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Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration

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THE DISTRIBUTION OF HUMPBACK WHALE WINTERING AREAS WORLDWIDE IN RELATION TO SEA-SURFACE TEMPERATURE

We conducted a review of the literature based on modern research to determine the location of humpback whale wintering areas worldwide, using the criteria described in the Methods section (see table A1 for a listing of sources). One known humpback whale population inhabiting the Arabian Sea was not included in this study because it does not appear to undertake seasonal migrations, but rather remains in tropical waters year-round (Mikhalev 1997). A total of 24 areas were identified, all within 30° of the equator. For three of these, information was inconclusive as to whether they are a true wintering area or part of the migratory route, but were still included in the analysis. Specifically, for the two Japanese areas, the Ryukyu and Bonin Island groups (F1 and F2 in figure 2 and table A1), calving may actually occur 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 & Aguayo-L 1987), suggesting that this area may be a migratory corridor for whales going further south.

A polygon delineating the approximate extent of each wintering area was drawn over digital maps of climatological sea-surface temperature (SST) for the month of peak calving occurrence: February for the Northern Hemisphere and August for the Southern Hemisphere (Chittleborough 1958; Clapham & Mead 1999). The average SST and the standard deviation for all pixels inside a polygon were computed for each one of the 24 areas identified. These values are reported in table A1, where a letter code is used to identify each area in figure 2 of the paper (these letter codes bear no relationship to the Southern Hemisphere stock designations by the International Whaling Commission, IWC). The average SST for all wintering areas was 24.6°C (± 1.9°C s.d.). The three ambiguous areas B1, F1, and F2 had the lowest SSTs (21.09-21.91°C), such that if they were excluded, the global average would be 25.1°C (±1.4°C s.d.).

The relationship between mean latitude and mean SST at the wintering areas is presented in figure A1 in the context of latitudinal global SST range. Most wintering areas occur at or above the global mean SST for that latitude (colored curves in figure A1), and they are generally closer to the upper end of the global SST range (shaded areas in figure A1). In addition, with a few noteworthy exceptions, humpback whale wintering areas do not occur within 10° of the equator. At these latitudes, there is an actual dip in SST due to wind-induced equatorial upwelling processes, as evidenced by the colored curves in figure A1. The exceptions are the wintering areas for eastern South Pacific and eastern South Atlantic humpback whales, which migrate to the warm waters found north of the equator (see figure 2), and the wintering area for eastern North Pacific whales off Panama and Costa Rica, which may migrate past (south) of the

localized upwellings that occur in the Gulfs of Tehuantepec and Papagayo during boreal winter (see figure 2). These observations indicate that there is a global correlation between the distribution of humpback whale wintering areas and SST.

Finally, the Cape Verde Islands, a wintering area for eastern North Atlantic humpback whales (Reiner *et al*. 1996; Hazevoet & Wenzel 2000; Jann *et al*. 2003), stand out as an outlier in SST-latitude space (figure A1) due to their low mean SST (22.1°C), which is, again, influenced by low-latitude upwelling processes. Similarly low SSTs occur at the Gálapagos Islands in the eastern equatorial Pacific (figure 1), where recent research suggests that this archipelago may be a wintering area for eastern South Pacific humpback whales (Félix *et al*. 2006; D. M. Palacios, unpublished observations). We suggest that humpback whales may winter in areas with less than optimal water temperatures in areas that offer shallow, protected conditions, especially as populations continue to recover from depletion.

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Table A1. Climatological sea-surface temperature (SST, °C) and standard deviation (s.d., °C) for humpback whale wintering areas in both the Northern and Southern Hemispheres shown in figure 2. The northernmost, southernmost, easternmost, and westernmost coordinates of each polygon are given. Literature sources are listed below.

				geographic coordinates			
	Northern Hemisphere	SST	SD	N	S	E	W
A	Hawaii[1,2]	24.15	0.31	22.44	17.74	-153.50	-160.59
B1	Mexico: Baja California[3]	21.09	0.79	25.65	21.81	-108.29	-112.33
B2	Mexico: mainland[3]	24.05	0.84	22.98	18.62	-103.85	-107.21
B3	Mexico: Revillagigedos[3]	24.32	0.30	20.11	17.96	-110.36	-115.31
C	Central America[4]	28.27	0.96	11.42	7.25	-80.79	-85.62
D	West Indies[5,6]	26.11	0.27	21.95	10.49	-60.03	-71.62
E	Cape Verde Islands[7,8,9]	22.10	0.36	17.37	14.47	-22.51	-25.68
F1	Japan: Ryukyu Islands[10,11,12,13]	21.60	0.44	29.81	24.66	131.31	126.32
F2	Japan: Bonin Islands[11,12,13,14,15,16]	21.91	1.13	28.74	23.33	143.47	140.30
F3	Mariana Islands[12,16]	26.96	0.42	20.06	12.92	146.56	144.43
	Southern Hemisphere	SST	SD	N	S	E	W
G	Tonga[17,18]	24.34	0.68	-18.00	-21.97	-173.18	-176.41
H	Cook Islands[17,18,19]	25.07	0.63	-18.07	-21.72	-156.02	-163.15
I	Polynesia[17,18,20]	25.93	0.88	-14.08	-22.05	-139.05	-153.04
J	Central America[4]	28.00	0.79	11.17	6.86	-78.27	-86.40
K	Colombia and Ecuador[21,22,23,24,25]	25.67	2.23	7.13	-2.79	-76.76	-81.70
L	Brazil[26,27,28]	25.37	1.05	-5.02	-19.73	-34.21	-40.72
M	West Africa[29,30,31,31]	24.89	2.79	7.11	-3.35	11.39	1.85
N	East Africa[29]	24.08	1.84	-14.92	-26.66	42.76	32.42
O	S Madagascar[29,33,34,35]	23.20	0.61	-21.77	-27.14	49.39	42.29
P	NE Madagascar[34]	24.02	0.22	-15.19	-18.06	51.22	48.30
Q	NW Australia[26,37,38,39]	25.54	0.90	-14.71	-19.86	126.08	120.61
R	NE Australia[40,41,42]	23.43	0.87	-17.08	-21.78	151.06	147.01
S	New Caledonia[17,18,43]	23.30	0.57	-18.99	-23.23	167.73	162.79
T	Samoa[18]	26.25	0.50	-13.70	-17.94	169.60	165.27

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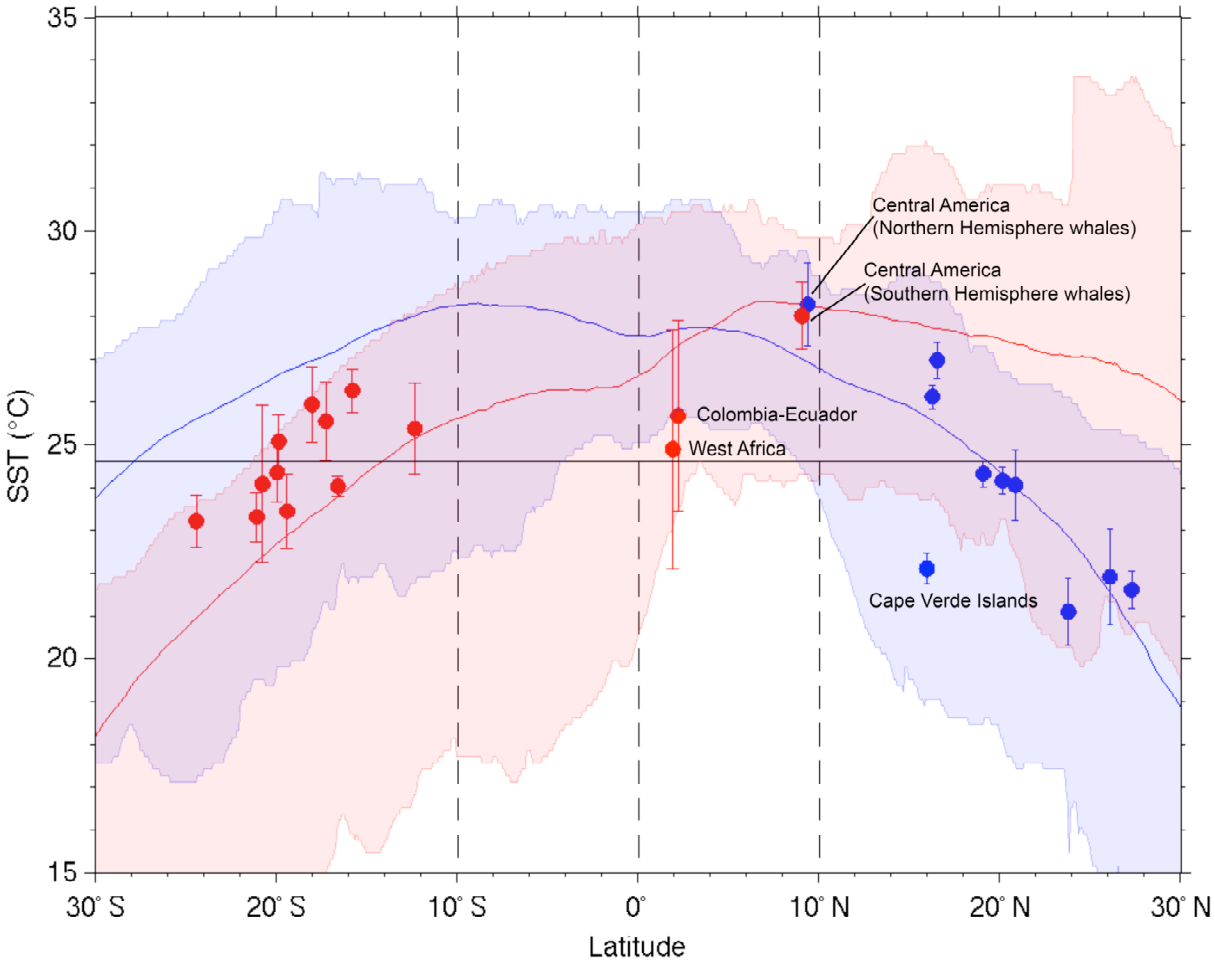

Figure A1. Mean latitude vs. mean SST at the wintering areas for Northern (blue circles) and Southern (red circles) Hemisphere humpback whale populations. Error bars are the standard deviations reported in table A1, and are a measure of the spatial variability of SST within each wintering area. Shaded areas represent the global range of SST at a given latitude for February (light blue) and for August (light red). Solid curves are the global mean (blue for February and red for August, respectively). Horizontal black line corresponds to the average SST for all wintering areas (24.6°C). Vertical black dashed lines at 10° S, 0°, and 10° N are drawn for reference. Names of selected wintering areas are mentioned in the text.