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# Sighting and environmental characteristics of humpback whale breeding habitat off Pacific Central America: comparison of Northern and Southern Hemisphere populations

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## ABSTRACT

Humpback whale (*Megaptera novaeangliae*) populations worldwide have been recovering from whaling, albeit at different rates. A recent global review of their population structure and conservation status under the USA Endangered Species Act led to the recognition of 14 Distinct Population Segments (DPS). In this study, we compare the sighting characteristics for two of these DPSs occurring in the Pacific Ocean that use the same habitat off Central America during their respective winters: the Central America DPS, which migrates from feeding areas off the west coast of North America during the boreal winter and is still considered endangered, and the Southeastern Pacific DPS, which migrates from feeding areas off the Antarctic Peninsula and Chile during the austral winter (also known as Breeding Stock G for IWC management purposes) and is no longer considered endangered. We also compare the characteristics of their breeding habitat in terms of seafloor depth, slope, and sea surface temperature (SST). We conducted non-systematic surveys off northwestern Costa Rica (NCR), southeastern Costa Rica (SCR), and western Panama (PAN) during both the boreal winter (22,866 km surveyed in 1996-2003) and the austral winter (6,011 km surveyed in 2000-2007), and made a total of 179 sightings of 305 whales in the boreal winter, and 177 sightings of 364 whales in the austral winter. Overall encounter rates were higher during the austral season than the boreal season (6.06 whales/100 km vs. 1.33 whales/100 km, respectively). Both seasons had a relatively high percentage of groups sighted with a calf, but this percentage was much higher for the austral than the boreal season (57% vs. 28%, respectively), suggesting different demographic parameters for these two DPSs. Although in general whales were seen in similar depth, slope, and SST habitats, significant differences between seasons were found in all three variables. A trend toward shallower depth and steeper slope in the austral winter can be explained by local differences in seafloor characteristics between SCR and PAN, while a trend toward lower SST reflects regionally cooler temperatures during this time of year. Groups with calves had a distinct preference for shallower depth, with most being found at 25 m in the boreal winter and 18 m in the austral winter. Because whales from these two DPSs use the similar habitat during their mating and calving season off Central America, we speculate that factors (natural or anthropogenic) on the feeding areas may be influencing their rates of recovery.

KEYWORDS: HUMPBACK WHALE, MEGAPTERA NOVAEANGLIAE, BREEDING AREA, NORTHERN HEMISPHERE, SOUTHERN HEMISPHERE, CENTRAL AMERICA, HABITAT, OCEANOGRAPHY, MONITORING, INDEX OF ABUNDANCE

## INTRODUCTION

In recent decades, humpback whale populations (*Megaptera novaeangliae*), which are found in all the world's major ocean basins, have been recovering from being decimated by commercial whaling during the 20<sup>th</sup> Century, albeit at different rates (Thomas et al. 2015). Recently the USA government reviewed the current level of threat for humpback whale populations worldwide and recognized 14 Distinct Population Segments (DPS). Of the 14, nine were removed from the Endangered Species List and are no longer considered under threat, while four are considered "Endangered" (the Cape Verde Islands/Northwest Africa, the Western North Pacific, Central America and the Arabian Sea) and one is considered "Threatened" (Mexico) (Bettridge et al. 2015, Federal Register 2016).

Two DPSs occurring in the Pacific Ocean use the coast of Central America as a breeding area. The Central America DPS, seen between December and April (i.e., the boreal winter), migrates from feeding areas off California, Oregon and Washington (Calambokidis et al. 2000, Calambokidis et al. 2008, Barlow et al. 2011, Rasmussen et al. 2012). The most recent population estimate for the Central America DPS is under 500 animals based on data from 2004-2006 (Calambokidis et al. 2008, Wade et al. 2016).

The Southeastern Pacific DPS (also known as Breeding Stock G for IWC management purposes), seen off Central America between July and October (i.e., the austral winter), migrates between feeding areas off the Antarctic Peninsula and Chile, to breeding areas off Peru, Ecuador, Colombia and Central America (Stone et al. 1990, Flórez-González 1991, Florez-Gonzalez et al. 1998, Stevick et al. 2004, Acevedo et al. 2007, Rasmussen et al. 2007). Whales from this DPS undertake the longest migration between a feeding and a breeding area of any population (Rasmussen et al. 2007). The Southeastern Pacific DPS was estimated at 6,500 individuals for the period 2005-2006, although this is likely an underestimate of the entire population (Felix et al. 2011). An

estimate also exists for the portion of this DPS using Las Perlas Archipelago (Gulf of Panama), during the austral winter at about 1,000 animals based on data for the period 2003-2009 (Guzmán et al. 2014).

Globally, humpback whale breeding areas have been generally described as occurring in warm water temperature (24-28°C) and relatively shallow depth (< 200 m) (Dawbin 1966, Herman and Antinaja 1977, Whitehead and Moore 1982, Clapham and Mead 1999). Females with their offspring (“mother/calf pairs”) appear to be the most closely associated with these parameters, showing a distinct preference for shallower depth (Smultea 1994, Felix and Haase 1997, 2001, Ersts and Rosenbaum 2003, Oviedo and Solís 2008, Felix and Botero-Acosta 2011, Cartwright et al. 2012, Trudelle et al. 2016, Oña et al. 2017). Rasmussen et al. (2007) conducted a systematic characterization of the thermal regime at all humpback whale breeding areas worldwide using remotely sensed sea surface temperature (SST), and demonstrated that they all occur in the range 21.1-28.3°C irrespective of latitude. These authors hypothesized that water temperature determines the location of the breeding areas at the basin-scale, while factors such as depth drive habitat choice at the local scale (Rasmussen et al. 2007). Further studies have examined the relationship between humpback whale distribution and these parameters at more local scales. Johnston et al. (2007) used SST and bathymetry for the Northwestern Hawaiian Islands to predict humpback whale habitat, and demonstrated that all sightings from one season of surveys corresponded to the predicted habitat. Smith et al. (2012) similarly used a predictive habitat model to find a relationship between SST (between 21 and 23°C), depth (between 30 and 58 m) and humpback whale sightings off the Great Barrier Reef, Australia. Finally, Guidino et al. (2014) showed that humpback whales at the southern limit of the Southeast Pacific breeding area off Peru were associated with shallow depths (< 200 m) while the temperature was slightly cooler than other studies (mean SST=22.09°C), likely due to the proximity of the Humboldt Current.

In this study, we surveyed areas off Central America during the austral (2001-2007) and boreal (1996-2003) winters in order to compare sighting rates and group composition for the Central America and Southeastern Pacific DPSs during their respective breeding season. We also used environmental data to characterize the habitat used by both DPSs and to determine if these two populations use the same areas in terms of seafloor depth, slope, and SST. Examining two separate populations that use the same habitat during the breeding season but have different recovery rates may provide insight into what potential factors are involved in their recovery.

## **METHODS**

### **Survey Effort**

This study was conducted off the Pacific coast of the Central American Isthmus, in the eastern tropical Pacific (Figs. 1 and 2). For the boreal winter season, our primary area of effort was off the northwest side of the Osa Peninsula, in southeastern Costa Rica (SCR) (Fig. 1). Surveys were conducted from 1996 to 2003 in small boats (5-7 m in length). Two boats were used every day for these surveys, and each boat covered a different search area. Additional small boat surveys were conducted in the Gulf of Chiriquí in western Panama (PAN) (2001-2003), and in northwestern Costa Rica (NCR) from the Gulf of Santa Elena to the Gulf of Papagayo and up to the Nicaraguan border (2000-2003) (Table 1). Austral winter season (July-October) surveys took place from 2001 to 2007 (Table 1). These surveys primarily occurred in the same areas as the austral season surveys, with effort in PAN (2002-2007), SCR (2001-2003), and NCR (2001-2003) (Fig. 2).

All surveys were conducted over the continental shelf, generally in water depth less than 1,000 m. During surveys, between two and eight observers were on board. 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.

Position 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 receiver, weather and sighting conditions, group size, group composition, and behaviors. Group composition was defined as one of seven types: single, pair, more than two adults, mother/calf, mother/calf and another adult (called an escort), mother/calf with more than one escort, and competitive groups, which were defined as groups of greater than three adults exhibiting aggressive behaviors towards each other. These groups typically contain one female (sometimes with a calf) and multiple males competing to mate with the female (Tyack and Whitehead 1983). Yearly mean encounter rates (whales seen per 100 km surveyed) were calculated for all three survey regions to indicate sightings per unit effort and adjust for bias in areas with greater effort, thus providing an index of relative abundance.

## **Bathymetry**

Digital bathymetry was extracted at every 1.5 km of effort and at each sighting location from the SRTM30\_PLUS global topography product (Becker and Sandwell 2009), version 3.0. The product has a grid resolution of 30 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/>). Sea-floor data in SRTM30\_PLUS are based on the Smith and Sandwell (1997) bathymetry, version 9.1 (1-minute resolution). A two-dimensional depth gradient (i.e., slope) was computed on the SRTM-30\_PLUS digital topography for the region using a Sobel operator (Gonzalez and Woods, 2002). Due to the resolution of the bathymetry data set, some of the depth values close to shore were reported as positive values (i.e., elevation). These values, and the corresponding slopes were discarded (n=1351, or 6.9% of effort, and n=17 or 4.6% of sightings). All values that were less than 5 m in depth but greater than 0 m were converted to 5 m (n=333 for effort and n=4 for sightings).

## **Sea-surface Temperature**

Satellite-measured SST products were similarly extracted for all 1.5 km effort segments and as well as for all sighting locations. The following global products, available through NOAA's CoastWatch West Coast Regional Node (<http://coastwatch.pfel.noaa.gov/index.html>), were used: AVHRR Pathfinder V.5.0: available from 1 January 1985 - 31 December 2006, with a grid resolution of 0.05 degrees (~5.5 km). Composites for the ascending and descending passes of 5 day, 8 day, and monthly averages were used. Multiple-satellite blended SST: available from 4 July 2002 - present, with a grid resolution of 0.1 degree (~11 km). This product combines measurements from both microwave and infrared sensors carried on multiple platforms (AVHRR, AMSR-E, MODIS/Aqua, and Imager/GOES), and is available on 5-day averages. The microwave instrument can measure ocean temperatures even in the presence of clouds, dramatically improving coverage in cloudy areas. The estimated measurement error of this product is < 0.2°C, which is superior to the measurement error for the AVHRR Pathfinder product, estimated at ~ 0.3°C (Powell et al. 2008).

An iterative search process was used on both the effort and sighting locations to find a SST value for each point. A first pass searched for AVHRR data at 5-day resolution at the pixel nearest to the effort or sighting location. If no data were available, the search radius was expanded by one pixel around the point (within 7.89 km), and then again by two pixels (15.76 km). Values within these search radii were averaged to obtain a single SST value. If SST data were still not available, then the AVHRR 8-day product was used within two surrounding pixels of the location. Finally, if SST data were still not available, the AVHRR monthly product was used within two pixels of the location. This process yielded 17,899 out of 19,335 SST values for effort, and 284 out of 353 SST values for sightings.

For all whale sighting data after 2002, an independent SST extract was conducted using the multiple satellite blended product. SST values were extracted at the pixel nearest the location, and if no data were available the search was expanded by one pixel surrounding the location (within 15.76 km), and then again by two pixels if data was still missing (31.52 km). This extraction yielded 4,114 results out of 4,794 effort points and 149 out of 168 sightings collected between 2002 and 2006.

Finally, these two sources of SST data were combined into our best SST estimates. The AVHRR data, due to its higher spatial resolution, is preferable to the blended product at the 5-day temporal and up to one pixel (7.89 km) spatial resolution. For any AVHRR value that was missing, or went beyond one pixel or beyond 5 days, the blended product was used. In this manner, we were sure to be using the best SST estimate for all sightings and effort points. Combining the two data sets yielded 19,152 valid SST values of 19,335 effort locations (99%) and 347 valid SST values of 353 sighting locations (98%).

## **Statistical Analyses**

One-way ANOVA tests were performed to quantify differences in encounter rates between the two seasons. A two-factor model-I ANOVA was conducted to test for differences in mean encounter rate among the three regions, and between the austral (2001-2004) and boreal (2000-2003) seasons. Tests for equal variances were performed on the residuals of the ANOVA analyses using Cochran's test, and normal distribution of the residuals was tested using the Kolmogorov-Smirnov test (Zar 1999). Chi-square analyses were conducted to test differences among group types of sightings.

Two-sample Kolmogorov-Smirnov tests (Zar 1999) were used to quantify if the distributions of the three environmental variables of interest (depth, slope and SST) were statistically significant between effort and sightings for each season, and for sightings between seasons. This test was also used to quantify the differences between sightings with calves and other group types for each season. All statistical analyses were conducted using Systat v. 13.

## RESULTS

### Survey Effort and Sightings

Survey effort was spatially similar for both seasons, with surveys in NCR, SCR, and PAN (Figs. 1 and 2). Total survey effort differed between the two seasons, with considerably more effort made during the boreal winter (22,866 km surveyed over eight years) than the austral winter (6,011 km surveyed over four years) (Table 1). For the boreal winter, the majority of the effort was off SCR, where two boats surveyed different areas each day for nearly all of our surveys (Fig. 1, Table 1), while most of the effort during the austral season was off PAN (Fig. 2, Table 1).

Humpback whales from both the Northern and Southern hemispheres were sighted in similar areas during their respective winters (Figs. 1 and 2). In PAN, sightings were near small islands or rocky outcroppings in the Gulf of Chiriquí. Off SCR, whales were seen between the mainland and Caños Island, or along the coastline. In NCR, all sightings during boreal winter occurred in the Gulf of Santa Elena and off the Gulf of Papagayo, whereas sightings during austral winter occurred only in the Gulf of Santa Elena (Figs. 1 and 2).

Encounter rates varied for each area and season. The highest encounter rates occurred off PAN during the austral season (6.949 whales/100 km), and the lowest occurred off PAN during the boreal season (0.386 whales/100 km) (Fig. 3). These regional differences in mean annual encounter rate were statistically significant for the boreal season (ANOVA,  $F=4.131$ ,  $p\text{-value}=0.043$ ), and just above significance for the austral season (ANOVA,  $F=4.394$ ,  $p\text{-value}=0.052$ ). When compared to the boreal winter, mean encounter rates for the three areas during the austral winter were greater and were significantly different than for the boreal winter (two-factor model I ANOVA,  $F=10.239$ ,  $p\text{-value}=0.008$ ; Fig. 3).

Mean group size for the austral season was 2.04 whales ( $SD \pm 1.02$  whales), and maximum group size was 7. More than half of the sightings (57%) contained calves, either as a mother/calf pair, a mother/calf escort trio, or a competitive group with a calf (Table 2). Of all the sightings that included calves, 77% were mother and calf only. All competitive groups sighted except one contained a calf. There were no significant differences among mean encounter rates of calves among the three regions surveyed in the austral season (ANOVA,  $F=1.856$ ,  $p\text{-value}=0.218$ ).

For the boreal season, mean group size was 1.71 animals ( $SD \pm 0.79$  whales) and maximum group size was 5. Not as many sightings contained a calf (28%) as the austral season. Fewer competitive groups were seen in the boreal season (1%) than in the austral season (5%). Mean encounter rates of calves among the three regions surveyed were not significantly different (ANOVA,  $F=0.519$ ,  $p\text{-value}=0.608$ ). In contrast, comparisons of the overall composition of groups types between the two seasons (Table 2) found a highly significant difference ( $\chi^2=108.08$ ,  $df=6$ ,  $p\text{-value} < 0.0001$ ).

### Bathymetry and SST

In the boreal season, effort occurred in depth between 5 and 1,953 m (mean 74.1 m,  $SD \pm 163$  m), slope between 0 and 411.7 m/km (mean 15.8 m/km,  $SD \pm 31.9$  m/km) and SST between 17.1 and 32.67°C (mean 28.82°C,  $SD \pm 1.82$ °C). Sightings occurred at depth between 5 and 119 m (mean 41 m,  $SD \pm 19$  m), and slope between 0.19 and 45.71 m/km (mean 7.89 m/km,  $SD \pm 7.24$  m/km). SST ranged between 21.85 and 31.05°C (mean 28.9°C,  $SD \pm 1.07$ °C).

Effort in the austral season occurred in depth between 5 and 847 m (mean 55 m,  $SD \pm 78$  m), slope between 0.19 and 235.8 m/km (mean 15.5,  $SD \pm 22.7$  m/km), and SST between 17.34 and 30.45°C (mean 28.21°C,  $SD \pm 1.18$ °C). Sightings occurred at depth between 5 and 320 m (mean 36 m,  $SD \pm 43$  m), and slope between 0.55 and 71.86 m/km (mean 10.07 m/km,  $SD \pm 10.22$  m/km). SST ranged between 24.22 and 30.03°C (mean 28.3°C,  $SD \pm 1.04$ °C).

The Kolmogorov-Smirnov statistic showed that the distribution of sighting depth was highly significantly different from the distribution of effort depth for both seasons ( $p\text{-value} < 0.0001$  in both cases) (Table 3). For the boreal season, the distribution of effort had a broad peak in the range 18-50 m, and a secondary minor peak at 68 m, while the distribution of sightings had a narrower peak at 37 m (range: 28-48 m) (Fig. 4). For the austral season, the distribution of effort had a broad peak in the range 6-32 m, and a secondary minor peak at 41 m, while the distribution of sightings had a narrower peak at 18 m (range: 12-26 m), and a secondary minor peak at 38 m (Fig. 4). Statistical comparison of the distribution of depth between sightings for the boreal and austral seasons indicated that they were highly significantly different (Kolmogorov-Smirnov test,  $p\text{-value} < 0.0001$ ) (Table 3).

The distribution for sighting slope was significantly different from the effort slope for the boreal season (Kolmogorov-Smirnov test,  $p\text{-value}=0.036$ ), but it was just above significance for the austral season

(Kolmogorov-Smirnov test,  $p$ -value=0.057) (Table 3). However, visually, the distribution of slope for effort and for sightings were virtually undistinguishable from each other, both for boreal and austral seasons (Fig. 4). Sightings primarily occurred in the range 2-10 m/km, with a strong peak at 3 m/km in all cases (Fig. 4). Statistical comparison of the distribution of slope between sightings for the boreal and austral seasons indicated a significant difference (Kolmogorov-Smirnov test,  $p$ -value=0.019) (Table 3), with more representation of steeper slope values in the austral winter (Fig. 4).

The distribution of SST was not significantly different between sightings and effort for either the boreal (Kolmogorov-Smirnov test,  $p$ -value=0.067) or the austral season (Kolmogorov-Smirnov test,  $p$ -value=0.869) (Table 3). Similar to slope, visually, the distribution of SST for effort and for sightings were virtually undistinguishable from each other, both for boreal and austral seasons (Fig. 4). These distributions were more symmetrical than those for depth and slope. A single clearly defined peak occurred at 28.6°C for the boreal winter (range: 28.3-29°C), and at 28.3°C for the austral winter (range: 27.5-29°C) (Fig. 4). These distributions also indicated that there were relatively fewer observations below 27.5°C and more observations above 30.5°C in the boreal winter than in the austral winter (Fig. 4). Statistical comparison of the distribution of SST between sightings for the boreal and austral seasons indicated that they were highly significantly different (Kolmogorov-Smirnov test,  $p$ -value < 0.0001) (Table 3).

When comparing sightings with calves against all other group types, the distribution of depth was highly significantly different for both seasons (Kolmogorov-Smirnov test,  $p$ -value=0.01 for both the boreal seasons and  $p$ -value=0.016 the austral season) (Table 3). For the boreal season, the distribution of sightings with calves was bimodal, with a primary peak at 25 m and a secondary peak at 46 m, while sightings of other groups types had a single peak at 35 m (range: 28-48 m) (Fig. 5). For the austral season, the distribution of calf sightings had a primary peak at 18 m (range: 12.5-25 m), and a secondary minor peak at 40 m, while the distribution of non-calf sightings had a broad, bimodal peak at 22 and 40 m (range: 12.5-28 m) (Fig. 5).

The distribution of slope was significantly different between calf and non-calf sightings for the boreal (Kolmogorov-Smirnov test,  $p$ -value=0.017) but not for the austral season (Kolmogorov-Smirnov test,  $p$ -value=0.756) (Table 3). As with the comparison between effort and sightings, this difference was visually less distinguishable; in all cases, sightings primarily occurred in the range 2-10 m/km, with a strong peak at about 3 m/km (Fig. 5).

Finally, the distribution of SST was not significantly different between calf and non-calf sightings for either boreal (Kolmogorov-Smirnov test,  $p$ -value=0.572) or austral season ( $p$ -value=0.229) (Table 3). As with the comparison between effort and sightings, SST had clearly defined peak at 28.6°C for the boreal winter (range: 28.3-29°C), and at 28.3°C for the austral winter (range: 27.5-29°C) (Fig. 5).

## DISCUSSION

The spatial distribution of sighting locations indicated the whales from both the boreal and austral winter seasons used the same general areas off Central America: the island groups and rocky outcroppings in the Gulf of Chiriquí (PAN), the waters between Caños Island and coastal SCR, and the islands and gulfs in NCR. These are all characterized by shallow, somewhat protected waters, as has been described for other breeding areas in previous studies (Dawbin 1966, Herman and Antinoya 1977, Whitehead and Moore 1982, Clapham and Mead 1999).

The overall encounter rate (6.056 whales/100 km) during the austral winter was much higher than the boreal (1.334 whales/100 km), which is likely a reflection of the current population sizes for the two DPSs studied here. While the data for the Southeastern Pacific DPS in this study go through 2007, more recent surveys in PAN have indicated that sighting rates have been increasing; whether this is due to population increase or habitat shift is unclear (Rasmussen and Palacios 2015). The geographic gradient in encounter rate seen for both seasons, with higher encounter rates off NCR and decreasing toward SCR and PAN during the boreal season, and higher encounter rates off PAN and decreasing toward SCR and NCR during the austral season, suggests that the closer to the feeding area, the higher the sighting rate. Oviedo and Solis (2008) also reported a higher encounter rate for the austral season than for the boreal season off SCR in 2005-2006 (11.85 vs. 3.0 whales/hour, respectively).

Sightings of groups with calves were higher during the austral winter season, consistent with the overall higher encounter rates during this season. In both seasons, the number of calves seen was greater than in other studies (range: 8-27%, Mattila and Clapham 1989, Mattila et al. 1994, Garrigue et al. 2001, Hauser et al. 2000, Zerbini et al. 2004). The higher sighting rate of calves during the austral (57 %) than the boreal season (28%), could indicate that the austral population has a greater calving rate than the boreal population. For both populations, it is clear that Costa Rica and Panama is an important nursery area.

Another significant difference was the greater number of competitive groups seen during the austral winter season (5%) compared with the boreal winter season (1%). Whereas the percentage of competitive groups of the austral season was less than other studies (range: 2-18%; Garrigue *et al.* 2001, Mattila *et al.* 1994, Mattila *et al.* 1989), the greater number of competitive groups in the austral winter could be a result of an overall greater density of animals during that season.

In terms of environmental characteristics, whales were not uniformly distributed with respect to the distribution of effort, but had specific habitat preferences within the areas studied and, in some cases, also between the boreal and austral winter seasons. Sightings generally occurred in depth shallower than 75 m in both seasons, although it appeared that most sightings occurred at deeper depth in the boreal (37 m) than in the austral (18 m) season. Indeed, the distribution of depth for both effort and sightings appeared to be shifted toward shallower depth for the austral season compared to the boreal season, which is explained by local differences in seafloor depth characteristics between SCR (which drove sample size in the boreal winter) and PAN (which drove sample size in the austral winter).

Seafloor slope did not appear to be a primary determinant of breeding habitat at local scales, given that the distribution of effort and of sightings for this variable was virtually the same in either season. Nevertheless, humpback whale breeding distribution can be generally characterized by a gentle slope in the range 2-10 m/km, with a peak at 3 m/km. As with depth, the significant difference in the distribution of slope for sightings between boreal and austral seasons is explained by local differences in seafloor slope characteristics between the areas surveyed off SCR and off PAN.

Humpback whale breeding distribution off Central America can be generally characterized by SST values peaking in the range 27-29°C, but like slope, SST does not appear to be a primary determinant of breeding habitat at the local scale, given that the distributions of effort and of sightings for this variable were very similar in either season. The differences in the distribution of SST for sightings between boreal and austral seasons are explained by the fact that the eastern tropical Pacific region is generally cooler during the austral winter due to the development of an equatorial cold tongue (Amador *et al.* 2006, Fiedler and Talley 2006), which Rasmussen *et al.* (2007) invoked as the reason why the breeding areas for the Southeastern Pacific DPS are found north of the equator.

Depth was the only variable that clearly separated groups with calves from other group types in both seasons, with most groups with calves being found at about 25 m in the boreal winter and at about 18 m in the austral winter, while groups without calves tended to occur in deeper depth (35-40 m). This preference for shallower depth by mother/calf pairs while in the breeding areas has been widely observed in studies in many other parts of the world (Smultea 1994, Felix and Haase 1997, Felix and Haase 2001, Ersts and Rosenbaum 2003, Oviedo and Solís 2008, Felix and Botero-Acosta 2011, Cartwright *et al.* 2012, Trudelle *et al.* 2016, Oña *et al.* 2017).

Pacific Central America provided a unique opportunity to examine the breeding habitat used at different times of the year by two distinct humpback whale populations. Although the data from this study are from 1996-2007 and the effort was not the same for both seasons, recent estimates indicate that the Southeastern Pacific DPS from the Southern Hemisphere continues to grow, while the Central America DPS from the Northern Hemisphere has not. Because these two populations are utilizing very similar habitat during their breeding season, both qualitatively and quantitatively, we speculate that factors in the feeding areas may be influencing their disparate growth rates. The Central America DPS feeds off California-Oregon-Washington in coastal areas with more human impacts, while the Southeastern Pacific DPS feeds in two main areas, the Antarctic Peninsula and the Strait of Magellan, which are both more remote. Fisheries, ship traffic, and availability of prey likely all influence the quality of these feeding areas, which in turn would affect the growth rate of the populations.

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Table 1. Survey effort, including dates and total kilometers surveyed (km), and humpback whale sightings, including total sightings, number of whales seen (Tot), number of calves, and encounter rate or number of whales seen per 100 km surveyed (Enc rate) off Central America 1996-2007 for both the Northern (NH) and Southern (SH) hemisphere winter seasons in northwestern Costa Rica (NCR), southeastern Costa Rica (SCR) and Panama (PAN).

| Seas          | Year | Region | Survey effort |          |            |               | Whale sightings |            |            |              |
|---------------|------|--------|---------------|----------|------------|---------------|-----------------|------------|------------|--------------|
|               |      |        | Start date    | End date | days       | km            | Sightings       | Tot        | Calves     | Enc rate     |
| NH            | 2000 | NCR    | 23-Jan        | 24-Jan   | 2          | 57            | 1               | 1          | 0          | 1.754        |
| NH            | 2001 | NCR    | 19-Jan        | 21-Jan   | 3          | 219           | 3               | 4          | 0          | 1.826        |
| NH            | 2002 | NCR    | 8-Mar         | 10-Mar   | 3          | 248           | 2               | 3          | 1          | 1.210        |
| NH            | 2003 | NCR    | 11-Mar        | 14-Mar   | 4          | 241           | 2               | 3          | 1          | 1.245        |
| NH            | 1996 | SCR    | 26-Jan        | 16-Feb   | 15         | 2,927         | 15              | 22         | 0          | 0.752        |
| NH            | 1997 | SCR    | 31-Jan        | 14-Feb   | 10         | 2,231         | 26              | 44         | 3          | 1.972        |
| NH            | 1998 | SCR    | 24-Jan        | 18-Feb   | 15         | 3,211         | 18              | 25         | 2          | 0.779        |
| NH            | 1999 | SCR    | 27-Jan        | 7-Feb    | 10         | 2,313         | 32              | 60         | 19         | 2.594        |
| NH            | 2000 | SCR    | 25-Jan        | 13-Feb   | 16         | 3,219         | 30              | 47         | 6          | 1.460        |
| NH            | 2001 | SCR    | 24-Jan        | 11-Feb   | 13         | 3,685         | 29              | 60         | 13         | 1.628        |
| NH            | 2002 | SCR    | 6-Feb         | 14-Mar   | 7          | 1,556         | 11              | 21         | 3          | 1.350        |
| NH            | 2003 | SCR    | 29-Jan        | 7-Feb    | 5          | 1,145         | 6               | 8          | 1          | 0.699        |
| NH            | 2001 | PAN    | 14-Feb        | 17-Feb   | 4          | 493           | 2               | 4          | 1          | 0.811        |
| NH            | 2002 | PAN    | 22-Feb        | 27-Feb   | 6          | 626           | 1               | 1          | 0          | 0.160        |
| NH            | 2003 | PAN    | 25-Feb        | 28-Feb   | 4          | 695           | 1               | 2          | 0          | 0.288        |
| <b>TOTALS</b> |      |        |               |          | <b>117</b> | <b>22,866</b> | <b>179</b>      | <b>305</b> | <b>50</b>  | <b>1.334</b> |
| SH            | 2001 | NCR    | 24-Aug        | 26-Aug   | 3          | 186           | 1               | 2          | 1          | 1.075        |
| SH            | 2002 | NCR    | 15-Aug        | 29-Sep   | 4          | 305           | 0               | 0          | 0          | 0.000        |
| SH            | 2003 | NCR    | 21-Sep        | 23-Sep   | 2          | 146           | 3               | 6          | 3          | 4.110        |
| SH            | 2001 | SCR    | 12-Aug        | 29-Aug   | 9          | 626           | 15              | 29         | 10         | 4.633        |
| SH            | 2002 | SCR    | 21-Aug        | 31-Aug   | 6          | 854           | 25              | 62         | 19         | 7.260        |
| SH            | 2003 | SCR    | 9-Sep         | 9-Sep    | 1          | 81            | 0               | 0          | 0          | 0.000        |
| SH            | 2002 | PAN    | 5-Sep         | 14-Sep   | 6          | 776           | 17              | 30         | 7          | 3.866        |
| SH            | 2003 | PAN    | 2-Sep         | 6-Sep    | 5          | 511           | 21              | 45         | 13         | 8.806        |
| SH            | 2004 | PAN    | 6-Sep         | 9-Sep    | 4          | 402           | 17              | 32         | 12         | 7.960        |
| SH            | 2006 | PAN    | 29-Aug        | 1-Sep    | 4          | 487           | 17              | 34         | 13         | 6.982        |
| SH            | 2007 | PAN    | 28-Jul        | 2-Oct    | 18         | 1,637         | 61              | 124        | 29         | 7.575        |
| <b>TOTALS</b> |      |        |               |          | <b>62</b>  | <b>6,011</b>  | <b>177</b>      | <b>364</b> | <b>107</b> | <b>6.056</b> |

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

|   | Boreal             |     | Austral            |     |
|---|--------------------|-----|--------------------|-----|
|   | winter (1996-2003) |     | winter (2001-2007) |     |
|   | #                  | %   | #                  | %   |
| Singles   | 84                 | 47% | 38                 | 21% |
| Pairs (not including m/c pairs)                     | 38                 | 21% | 27                 | 15% |
| Mother/calf   | 31                 | 17% | 86                 | 49% |
| Mother/calf/escort                                  | 20                 | 11% | 15                 | 8%  |
| Groups larger than 2 (excluding competitive groups) | 4                  | 2%  | 3                  | 2%  |
| Competitive Groups                                  | 2                  | 1%  | 1                  | 1%  |
| Competitive Groups w calf                           | 0                  | 0%  | 7                  | 4%  |
| Total groups with calf                              | 51                 | 28% | 101                | 57% |
| <b>Total</b>  | <b>179</b>         |     | <b>177</b>         |     |

Table 3. Summary of the Kolmogorov-Smirnov tests for distribution of the environmental variables between the boreal (NH) and austral (SH) winter seasons.

| Distribution tested                          | Variable | P-value |
|--|----------|---------|
| NH sightings (n=177) vs. effort (n=14,468)   | Depth    | <0.0001 |
| NH sightings (n=177) vs. effort (n=14,468)   | Slope    | 0.036   |
| NH sightings (n=178) vs. effort (n=14,905)   | SST      | 0.067   |
| SH sightings (n=159) vs. effort (n=3,516)    | Depth    | <0.0001 |
| SH sightings (n=159) vs. effort (n=3,516)    | Slope    | 0.057   |
| SH sightings (n=169) vs. effort (n=3,406)    | SST      | 0.869   |
| NH sightings (n=177) vs SH sightings (n=159) | Depth    | <0.0001 |
| NH sightings (n=177) vs SH sightings (n=159) | Slope    | 0.019   |
| NH sightings (n=178) vs SH sightings (n=169) | SST      | <0.0001 |
| NH calf (n=50) vs. non-calf (n=127)          | Depth    | 0.010   |
| NH calf (n=50) vs. non-calf (n=127)          | Slope    | 0.017   |
| NH calf (n=51) vs. non-calf (n=127)          | SST      | 0.572   |
| SH calf (n=99) vs. non-calf (n=60)           | Depth    | 0.016   |
| SH calf (n=99) vs. non-calf (n=60)           | Slope    | 0.756   |
| SH calf (n=102) vs. non-calf (n=67)          | SST      | 0.229   |

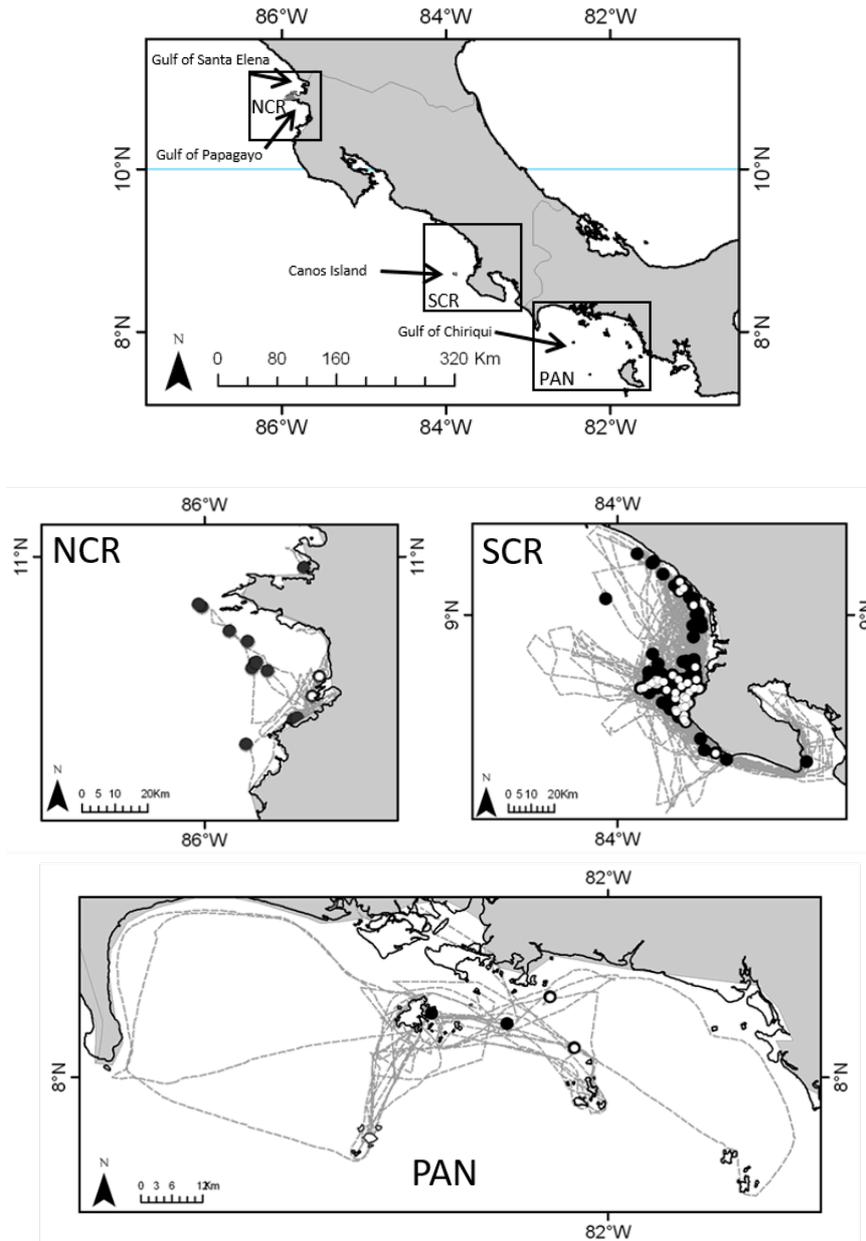


Figure 1. Survey effort and sightings in three regions (NCR: northwestern Costa Rica, SCR: southeastern Costa Rica, and PAN: western Panama) for the boreal winter season (January-March) between 1996 and 2003. Survey effort shown in hatched grey lines, sightings of humpback whales shown by black circles, and sightings with calf by white circles.

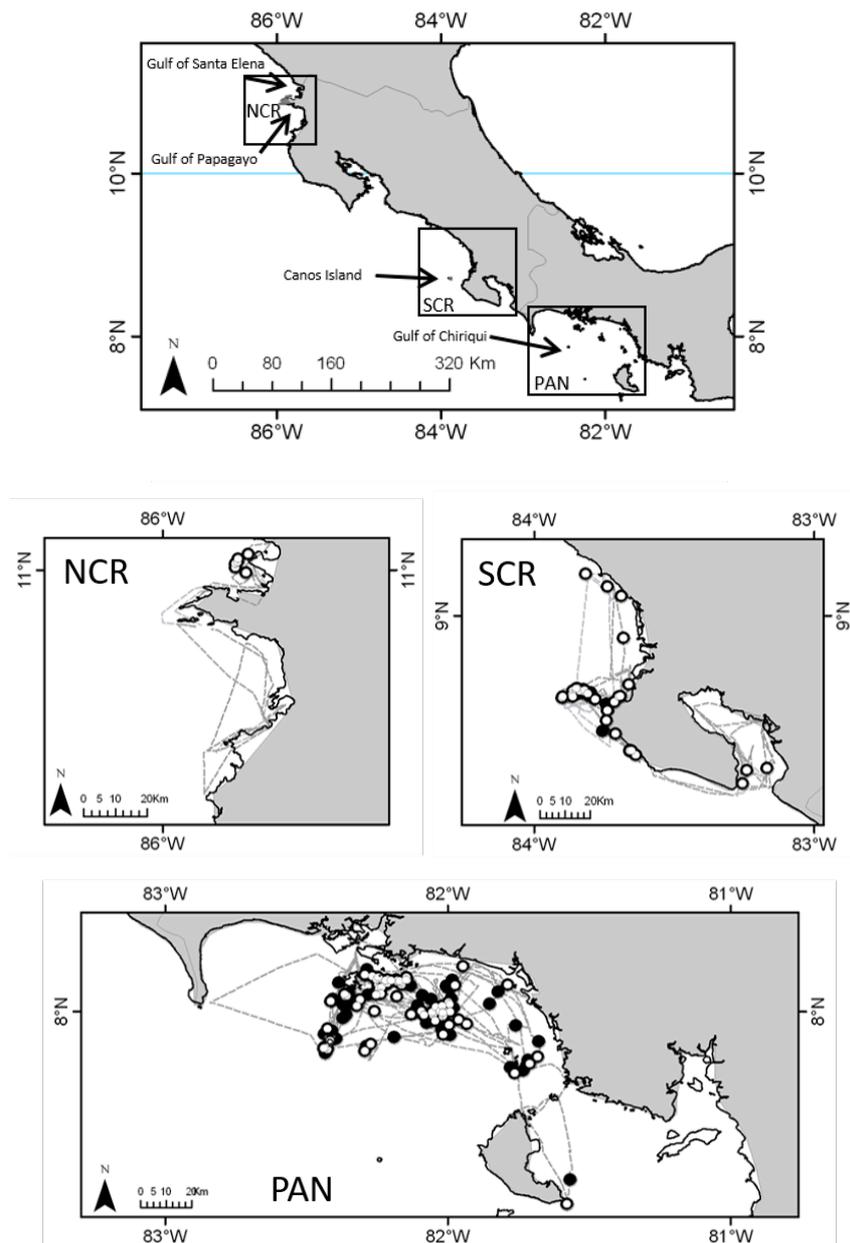


Figure 2. Survey effort and sightings in three regions (NCR: northwestern Costa Rica, SCR: southeastern Costa Rica, and PAN: western Panama) for the austral winter season (July-October) between 2001 and 2007. Survey effort shown in hatched grey lines, sightings of humpback whales shown by black circles, and sightings with calf by white circles.

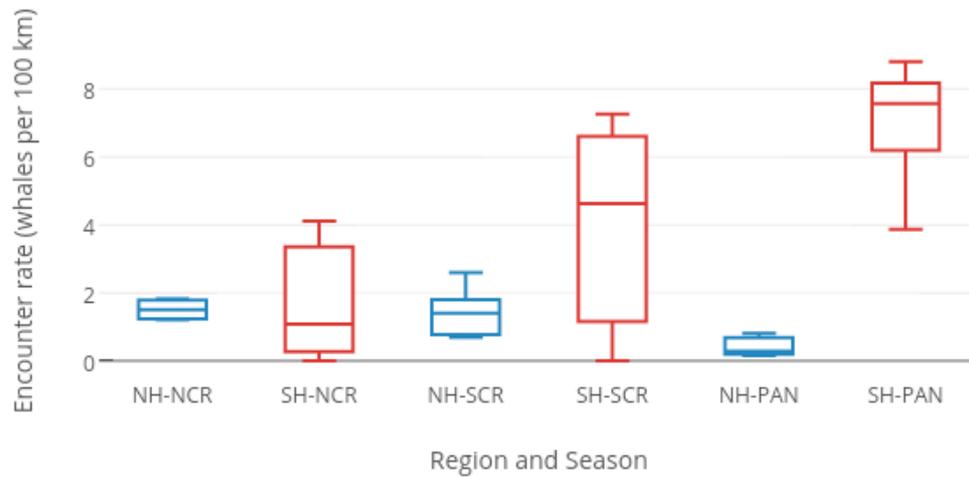


Figure 3. Mean yearly encounter rates (number whales per km) of boreal (NH) and austral (SH) winter humpback whale sightings for three regions (NCR=northwestern Costa Rica, SCR=southeastern Costa Rica, PAN=western Panama). Boxes represent 95% confidence intervals, horizontal line represents the median, and vertical bars represent the minimum and maximum encounter rate values.

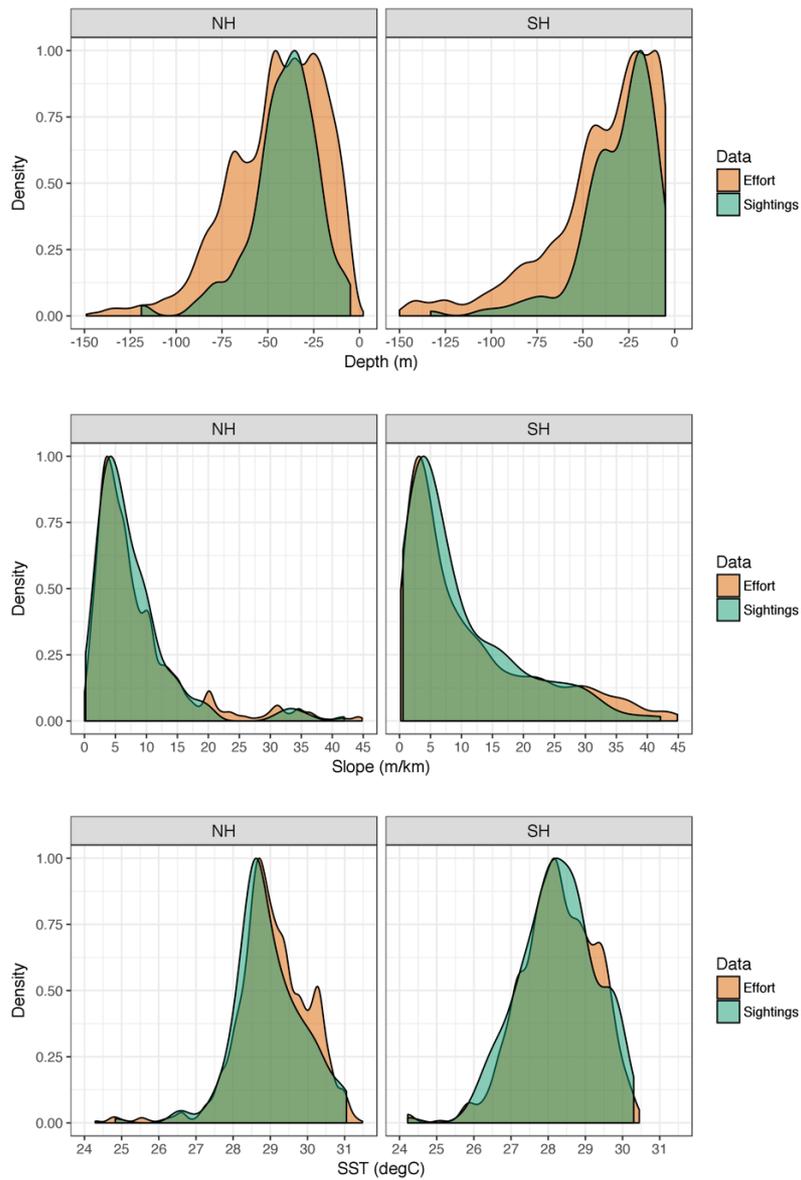


Figure 4. Probability density plots comparing the distribution of effort and of sightings (y axis) against three environmental variables, Depth (top), Slope (middle) and SST (bottom) for both boreal (NH) and austral (SH) seasons. Note that for optimal visual examination, the extent of the x axis for all variables has been limited to the range where most observations occurred to avoid long tails caused by a few extreme values. The full ranges of the variables are reported in the Results section.

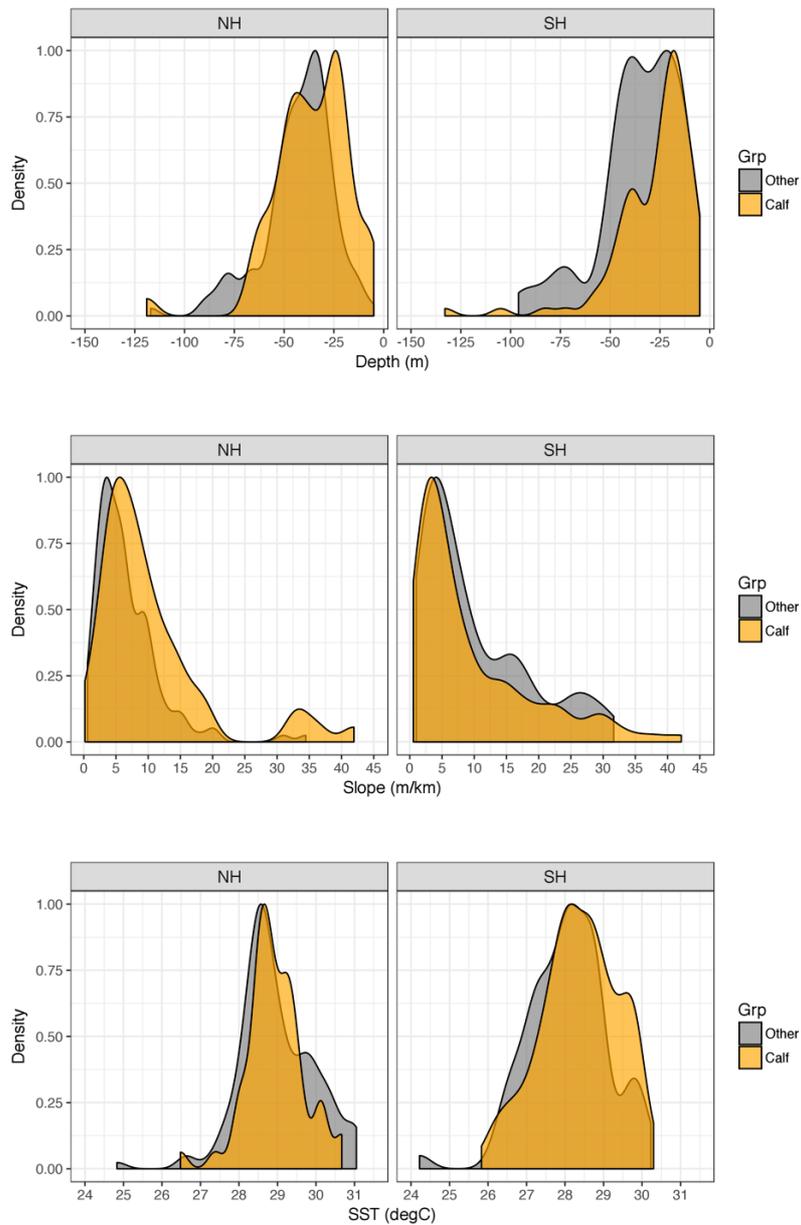


Figure 5. Probability density plots comparing the distribution of sightings with a calf and sightings without a calf (y axis) against three environmental variables, Depth (top), Slope (middle) and SST (bottom) for both boreal (NH) and austral (SH) seasons. Note that for optimal visual examination, the extent of the x axis for all variables has been limited to the range where most observations occurred to avoid long tails caused by a few extreme values. The full ranges of the variables are reported in the Results section.