless an important and unique area for humpback whales.

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Table 1. Survey effort, including dates and total kilometers surveyed, and humpback whale sightings, including total sightings and number of whales seen, off Central America 1996-2004 with mean sea surface temperatures and standard deviation for each region.

		Survey effort			Whale sightings			Temperature	
Year	Region	Start date	End date	km surveyed	Sightings	Animals	Whales/km	Mean SST	SD
2001	Panama	14-Feb	17-Feb	493	2	4	0.008	29.2	0.2
2002	Panama	22-Feb	27-Feb	626	1	1	0.002	29.8	0.3
2003	Panama	25-Feb	28-Feb	695	1	2	0.003	29.3	0.4
1996	S Costa Rica	26-Jan	16-Feb	2,927	15	19	0.006	28.6	0.3
1997	S Costa Rica	31-Jan	14-Feb	2,231	27	45	0.020	28.9	0.2
1998	S Costa Rica	24-Jan	18-Feb	3,211	18	25	0.008	30.1	0.1
1999	S Costa Rica	27-Jan	7-Feb	2,313	32	60	0.026	28.4	0.3
2000	S Costa Rica	25-Jan	13-Feb	3,219	29	46	0.014	28.2	0.2
2001	S Costa Rica	23-Jan	11-Feb	3,685	28	59	0.016	28.5	0.1
2002	S Costa Rica	6-Feb	14-Mar	1,556	11	21	0.013	29.6	0.2
2003	S Costa Rica	29-Jan	7-Feb	1,145	6	8	0.007	29.6	0.3
2004	S Costa Rica	22-Jan	9-Feb	1,887	13	17	0.009	29.0	0.3
2004	S Nicoya Peninsula	6-Mar	7-Mar	220	1	2	0.009		
1999	N. Costa Rica	2-Mar	10-Mar	67	8	12	0.180 *	27.7	0.7
2000	N Costa Rica	23-Jan	24-Jan	57	1	1	0.017	26.3	0.6
2001	N Costa Rica	19-Jan	21-Jan	219	3	4	0.018	27.1	0.5
2002	N Costa Rica	8-Mar	10-Mar	248	2	3	0.012	28.0	1.1
2003	N Costa Rica	11-Mar	14-Mar	241	2	3	0.012	28.4	0.8
2004	N Costa Rica	25-Jan	22-Mar	344	9	17	0.049	27.5	0.5
1999	Nicaragua	1-Mar	1-Mar	107	0	0	0.000 *		
1999	El Salvador	28-Feb	28-Feb	100	1	2	0.020 *		
1999	Guatemala	26-Feb	27-Feb	191	4	5	0.026 *		
2004	Nicaragua	26-Feb	16-Mar	922	9	17	0.018		
2004	El Salvador	27-Jan	29-Jan	339	0	0	0.000		
2004	Guatemala	14-Jan	5-Feb	880	6	9	0.010		
			TOTAL	27,923	229	382	0.014		

* Surveys in 1999 were done from an 18 meter sailboat so observation methods differed

Table 2. Group composition of humpback whale sightings in the study area off Central America, 1996-2004 including total sightings (#) and overall percentage (%) for each category.

	1996		1997		1998		1999		2000		2001		2002		2003		2004		Total	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
Lone singers	5	33	2	7	7	39	5	11	14	47	4	12	4	29	4	44	4	11	49	21
Singles	5	33	6	22	4	22	12	27	7	23	7	21	2	14	0	0	15	39	58	25
Pairs	3	20	15	56	5	28	8	18	2	7	7	21	3	21	1	11	5	13	49	21
Mother/calf	0	0	3	11	2	11	14	31	1	3	4	12	4	29	3	33	9	24	40	17
Mother/calf/escort	0	0	0	0	0	0	6	13	5	17	10	30	0	0	0	0	3	8	24	10
Groups larger than 2	1	7	0	0	0	0	0	0	1	3	1	3	0	0	0	0	1	3	4	2
Competitive Groups	1	7	0	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	2	1
Competitive Groups w calf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1	0
Undetermined	0	0	1	4	0	0	0	0	0	0	0	0	0	0	1	11	0	0	2	1
Total groups with calf	0	0	3	11	2	11	20	44	6	20	14	42	4	29	3	33	12	32	64	28
Total	15		27		18		45		30		33		14		9		38		229	

Table 3. Results of photographic identification research of humback whales off Central America 1996-2004. ID's is the total number of identification photographs taken, unique whales is the number of unique whales of the total identifications, new whales are whales that had not been identified in previous years, no. matching California are total number that have also been identified off California,% matching California is the percentage of whales identified that year that have also been seen off California.

	ID's	Unique whales	New whales	# matching California	% matching California
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%
2004	24	19	15	11	73%
All Years	175	92		80	87%

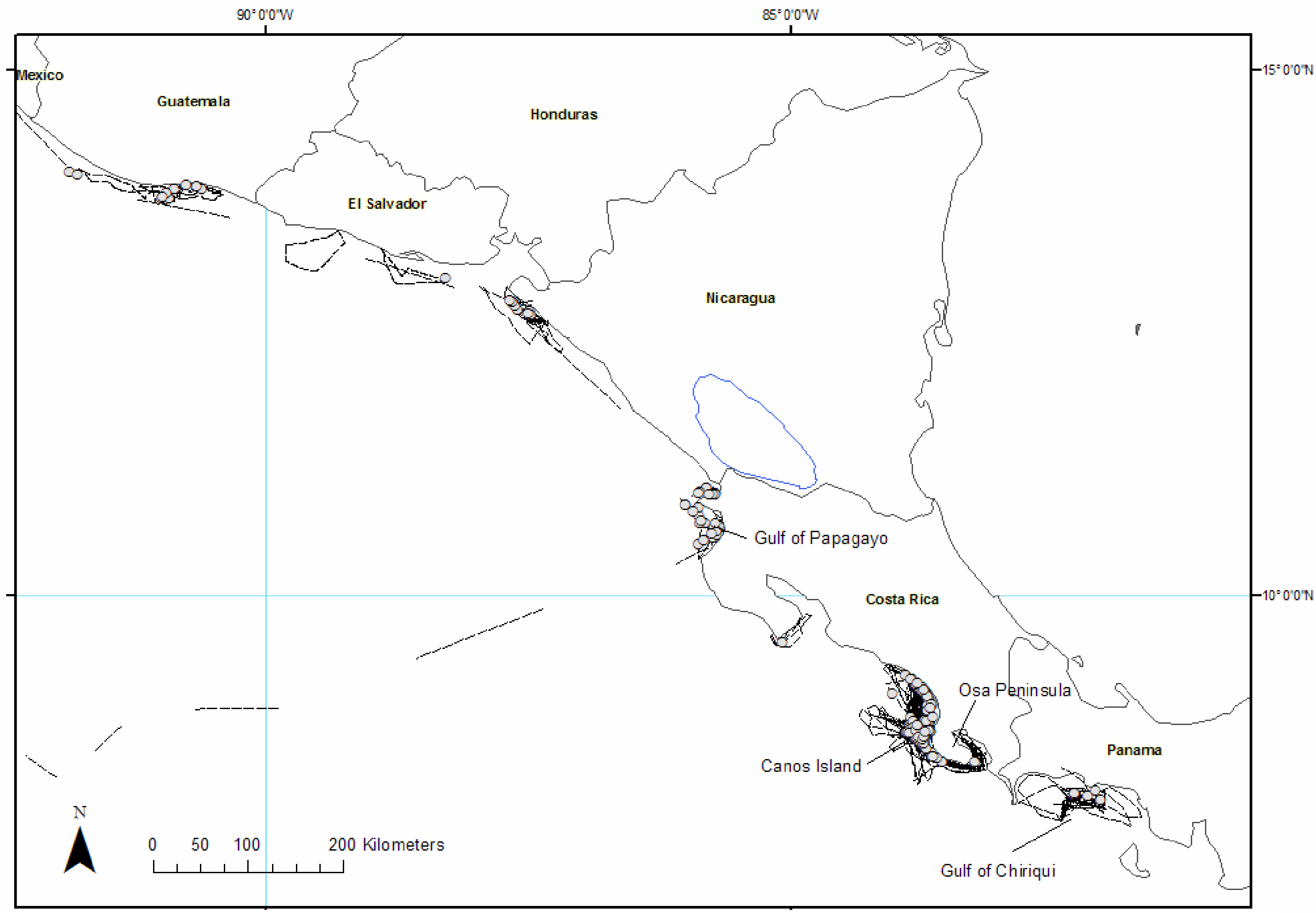

Figure 1. Survey effort and humpback whale sightings off Central aMerica boreal winte s 1996-2004. Hatched lines show survey tracklines, circles represent sightings.

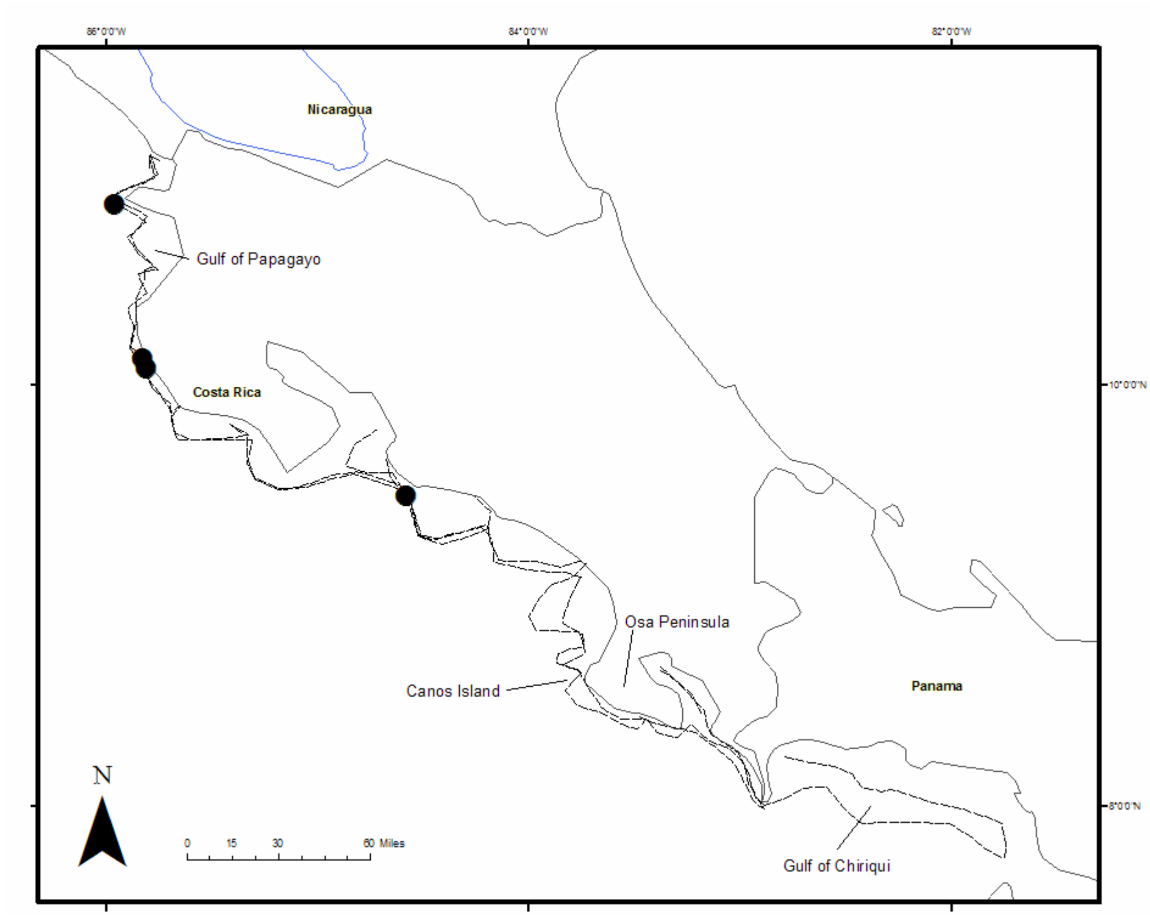

Figure 2. Aerial surveys off Costa Rica and Panama in 2002. Hatched line indicates survey tracklines, black circles represent location of humpback whale sightings.

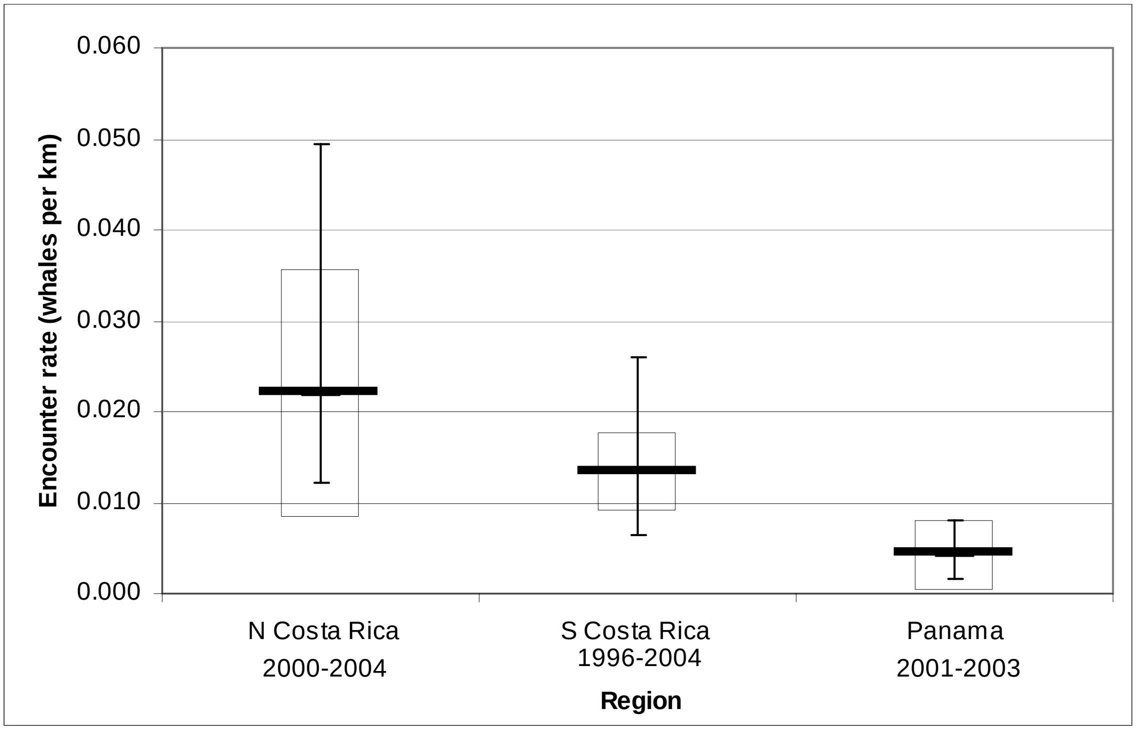

Figure 3. Mean annual encounter rates (number of whales per km) by region. Boxes represent the 95% confidence intervals, vertical bars represent the minimum and maximum encounter rate, and solid horizontal line represents the mean.

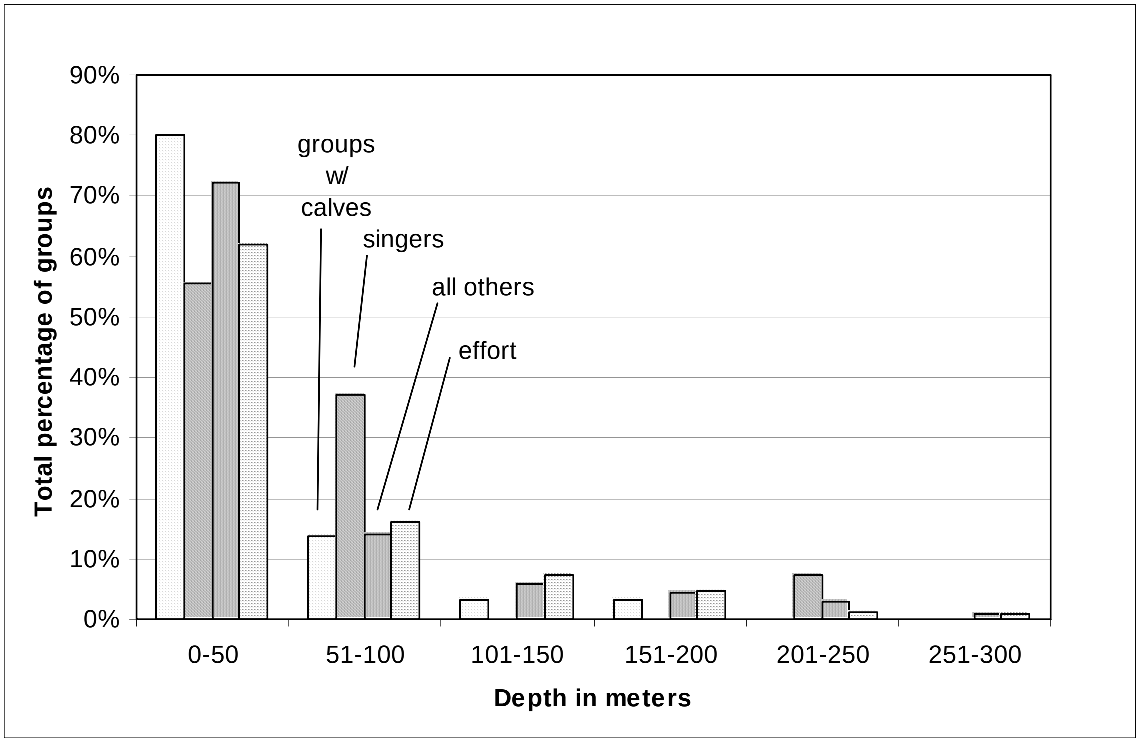

Figure 4. Total percentage of sightings in 50 meter water depth bin categories for calves, singers, all other groups, and amount of effort in each category. (N= 228)

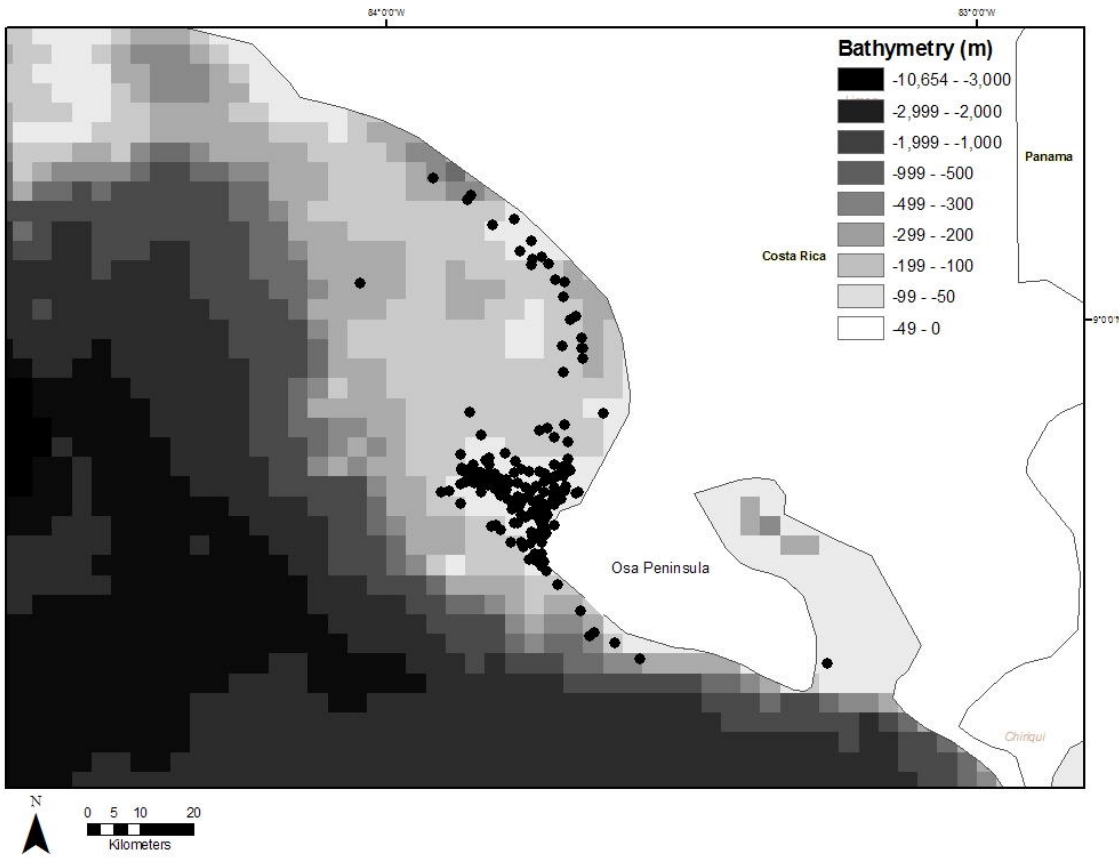

Figure 5. Humpback whale sightings (indicated by circles) off Southern Costa Rica 1996-2004 over bathymetry in meters.

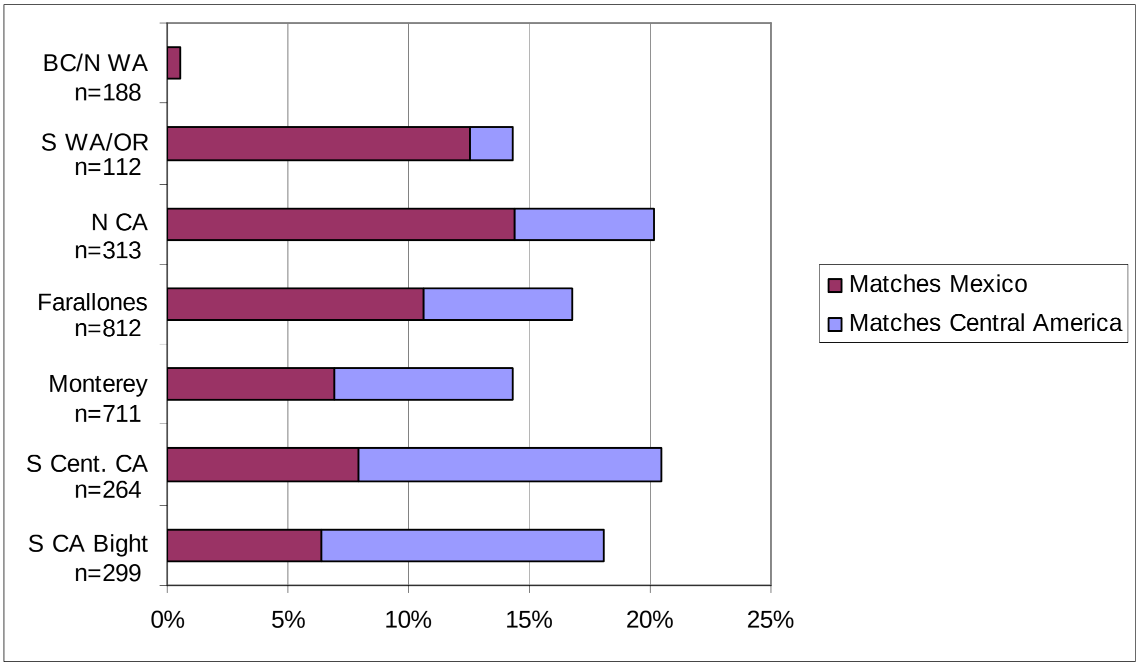

Figure 6. Percentage of whales seen off Central America and Mexico that have been seen off areas off California, Oregon, and Washington. (BC/N WA=British Columbia northern Washington, S WA/OR= southern Washington Oregon, N CA= northern California, S Cent. CA= southern Central California, S CA Bight= southern California bight). (N=2,699)

CHAPTER TWO

Distribution of humpback whales during the austral winter off Pacific Central America

Kristin Rasmussen

INTRODUCTION

The Pacific coast of Central America is an area used during winter by humpback whales primarily migrating from areas used for feeding off California (Chapter One, Rasmussen *et al*. 1995, (Calambokidis et al., 2000). The greatest number of sightings off Central America for humpback whales migrating from California is during the boreal winter, between December and April. Humpback whales also are observed off Central America between July and October (Tim Gerrodette pers. comm., Marco Saborío pers comm., Acevedo and Smultea 1995, this study), which corresponds with the southern hemisphere (austral) winter when humpback whales reproduce (Chittleborough 1958). Historical whaling records also indicated that humpback whales were killed off Central America during the austral winter, primarily in the Gulf of Panama (Townsend 1935).

Common characteristics of areas used by humpback whales during winter include: shallow waters often associated with island groups or reefs (Dawbin 1966, Whitehead and Moore 1982, Clapham and Mead, 1999), warm waters with temperatures between 24° and 28° C (Dawbin 1966, Herman and Antinoja 1977, Whitehead and Moore 1982), and presence of small calves and mating behavior. Behaviors associated with mating may include competitive groups, in which a group of males aggressively vie for the opportunity to mate with a female, and single males escorting cow/calf pairs, which can potentially lead to a larger competitive group (Tyack and Whitehead 1983, Baker and Herman 1984,(Clapham et al., 1992). Humpback whales also produce song in areas used during winter. Only male humpback whales sing, and the greatest song production coincides with winter. Although the exact role of song it is still unclear, because whales sing primarily during the period of mating and calving, it is presumed song has something to do with the mating system (Payne and McVay 1971, Winn and Winn 1978).

Humpback whales in the southern hemisphere feed off Antarctica during summer, and migrate towards the equator during winter. There are six stocks that feed in separate areas in Antarctic waters and these stocks correspondingly spend winter in separate areas. Most areas used during winter are found on either side of the major continents (South America, Africa, and Australia), and island groups in the south Pacific (Mackintosh 1942). In the southeast Pacific, humpback whales from the southern hemisphere spend winter off Ecuador and Colombia (Florez-Gonzalez, 1991, Felix and Haase, 2001, Scheidat et al., 2000). Whales wintering off Ecuador and Colombia are thought to be primarily migrating from areas used for feeding off the Antarctic Peninsula (Stone 1990, (Stevick et al.). No studies have been previously conducted to determine if the areas used during winter by humpback whales from the southern hemisphere extend further north of South America and into Central America.

In this study, we surveyed areas off Costa Rica and Panama during the austral winter. We compared data from these surveys to data collected during the boreal winter (Chapter one) to determine the extent of spatial overlap, and to assess whether temporal overlap existed between the two populations. Our hypotheses were; (1) humpback whales sighted during the austral winter off Central America were using this area for mating and calving, similar to other areas used during winter by humpback whales, and (2) there was some degree of spatial and temporal overlap with humpback whales from the northern hemisphere.

METHODS

Surveys using small boats with one to two observers were conducted off Costa Rica and Panama between 2001 and 2004. Areas surveyed included northern Costa Rica, southern Costa Rica, (for this study 9°30'N divides northern and southern Costa Rica) and western Panama in the Gulf of Chiriquí (Fig. 1). Survey design was non-systematic, and areas where humpback whales had been seen previously were targeted to increase the likelihood of finding whales. This is optimal for photo identifications but can introduce bias in distribution analyses. When whales were encountered, we photographed the underside of their flukes, and recorded sighting time and location, group size, group composition, and behaviors (Chapter One).

Acoustic monitoring was conducted every half hour to listen for humpback whale songs. Hydrophones designed by Cetacean Research Technology were used, with a sensitivity of -180 dBV/uPa ± 4 dB, and a frequency response from 0.02 kHz to 60 kHz, and 100 kHz to 250 kHz. When a song was heard, we recorded at least 30 minutes of it onto a Digital Audio Tape (DAT) using a Sony TCD-D7 or D8 DAT recorder (frequency response 20-14,000 Hz, 32 Hz sampling rate). Due to the density of whales and the likelihood of more than one singer being heard at one time, singers were not pursued for photo-identification purposes. For the analysis, singer "detections" were determined based on the number of whales heard singing within a survey. We determined for each day the minimum number of singers possible in the survey area, and those data were included in analyses of the group composition of sightings. Chi-square analyses were conducted to test differences among these group types.

Water depths at each sighting were obtained using Global Digital Elevation Models from ETOPO2 (USDC 2001). These data provide grided (2 minute by 2 minute) bathymetry derived from the National Geophysical Data Center Marine Geology and Geophysics dataset (ETOPO2) and University of California, San Diego, Seafloor Topography. Depth values for each sighting were grouped into 50-meter classes using ArcGIS version 9 (ESRI 2004), and all analyses were conducted on these groups to account for the relatively low resolution of the data. All values were compared with nautical charts and personal knowledge of the area to determine whether the values were reasonable. Chi square analyses were conducted on group types in each 50 meter water depth bin (Zar 1999).

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 monthly, 4-km resolution data (ascending pass and descending passes were combined to increase coverage). A single SST value of a monthly average was computed for each area and survey period.

These monthly averages were used due to insufficient data on a daily or weekly scale because of seasonal cloud cover in the eastern tropical Pacific.

Yearly mean encounter rates (whales seen per kilometer surveyed) were calculated for all three survey regions to indicate sightings per unit effort and adjust for bias of areas of greater effort, thus providing an index of relative density. A two factor model-I ANOVA was conducted to test differences in mean encounter rate among the three regions, and between the austral and boreal season for 2001-2004 (Zar 1999).

For all three survey regions we placed 4km x 4km grids over the survey tracklines. Encounter rates (whales per kilometer surveyed) were calculated for each individual square within the grid.

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

A total of 3700 nautical miles were surveyed during a four year period. Surveys off Panama accounted for almost half of this effort (Table 1). Whales were sighted in all three regions surveyed (Fig. 1). The mean annual encounter rate varied with each region, although these differences were not statistically significant (two factor model I ANOVA $F=1.771$, $P= 0.212$). The encounter rate was greatest off Panama, and least off northern Costa Rica. Mean encounter rates during the austral winter were greater than during the boreal winter (two factor model I ANOVA, F=10.437, P=0.007; Fig. 2).

Humpback whales from the northern and southern hemispheres were sighted in similar areas during their respective winters (Fig. 3). In the Gulf of Chiriquí in Panama, sightings were near small islands or rocky outcroppings. Off southern Costa Rica, whales were seen between the mainland and Caños Island, or along the coastline. In northern Costa Rica, all sightings during austral winter occurred in the Gulf of Santa Elena, whereas sightings during boreal winter occurred there and off the Gulf of Papagayo. The grid analysis indicated differences in relative density among the three regions. Relative density decreased southward during the boreal season, and decreased northward during the austral season. Overall, the austral season had a greater relative density than the boreal season. Both southern Costa Rica and Panama had a greater relative density during the austral season (Fig 3).

Most sightings of groups with calves occurred in depths less than 50 meters, both in the austral and boreal winter (Fig. 4). A slightly greater percentage of whales were seen in the 100-150 meter water depth category in the austral winter (Fig. 5).

Mean SSTs during the austral winter for all regions and years was 28.4° C (± 0.8 SD; Table 1). The least mean SST of this season (27.9° ± 0.5 SD) occurred in Panama during 2003, and the greatest SST (28.9° ± 0.6 SD) occurred off southern Costa Rica in 2002. These variations were not extreme, particularly compared with the boreal winter SSTs of 26.3° to 30.1°.

Mean group size was 2.04 whales (± 1.02 SD), and maximum group size was 7. Almost half of the sightings contained calves, either as a mother/calf pair, a mother/calf escort trio (a mother/calf pair with an additional juvenile or adult whale accompanying them), or a competitive group with a calf (Table 2). Of all the sightings that included calves, 77% were mother and calf only. No competitive groups were seen that did not contain a calf. There were no significant differences among mean encounter rates of calves among the three regions surveyed (ANOVA, F=1.344, P=0.33). When compared with group types found during the boreal winter (Table 2), there was a highly significant difference between the two seasons (x^2=325.08, df=8, P<0.001). Subdividing the chi-square into two groups indicated that the frequency of mother/calf pairs, competitive groups with calves, pairs, single whales, and undetermined groups were significantly different between the two seasons (x^2= 318.01, df=4, P<0.001), whereas frequency of singers, mother/calf/escort, competitive groups without a calf, and groups larger than two were not significantly different than expected (x^2=7.07, df=3, P=0.07).

DISCUSSION

Panama and Costa Rica have all the typical characteristics of an area used by humpback whales during the austral winter season. The waters were warm (mean=28.4°C ±0.8 SD), although the temperatures in our study area were slightly greater than reported for other areas (24°C-28°C; Dawbin 1966, Herman and Antinoja 1977, Whitehead and Moore 1982). Sightings of humpback whales in other areas used during winter usually occur in less than 200 meters water depth (Winn et al., 1975, Herman and Antinoja, 1977, Whitehead and Moore, 1982), which our data corroborates. Areas used during winter also are characterized by mating behavior such as singing (Payne and McVay, 1971, Winn and Winn, 1978), presence of competitive groups (Tyack and Whitehead, 1983, Baker and Herman, 1984), and presence of small calves. We observed all of these, supporting the hypothesis that Costa Rica and Panama is an area used by humpback whales for mating and calving during the austral winter.

Some whales identified during the austral winter off Costa Rica and Panama migrated from areas used for feeding off Antarctica (Chapter 3). Whales photographed off Colombia also were identified off Antarctica (Stone *et al.* 1990), Ecuador, Panama, and Peru (Florez-Gonzalez et al., 1998). The season of our sightings, and the identification of the same whales off Central America and the southern hemisphere indicated that whales seen off Central America between July and October were migrating from areas used for feeding in the southern hemisphere. Whales migrating from the Antarctic Peninsula to Costa Rica are making the longest known mammalian migrations (Chapter 3).

It is unclear how much interchange occurs between Ecuador, Colombia, and Central America during the austral winter. Individual whales photo-identified off Panama and Colombia, and Colombia and Ecuador (Florez-Gonzalez *et al*. 1998) indicate some degree of interchange. Interchange is common between sub areas used during winter (Baker and Herman, 1981, Darling and McSweeney, 1985, Calambokidis et al., 2001).

Typically, humpback whales do not have the same degree of site fidelity with areas used during winter as they do with areas used for feeding (Baker et al., 1986, Darling and McSweeney, 1985, Perry et al., 1990, Calambokidis et al., 2001). Of forty-one individual whales identified off Panama and Costa Rica in four years, only two were seen in more than one year. This low resight rate does not necessarily indicate lesser site fidelity; it could be due to a large population that was not completely sampled.

What is particularly unique about this area is that whales from two different populations of different hemispheres are using this same area during winter at different times of the year. This situation provides us with a natural experiment: if two distinct humpback whale populations use the same region at different times, will they use the same habitat? It appears that the same areas within our survey sites were attractive to both populations; the island groups and rocky outcroppings in the golf of Chiriquí, the waters between Caños Island and coastal southern Costa Rica, and the islands and gulfs in northern Costa Rica. These are all characterized by shallow, somewhat protected waters. Because we also targeted shallow waters, we cannot definitively say that humpback whales do not occur in waters of greater depth off Central America, only that clearly they occur in shallow waters.

The minimum area of spatial overlap between these two populations can be inferred based on the limits of sightings from each season. The farthest north a southern hemisphere whale was sighted was 11.05° N, near the Costa Rican/ Nicaraguan border. The farthest south a northern hemisphere whale was sighted was off coastal Panama

(8.05° N). Sightings of northern hemisphere whales also have been reported near Cocos Island, at 5.55° N (Acevedo and Smultea, 1995) and stranded dead calves, presumably from the northern hemisphere have been reported off Colombia at 6.08° N and 6.25° N (Alzueta et al., 2001). The minimum latitudinal overlap between the southern and northern hemisphere populations, therefore, could be considered between 11° N and 5.5° N. This represents a latitudinal distance of 606 km.

While there is clearly spatial overlap, the degree of temporal overlap remains unclear. Greatest numbers of sightings occurred between December and April for whales migrating south from the northern hemisphere, and between July and October for whales migrating north from the southern hemisphere, but whales have been sighted in other months of the year. Sightings have been recorded by Southwest Fisheries Science Center off this region of Central America in all months of the year (Tim Gerrodette, pers. comm.). The origin of whales seen in May, June, and November is unclear, and it is possible that they could be from either population. Although sighting rates were less during these months, it is conceivable that whales from these two populations encounter each other, as has been previously suggested by Acevedo and Smultea (1995), Florez-Gonzalez *et al.* (1998), and (Baker et al., 1993). Genetic data indicates these two populations share common traits, and have had the most recent genetic interchange of all the distinct populations worldwide (Baker et al., 1993). These similarities are likely the result of mixing between these two populations off Central America, although the time period of such interchange is unclear.

Scientific reports from the whaling era also indicated the potential for overlap of humpback whales from the northern and southern hemispheres. Mackintosh (1942) and Mathews (1937) noted that whales from the southern hemisphere crossed the equator into the northern hemisphere off the west coasts of South America and Africa, and interchange between the two hemispheres was possible. It is likely that this potential for overlap was greater before humpback whale populations were drastically decreased by whaling.

Humpback whale song can be used as an indicator of interchange between two populations (Darling and Sousa-Lima 2005). All humpback whales breeding within a distinct area will sing the same song, and this song will progressively change during the season (Winn et al., 1981, Cerchio et al., 2001, Winn and Winn, 1978, Payne and Payne, 1985). Although it is unclear the exact mechanisms that results in changes of song, it has been hypothesized it is brought about by the introduction of new phrases from other populations, possibly by migrant whales (Noad et al., 2000) or by interchange of individuals during periods of feeding (Clark and Clapham, 2004). If interaction between these two populations was occurring, we would expect some shared components of the songs of each of these populations. We conducted a cursory analysis of song from both seasons which indicated no shared components. Because our sample size was minimal, we were unable to definitively detect interchange between these two populations. A more comprehensive sampling of song throughout both seasons, with a greater sample size of individuals may provide a better indication of the degree of temporal overlap (Sal Cerchio pers. comm.).

A unique aspect of this area is that it represents the extreme range of humpback whales during winter for the both the austral and boreal populations. Individuals from both populations are traveling beyond other areas used during winter to reach southern Central America (Mexico for the North Pacific population, Ecuador and Colombia for the South Pacific population). What would drive these whales to migrate a greater distance than they need to? During the boreal winter, the number of groups containing calves (28%) was greater than many other studies (see chapter one). During austral winter, the number of groups that contained a calf was almost 50%, considerably greater than other areas used during winter (other studies ranged 8%-27%) (Mattila and Clapham, 1989, Mattila et al., 1994, Garrigue et al., 2001, Hauser et al., 2000, Zerbini et al., 2004). While this result could be an artifact of the season of our sampling (more calves would be seen late in the sampling period), it is possible that this area represents a nursery area for cow/calf pairs from the southern hemisphere, as was suggested for the whales of the northern hemisphere (see chapter one). Cow/calf pairs isolate themselves from other groups, usually in shallower waters (Martins et al., 2001, Smultea, 1994, Craig and Herman, 2000, Ersts and Rosenbaum, 2003). It may be that mothers with calves are avoiding the greater density areas found closer to their summer areas where they feed.

Another significant difference is the greater number of competitive groups seen during the austral winter season compared with the boreal winter season. Whereas the percentage of competitive groups of the austral season was less than other studies (other studies ranged 2%-18%; Garrigue *et al* 2001, Mattila *et al* 1994, Mattila *et al* 1989), the increase in number of competitive groups of the boreal winter could be a result of an overall greater density in the austral winter. There was simply a greater density of whales available to form larger competitive groups.

Central America is a unique area used by humpback whales during winter for a variety of reasons. It is currently the only area in the world used during winter by humpback whales from two distinct populations from the northern and southern hemispheres. It is highly possible whales from each population have a chance to encounter each other as one population leaves and the other arrives. The implications for this in terms of genetic flow between the two hemispheres are great. Because two populations are using the same area, it allows us to test the theories of what comprises suitable humpback whale breeding habitat. Both populations were using similar habitat, which supported the hypothesis that humpback whales sought warm shallow waters in wintertime. For both populations, Central America is the extent of their winter range. It is possible that animals are segregated in terms of age class and reproductive status with more cow/calf pairs found at the extreme of their range. Because this area is unique in these ways, it allows us to have insight into the migratory habits of humpback whales. Central America should be considered an important area used during winter for humpback whales because of these unique characteristics.

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Table 1. Survey effort (start and end date and kilometers surveyed) off Panama and Costa Rica and number of humpback whale sightings, total number of whales, encounter rates (whales per kilometer surveyed), and mean sea surface temperatures (SST) and standard deviation (SD).

		Survey effort			Whale sightings		Sighting rates		
Location	Year	Start date	End date	Survey Km	Sightings	Animals	Whales per km	SST	SD
Panama	2002	5-Sep	14-Sep	872	19	32	0.037	28.1	0.6
	2003	2-Sep	6-Sep	441	21	45	0.102	27.8	0.5
	2004	6-Sep	9-Sep	402	18	33	0.082	28.4	0.6
S Costa Rica	2001	12 Aug,28 Aug	20 Aug, 29 Aug	356	15	29	0.082	28.2	0.3
	2002	21-Aug	31-Aug	854	25	62	0.073	28.9	0.6
	2003	12-Sep	12-Sep	81	0	0	0.000		
N Costa Rica	2001	24-Aug	26-Aug	146	1	2	0.014	28.6	0.5
	2002	15 Aug, 27 Sep	16 Aug, 28 Sep	404	0	0	0.000	28.6	0.6
	2003	21-Sep	23-Sep	146	2	4	0.027	28.7	0.4
			TOTAL	3,702	101	207	0.056	28.4	0.8

Table 2. Group types of sightings for the austral and boreal winters, total numbers of sightings observed (#) and total percentage of all sightings (%)

	Austral winter		Boreal winter	
	#	%	**#**	**%**
Lone singers	32	24	49	21
Singles	14	11	58	25
Pairs (not including m/c pairs)	11	8	49	21
Mother/calf	49	37	40	17
Mother/calf/escort	9	7	24	10
Groups larger than 2 (excluding competitive groups)	1	1	4	2
Competitive Groups	0	0	2	1
Competitive Groups w calf	6	5	1	0
Undetermined	11	8	2	1
Total groups with calf	64	48	64	28
Total	133		229	

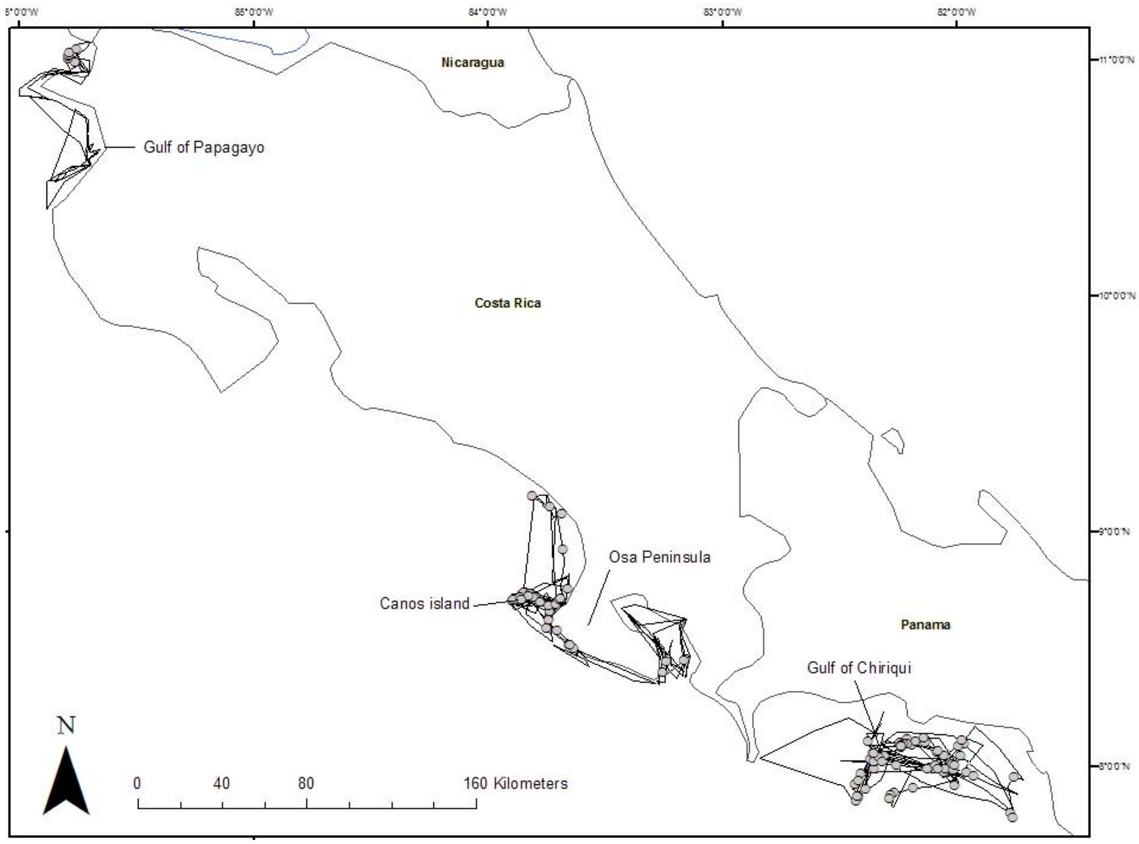

Figure 1. Survey effort during the austral winter between 2001-2004 off three areas in Central America (northern Costa Rica, southern Costa Rica, and Panama) shown by solid black lines, and sightings locations of humpback whales shown by circles.

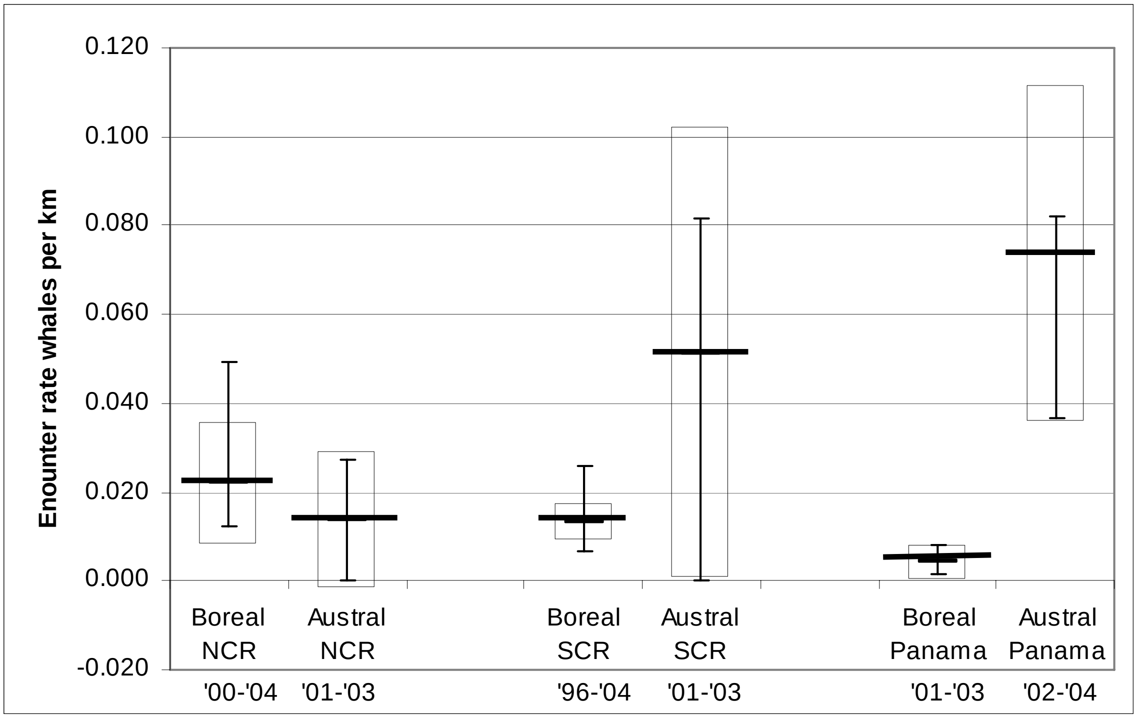

Figure 2. Mean yearly encounter rates (number whales per km) of boreal and austral winter humpback whale sightings for three regions (NCR=northern Costa Rica, SCR=southern Costa Rica, Panama). Boxes represent 95% Confidence intervals, horizontal line represents the mean, and vertical bars represent the minimum and maximum encounter rate values.

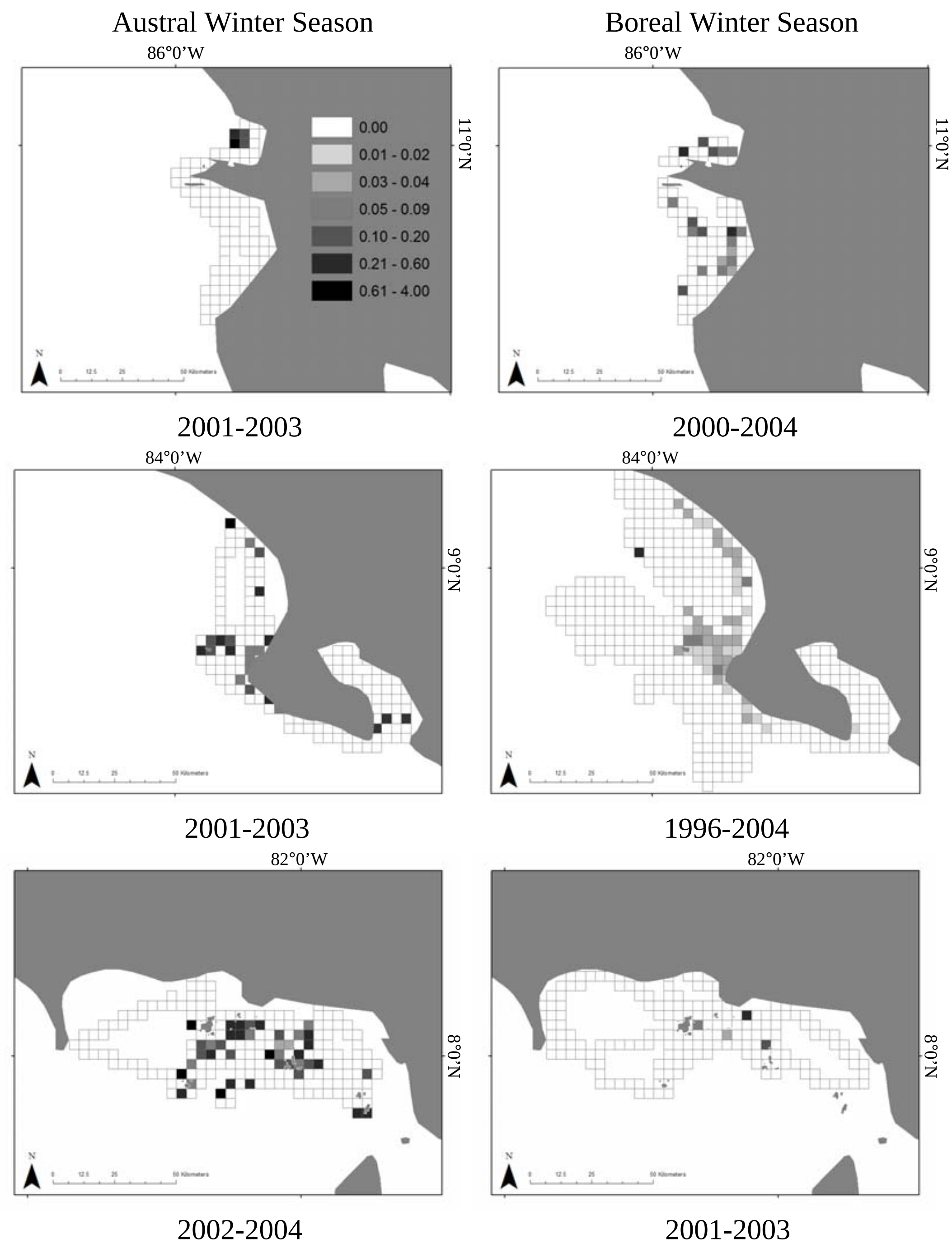

Figure 3. Relative density (whales seen per kilometer surveyed) shown in 4km by 4km grid squares for three regions off Central America (Northern Costa Rica, Southern Costa Rica and Panama).

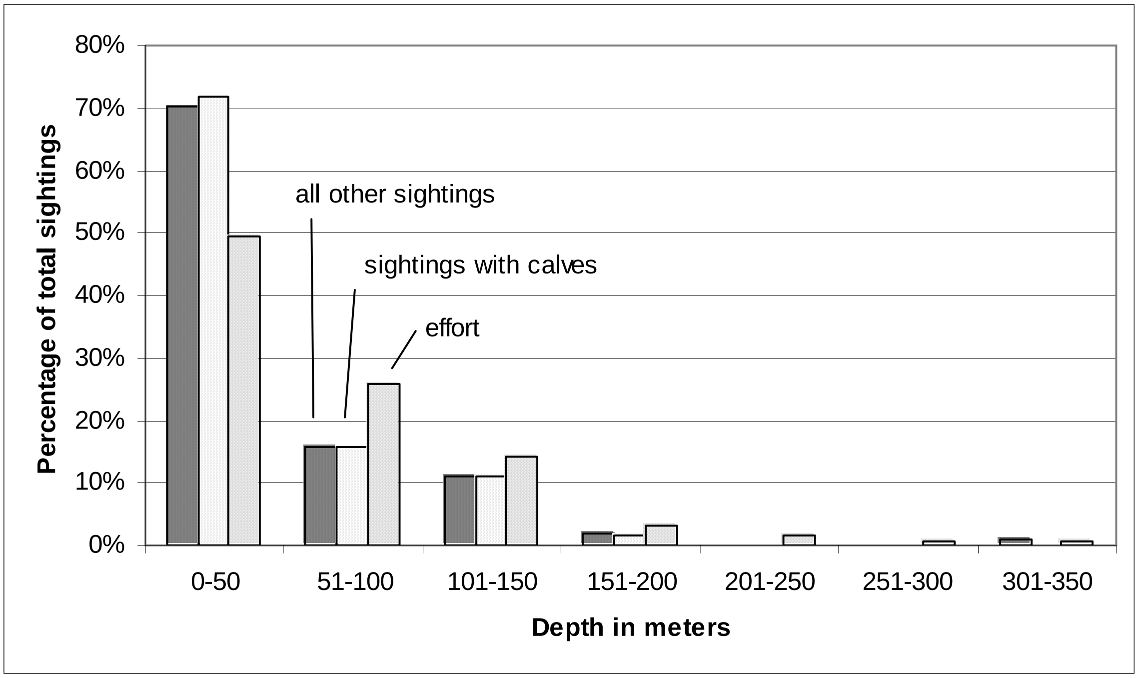

Figure 4. Percentage of sightings and survey effort in 50 meter bins of water depth for calves and all other group types during the austral winter (n=101).

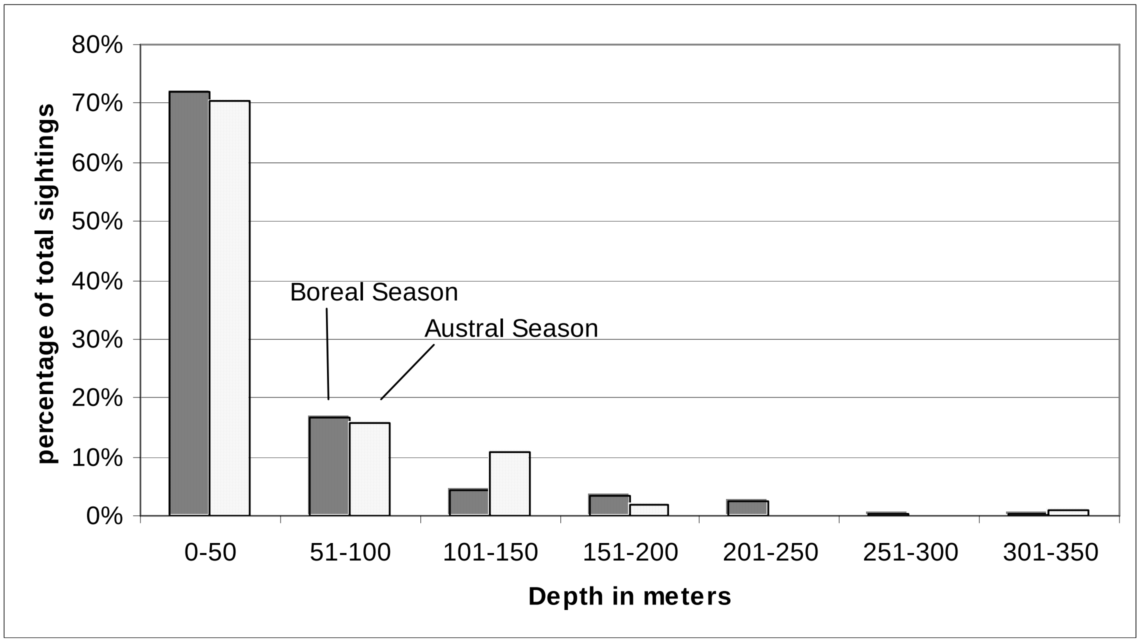

Figure 5. Comparison of percentage of all sightings in 50 meter bins of water depth for both the austral season (2001-2004, n=101) and the boreal season (1996-2004, n=228).

CHAPTER THREE

On the trans-equatorial migration of Southeast Pacific humpback whales

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INTRODUCTION

The long annual migrations of baleen whales from productive, high-latitude areas used for feeding ("feeding areas") to low-latitude, resource-poor areas used for breeding ("wintering areas") are well known, but the selective forces that drive them remain largely unexplained. Several hypotheses have been proposed, including: migration as vestigial behaviour from a past era when ocean basins were smaller and feeding and wintering areas were closer together (Evans 1987); the optimization of energy budgets by spending winter in warm waters (Brodie 1975); increased offspring (calf) growth and survivorship in warm, protected waters (Norris 1967); and avoidance of killer whale (*Orcinus orca*) predation, specifically on the vulnerable calves at low latitudes (Corkeron and Connor 1999).

For humpback whales (*Megaptera novaeangliae*), which occur in all major ocean basins, wintering areas are found at about 20 degrees of latitude in the northern and southern hemispheres (Clapham and Mead 1999). Mackintosh (1942) and Mathews (1937), however, reported humpback whale catches north of the equator during the austral winter off the west coasts of South America and Africa, leading these authors to suggest that some southern hemisphere whales might spend winter in areas north of the equator. Indeed, modern researchers have confirmed the existence of a wintering area north of the equator off western Colombia for humpback whales from the Southeast Pacific (Flórez-González 1991). Sightings of whales from this population have been reported at additional sites in the Northeast tropical Pacific (Acevedo and Smultea 1995; Flórez-González *et al*. 1998).

We report here on a wintering area in coastal waters of Central America for humpback whales in the Southeast Pacific. We also document the migratory destinations of several animals through photo-identification. Finally, we examine the water temperature regime at this wintering area, and compare it with those of all other known humpback whale wintering areas world-wide to investigate the influence of temperature on humpback whale distribution at the low latitudes.

METHODS

Coastal marine mammal surveys were conducted yearly off Central America from 2001 to 2004 (additional opportunistic observations were made since in 1993) during the austral winter between latitudes 7°46'N and 11°06'N (Fig. 1). Whenever encountered, humpback whales were identified using photographs of the unique markings on the ventral surface of the tail flukes (Katona and Whitehead 1981). Whales were photographed also off the Antarctic Peninsula between latitudes 61°14'S and 66°43'S during the austral summer from 1981 to 2004 by a variety of contributors, including research groups and naturalists aboard whale watching boats and cruise ships. This collection of photographs (n=587) is part of the Antarctic Humpback Whale Catalogue, maintained by the College of the Atlantic. We compared these two photographic collections to determine individual whales common to both areas.

We reviewed the geographic distribution of present-day humpback whale wintering areas world-wide based on the published literature, to investigate a possible explanation to the extreme northern occurrence of an austral humpback whale wintering area off Central American wintering area. For inclusion as a wintering area, we considered those areas where small calves had been observed, and where there were other behaviours by adults indicative of breeding such as singing and competitive groups (Payne and McVay 1971; Winn and Winn 1978; Tyack and Whitehead 1983; Baker and Herman 1984; Clapham *et al*. 1992).

A total of 24 wintering areas were determined, all within 30 degrees of the equator (Fig. 2). Ten were in the northern hemisphere (A-F in Table 1 and Fig. 2) and 14 in the southern hemisphere (G-T in Table 1 and Fig. 2). For three of these, information was inconclusive as to whether they were a true wintering area or part of the migratory route, but they were still included in the analysis. For two of the Japanese wintering areas, the Ryukyu and Bonin Island groups (F1 and F2), it has been suggested that calving occurs further south (Mori *et al*. 1998; Ohizumi *et al*. 2002). It also is unclear whether Baja California (B1), Mexico, is an area used for calving, as humpback whales there are seen as early as September (Urban-R and Aguayo-L 1987), indicating this area may be a migratory corridor for whales going further south. One known humpback whale population inhabiting the Arabian Sea, northern Indian Ocean, was not included in the analysis because its migratory movements are not well understood (Reeves *et al.* 1991; Mikhalev 1997).

Long-term average sea-surface temperature (SST) for the month of peak whale occurrence in each wintering area (February for the northern hemisphere and August for the southern hemisphere) were extracted from satellite-derived global monthly climatologies at 4-km grid resolution for the base period 1985-2001 [see Casey and Cornillon (1999) for details on an earlier version of this product]. These climatologies are distributed by NOAA's National Oceanographic Data Center (http://www.nodc.noaa.gov/sog/pathfinder4km/).

RESULTS

A total of 207 whales were sighted off Central America (between 7˚47'N and 11˚06'N) during the 2001-2004 austral winter surveys (Fig.1b). Mother/calf pairs, groups of competing males, and singing males were all documented (see chapter two). Forty-one individual whales were photo-identified; seven of these also were photographed off the Antarctic Peninsula. Three of the whales were seen within the same year; one off Costa Rica 262 days after it was seen off Antarctica, and two (a mother and calf pair) off Antarctica 161 days after being seen off Costa Rica (Table 2). The minimum distances between these locations (based on straight great-circle distances around land masses) ranged from 8,299 to 8,461 km.

The overall mean SST for all wintering areas was 24.6°C (± 1.9°C SD), or 25.1°C (±1.4°C SD) if the three areas B1, F1, and F2 are excluded. Mean SST in all areas were 21.1°C to 28.3°C, with no significant difference between northern and southern hemispheres (t-test on the log-transformed data to homogenize the variance, p-value=0.23). There were seven wintering areas with mean SST less than the lower 95% confidence interval (23.8°C) for the mean of this sample (Table 1, Fig. 2): Baja California (B1), two Japanese areas (F1 and F2), the Cape Verde Islands (E), south Madagascar (O), northeast Australia (R) and New Caledonia (S). Of these, Madagascar, Australia, and New Caledonia all seem reasonably close to 23.8°C (Table 1), whereas Baja California and the two Japanese areas have not been conclusively determined as wintering areas. The Cape Verde Islands have been confirmed as a wintering area, with sightings of small calves, competitive groups, and singers (Jann *et al*. 2003).

DISCUSSION

The extensive migrations between Antarctica and Central America documented here (~8,300 km) were not anomalous movements by a few individuals, but rather were common or even the norm for at least part of the population of humback whales in the Southeast Pacific. Whales were regularly sighted off Panama and Costa Rica during the austral winter as far north as 11˚N. Group composition (mother/calf pairs) and behaviours (competing males, singing males) were indicative of an area used for calving and mating (Payne and McVay 1971; Winn and Winn 1978; Tyack and Whitehead 1983; Baker and Herman 1984; Clapham *et al*. 1992). Previously Stone *et al*. (1990) reported movements of whales between the Antarctic Peninsula and Colombia, and it is likely that the Central American wintering area is an extension of the wintering area off Ecuador and Colombia (Flórez-González 1991; Flórez-González *et al.* 1998; Scheidat *et al.* 2000; Félix and Haase 2001) (Fig. 1b).

Another unique aspect of this area is the spatial overlap with whales from the northern hemisphere. Work we have conducted off Central America during the boreal winter season (December-April) since 1996 (Fig. 1a) has indicated that this also is a wintering area for Northeast Pacific humpback whales migrating from feeding areas off California (Calambokidis *et al.* 2000). In fact, whales have been reported every month off Central America (see chapter two), although the population identity of animals seen during the non-peak sighting months has not been determined. There are shared genetic traits between Northeast and Southeast Pacific populations indicating trans-equatorial exchange has occurred, likely off Central America (Medrano-González *et al.* 2001).

The mean August SST in this wintering area is 28°C (Table 1). Temperatures were reported between 24°C and 28°C at other humpback whale wintering areas (Dawbin 1966; Herman and Antinoja 1977; Whitehead and Moore 1982), consistent with our global SST analysis (Fig. 2 and Table 1). Coastal upwelling and cold tongue development during the austral winter in the eastern equatorial Pacific causes lesser SST, and SST > 24˚C do not occur until north of the equator (Fig. 2), explaining why humpback whales in the Southeast Pacific need to migrate farther north. Furthermore, this pattern is consistent with observations off the west coast of Africa at a wintering area for humpback whales in the Southeast Atlantic (Mackintosh 1942; Findlay *et al*. 1994; Walsh *et al*. 2000; Van Waerebeek *et al*. 2001), where the Atlantic cold tongue also limits SST > 24°C to north of the equator (Fig. 2).

World-wide humpback whale wintering areas are found in waters warmer than 24°C irrespective of latitude, indicating that whales seek warm waters during the low latitude phase of their migration. If, as suggested by Corkeron and Connor (1999), avoidance of killer whale predation is the main reason for migration, we would expect a lesser occurrence of these predators in the wintering areas, and no correlation between SST and the distribution of wintering areas. However, killer whale attacks on humpback whales have been observed off Colombia (Flórez-González *et al*. 1994), and Ecuador (Palacios 1993). In addition, we have sighted killer whales in the vicinity of humpback whales in our study area and we have documented killer whale-inflicted scars on small calves. Therefore, it is more likely that the factors driving migration are more related to the environmental conditions found in the wintering areas than to avoidance of predation. Perhaps these factors are linked to the developmental advantage that calves have in warm water, leading to increased reproductive success later in life (Dawbin 1966; Clapham 2000).

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Table 1. Sighting information for the seven matches between Antarctica and Central America. Identification numbers are shown for Cascadia Research Collective (CRC) and the Antarctic humpback whale catalog (AHWC). Sighting information includes dates and locations, and the minimum distance between the two sighting locations. The group composition for the Central American sightings is shown, M/C/E =(mother/calf/escort).

CRC	AHWC	Antarctica			Central America			Minimum	
ID	ID	Date	Lat	Long	Date	Lat	Long	Distance (km)	Group composition
1002	0010	16-Apr-86	64˚22'S	63˚17'W	25-Sep-99	8˚31'N	83˚15'W	8,346	Adult of M/C/E trio
1004	0021	16-Apr-86	64˚30'S	63˚09'W	25-Sep-99	8˚31'N	83˚15'W	8,361	Adult of M/C/E trio
1015	0529	4-Jan-95	65˚21'S	64˚58'W	23-Sep-95	8˚39'N	83˚43'W	8,409	Cow
1006		10-Dec-03	64˚37'S	62˚36'W	28-Aug-01	9˚09'N	83˚49'W	8,461	1 of M/C/2E
1033	0147	Jan-89	64°48'S	64°00'W	3-Sep-03	7°55'N	82°01'W	8,299	Adult in M/C/E trio
1013		30-Jan-02	64°37'S	62°15'W	17-Aug-01	8°44'N	83°49'W	8,425	Cow
1012		30-Jan-02	64°37'S	62°15'W	17-Aug-01	8°44'N	83°49'W	8,425	Calf

Table 2. Mean sea surface temperatures (SST) and standard deviation (SD) for world-wide humpback whale wintering areas for both the northern and southern hemispheres.

	Northern hemisphere wintering areas	SST	SD
A	Hawaii[1,2]	24.15	0.31
B1	Mexico: Baja California[3]	21.09	0.79
B2	Mexico: mainland[3]	24.05	0.84
B3	Mexico: Revillagigedos[3]	24.32	0.30
C	Central America[4]	28.27	0.96
D	West Indies[5,6]	26.11	0.27
E	Cape Verde Islands[7,8,9]	22.10	0.36
F1	Japan: Ryukyu Islands[10,11,12,13]	21.60	0.44
F2	Japan: Bonin Islands[11,12,13,14,15,16]	21.91	1.13
F3	Japan: Mariana Islands[12,16]	26.96	0.42
	Southern hemisphere wintering areas	**SST**	**SD**
G	Tonga[17,18]	24.34	0.68
H	Cook Islands[17,18,19]	25.07	0.63
I	Polynesia[17,18,20]	25.93	0.88
J	Central America[4]	28.00	0.79
K	Colombia and Ecuador[21,22,23,24,25]	25.67	2.23
L	Brazil[26,27,28,]	25.37	1.05
M	West Africa[29,30,31,32]	24.89	2.79
N	East Africa[29]	24.08	1.84
O	S Madagascar[29,33,34,35]	23.20	0.61
P	NE Madagascar[34]	24.02	0.22
Q	NW Australia[26,37,38,39]	25.54	0.90
R	NE Australia[40,41,42]	23.43	0.87
S	New Caledonia[17,18,43]	23.30	0.57
T	Samoa [18]	26.25	0.50

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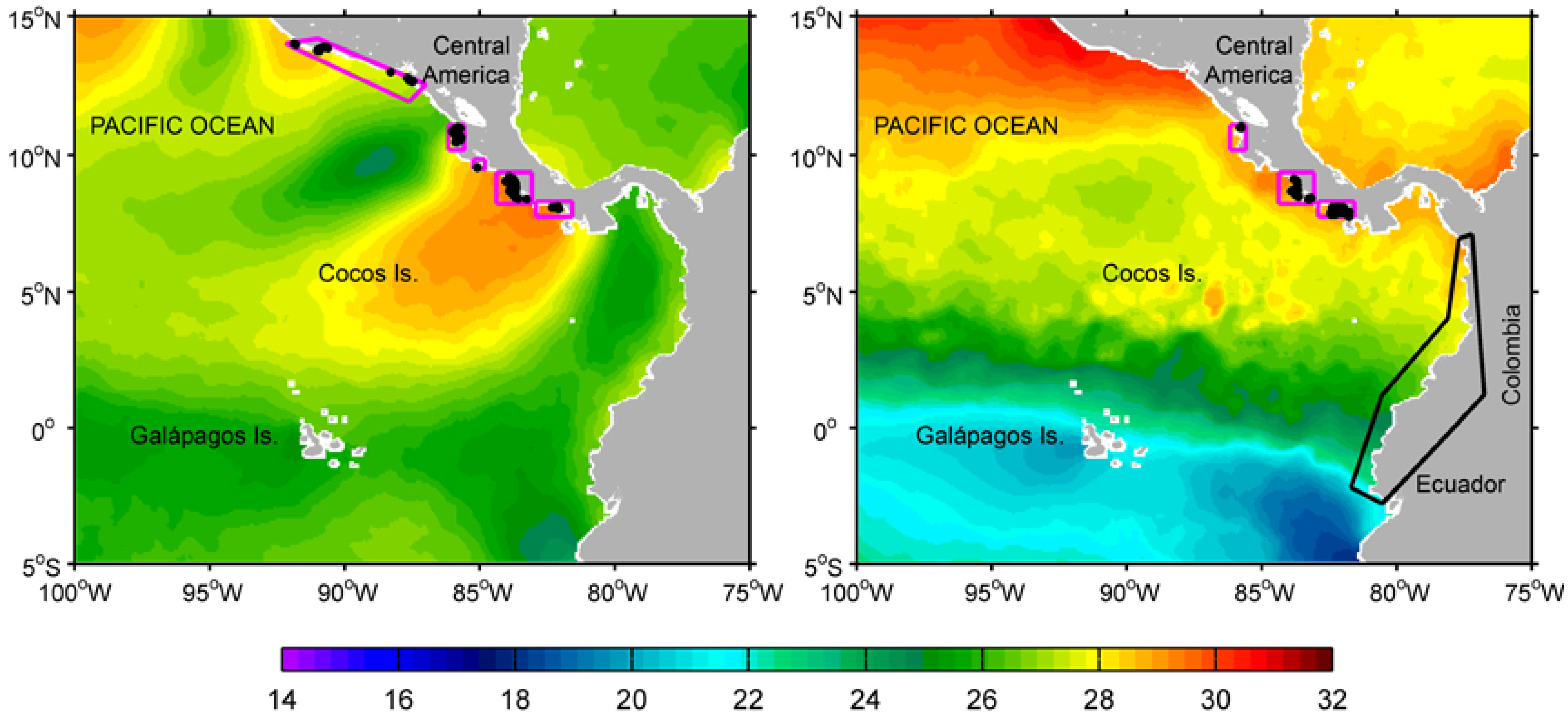

Figure 1. Survey areas (magenta boxes) off Central America and humpback whale sighting locations during (a) boreal (n=229), and (b) austral (n=101) winters, overlaid on mean SST for February and for August, respectively. Black polygon in (b) is the “Colombia and Ecuador” wintering area.

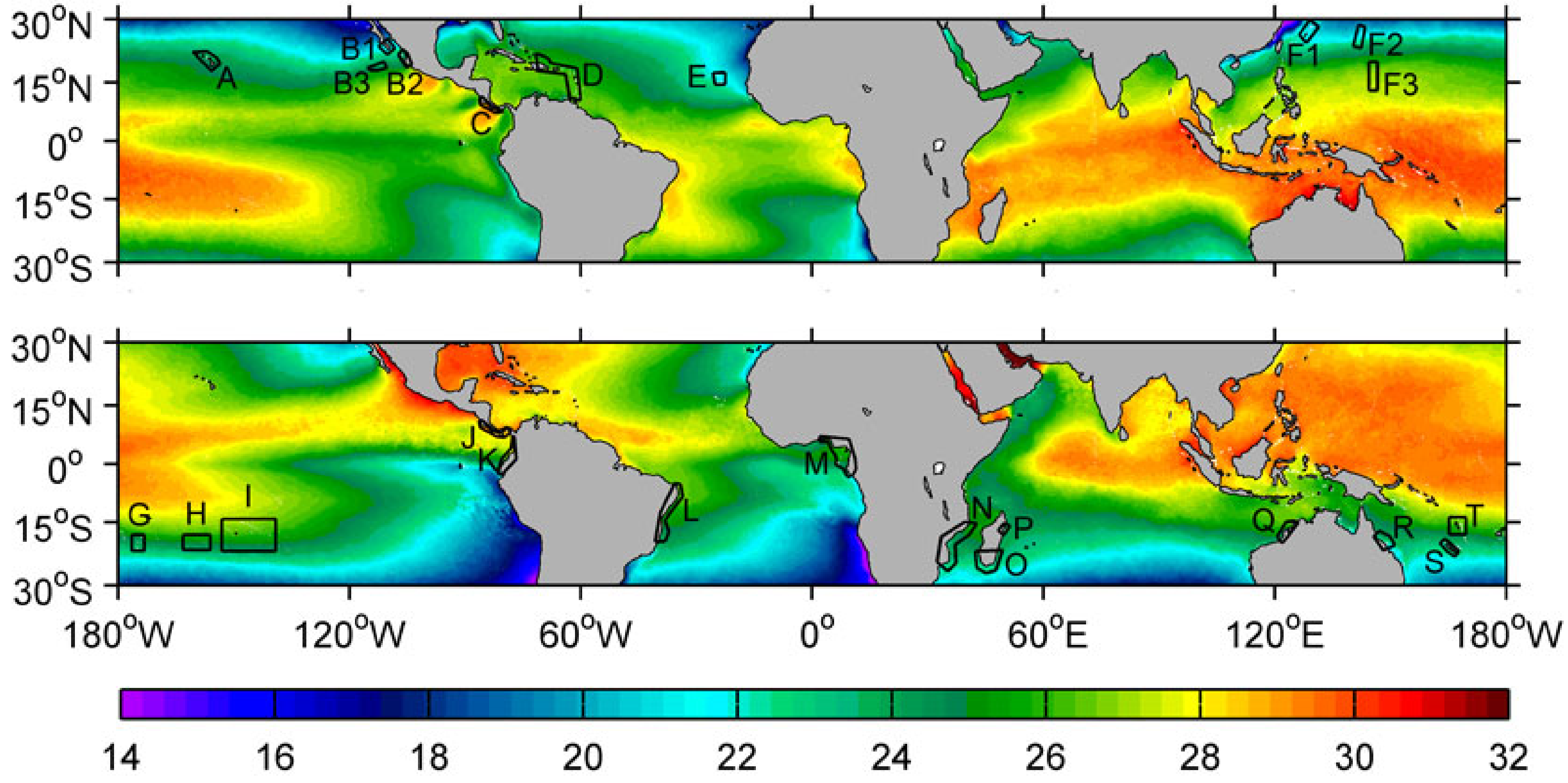

Figure 2. World-wide distribution of wintering areas (black polygons) for (a) ten northern (A-F) and (b) 14 southern (G-T) hemisphere humpback whale populations, overlaid on mean SST for February and for August, respectively (see Table 2 for sources).