biology letters
Marine biology

Biol. Lett.
doi:10.1098/rsbl.2007.0067
Published online

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

Kristin Rasmussen[1,2,*], Daniel M. Palacios[3,4], John Calambokidis[1], Marco T. Saborío[5], Luciano Dalla Rosa[6,7], Eduardo R. Secchi[7], Gretchen H. Steiger[1], Judith M. Allen[8] and Gregory S. Stone[9]

[1]*Cascadia Research Collective, 218 1/2 West Fourth Avenue, Olympia, WA 98501, USA*
[2]*Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA*
[3]*Joint Institute for Marine and Atmospheric Research, 1000 Pope Road, MSB 312, Honolulu, HI 96822, USA*
[4]*NOAA/NMFS/SWFSC/Environmental Research Division, 1352 Lighthouse Avenue, Pacific Grove, CA 93950, USA*
[5]*Apartado 292-2300, San José, Costa Rica*
[6]*Department of Zoology and Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*
[7]*Brazilian Antarctic Program, Museu Oceanográfico 'Prof. Eliézer C. Rios', FURG, Rio Grande, RS 96200-970, Brazil*
[8]*College of the Atlantic, 105 Eden Street, Bar Harbour, ME 04609, USA*
[9]*New England Aquarium, Central Wharf, Boston, MA 02110, USA*
**Author for correspondence (krasmussen@mlml.calstate.edu).*

We report on a wintering area off the Pacific coast of Central America for humpback whales (*Megaptera novaeangliae*) migrating from feeding areas off Antarctica. We document seven individuals, including a mother/calf pair, that made this migration (approx. 8300 km), the longest movement undertaken by any mammal. Whales were observed as far north as 11° N off Costa Rica, in an area also used by a boreal population during the opposite winter season, resulting in unique spatial overlap between Northern and Southern Hemisphere populations. The occurrence of such a northerly wintering area is coincident with the development of an equatorial tongue of cold water in the eastern South Pacific, a pattern that is repeated in the eastern South Atlantic. A survey of location and water temperature at the wintering areas worldwide indicates that they are found in warm waters (21.1–28.3°C), irrespective of latitude. We contend that while availability of suitable reproductive habitat in the wintering areas is important at the fine scale, water temperature influences whale distribution at the basin scale. Calf development in warm water may lead to larger adult size and increased reproductive success, a strategy that supports the energy conservation hypothesis as a reason for migration.

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2007.0067 or via http://www.journals.royalsoc.ac.uk.

Received 2 February 2007
Accepted 13 March 2007

Keywords: humpback whale; *Megaptera novaeangliae*; migration; Central America; Antarctica; sea-surface temperature

1. INTRODUCTION

The long annual migrations of baleen whales from productive high-latitude areas used for feeding (feeding areas) to low-latitude oligotrophic areas used for breeding (wintering areas) are well known, but the selective forces driving them remain unclear. Several hypotheses have been proposed that include: a vestigial behaviour from when smaller ocean basins meant closer feeding and wintering areas (Evans 1987); the optimization of energy budgets by wintering in warm waters (Brodie 1975); increased calf (offspring) growth and survivorship in warm protected waters (Norris 1967); and avoidance of killer whale (*Orcinus orca*) predation at low latitudes (Corkeron & Connor 1999).

For humpback whales (*Megaptera novaeangliae*), which occur in all major ocean basins, wintering areas are at approximately 20° latitude in both hemispheres (Clapham & Mead 1999), while the feeding areas are found in temperate to polar waters within the same hemisphere. Both Mathews (1937) and Mackintosh (1942), however, reported humpback whale catches near the equator during the austral winter (July–October) off the western coasts of South America and Africa, and suggested that some Southern Hemisphere whales winter in areas north of the equator. Modern research has confirmed this off Ecuador and Colombia (approx. 0–7° N; Flórez-González *et al.* 1998; Félix & Haase 2001). We report on a wintering area in coastal Central America for humpback whales feeding off the Antarctic Peninsula, resulting in the longest documented mammalian migration. We also examine the water temperature at this wintering area and compare it with all other wintering areas worldwide to investigate the influence of temperature on humpback whale distribution at low latitudes.

2. MATERIAL AND METHODS

Data collection consisted of coastal marine mammal surveys conducted yearly off Central America between latitudes 7°46′ N and 11°06′ N during the austral winter from 2001 to 2004 (figure 1; Rasmussen 2006). Additional opportunistic observations made since 1993 were also included. Whenever encountered, humpback whales were identified using photographs of the unique markings on the ventral surface of the tail flukes (Katona & Whitehead 1981). Photographs were also collected off the Antarctic Peninsula between latitudes 61°14′ S and 66°43′ S during the austral summer from 1981 to 2004, as part of the Antarctic humpback whale catalogue (AHWC, $n=965$; Allen *et al.* 2006). These two photographic collections were compared to determine individual whales common to both areas.

We reviewed the geographical distribution of current humpback whale wintering areas worldwide based on the published literature (electronic supplementary material). For inclusion as a wintering area, we considered areas where small calves had been observed and where there were other behaviours by adults indicative of breeding, such as competitive groups and singing (Winn & Winn 1978; Tyack & Whitehead 1983; Baker & Herman 1984). Long-term mean sea-surface temperature (SST) for the month of peak whale occurrence in each wintering area was extracted from satellite-derived global monthly climatologies at 4 km grid resolution for the base period 1985–2001. These climatologies are distributed by NOAA's National Oceanographic Data Center (http://www.nodc.noaa.gov/sog/pathfinder4km/).

Report Documentation Page

Form Approved
OMB No. 0704-0188

1. REPORT DATE	2. REPORT TYPE	3. DATES COVERED
FEB 2007		**00-00-2007 to 00-00-2007**

4. TITLE AND SUBTITLE	5a. CONTRACT NUMBER
Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration	5b. GRANT NUMBER
	5c. PROGRAM ELEMENT NUMBER
6. AUTHOR(S)	5d. PROJECT NUMBER
	5e. TASK NUMBER
	5f. WORK UNIT NUMBER
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) **Cascadia Research Collective,218 W. 4th Avenue,Olympia,WA,98501**	8. PERFORMING ORGANIZATION REPORT NUMBER
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)	10. SPONSOR/MONITOR'S ACRONYM(S)
	11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution unlimited

13. SUPPLEMENTARY NOTES

14. ABSTRACT

15. SUBJECT TERMS

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			
unclassified	**unclassified**	**unclassified**	**Same as Report (SAR)**	**13**	

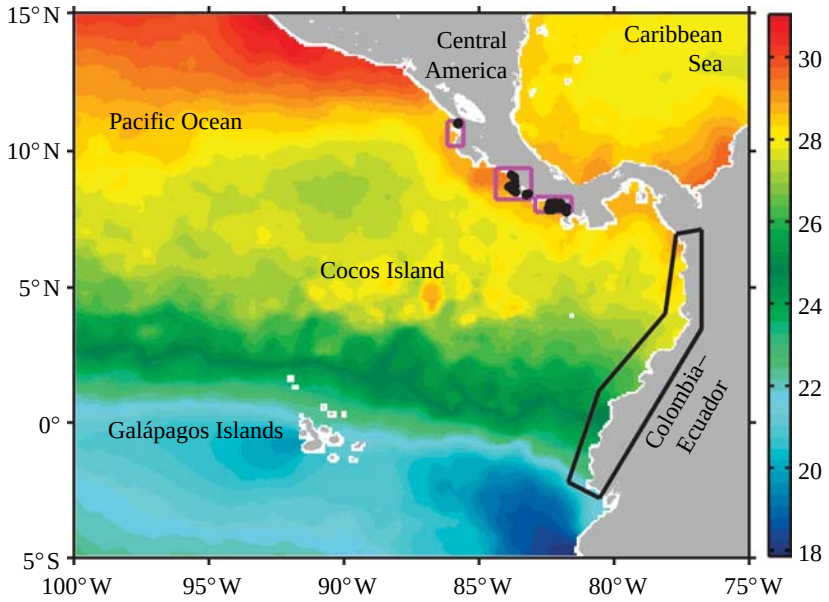

Figure 1. Survey areas (magenta boxes) off Central America and humpback whale sighting locations (black dots; $n=101$) during austral winters 2001–2004, overlaid on climatological SST for August. Black polygon is the 'Colombia and Ecuador' wintering area.

Table 1. Sighting information for seven photographic matches between Antarctica and Central America. (Identification numbers are shown for Cascadia Research Collective (CRC) and the Antarctic humpback whale catalogue (AHWC). Group composition for the Central American sightings is shown (M/C/E = mother/calf/escort).)

CRC ID	AHWC ID	Antarctica			Central America			distance (km)	group composition
		date	latitude	longitude	date	latitude	longitude		
1002	0010	16 Apr 1986	64°22′ S	63°17′ W	25 Sep 1999	8°31′ N	83°15′ W	8346	adult in M/C/E trio
1004	0021	16 Apr 1986	64°30′ S	63°09′ W	25 Sep 1999	8°31′ N	83°15′ W	8361	adult in M/C/E trio
1015	0529	4 Jan 1995	65°21′ S	64°58′ W	23 Sep 1995	8°39′ N	83°43′ W	8409	mother of M/C pair
1006	1212	10 Dec 2003	64°37′ S	62°36′ W	28 Aug 2001	9°09′ N	83°49′ W	8461	1 of M/C/2E
1033	0147	Jan 1989	64°48′ S	64°00′ W	3 Sep 2003	7°55′ N	82°01′ W	8299	adult in M/C/E trio
1013	1218	30 Jan 2002	64°37′ S	62°15′ W	17 Aug 2001	8°44′ N	83°49′ W	8425	mother of M/C pair
1012	1214	30 Jan 2002	64°37′ S	62°15′ W	17 Aug 2001	8°44′ N	83°49′ W	8425	calf of M/C pair

3. RESULTS

A total of 207 whales were sighted off Central America during the 2001–2004 austral winter surveys (figure 1). Mother/calf pairs, groups of competing males and singing males were all documented (Rasmussen 2006). Forty-one whales were individually identified photographically; of these, seven were also photographed off the Antarctic Peninsula. Three of these whales were seen within the same year; one off Costa Rica 262 days after it was seen off Antarctica and two (a mother/calf pair) off Antarctica 161 days after being seen off Costa Rica (table 1). The minimum distances between these locations, as determined by great-circle distances between straight segments around land masses, ranged from 8299 to 8461 km.

A total of 24 wintering areas were determined worldwide, all within 30° of the equator (figure 2; electronic supplementary material). A humpback whale population inhabiting the Arabian Sea was excluded from the analysis because it does not appear to undertake seasonal migrations (Mikhalev 1997). Climatological SSTs in all wintering areas were 21.1–28.3°C (electronic supplementary material), with no significant difference between Northern and Southern Hemispheres (*t*-test on the log-transformed data to homogenize the variance, p-value = 0.23). The interquartile SST range for all areas was 23.4–25.7°C, and the average was 24.6°C (±1.9°C s.d.).

4. DISCUSSION

The migrations reported here (up to 8461 km minimum travelling distance) are the longest movements documented for any mammal. The longest previously known migration was reported by Stone *et al.* (1990) for a humpback whale that moved between the Antarctic Peninsula and Colombia (7878 km according to our method; their reported 8334 km is probably an overestimate).

These trans-equatorial migrations between Antarctica and Central America are common for at least part of the humpback whale population in the eastern South Pacific. During this study, whales were regularly sighted off Panama and Costa Rica in the austral winter as far north as 11° N. Group composition (mother/calf pairs) and behaviours (competing males

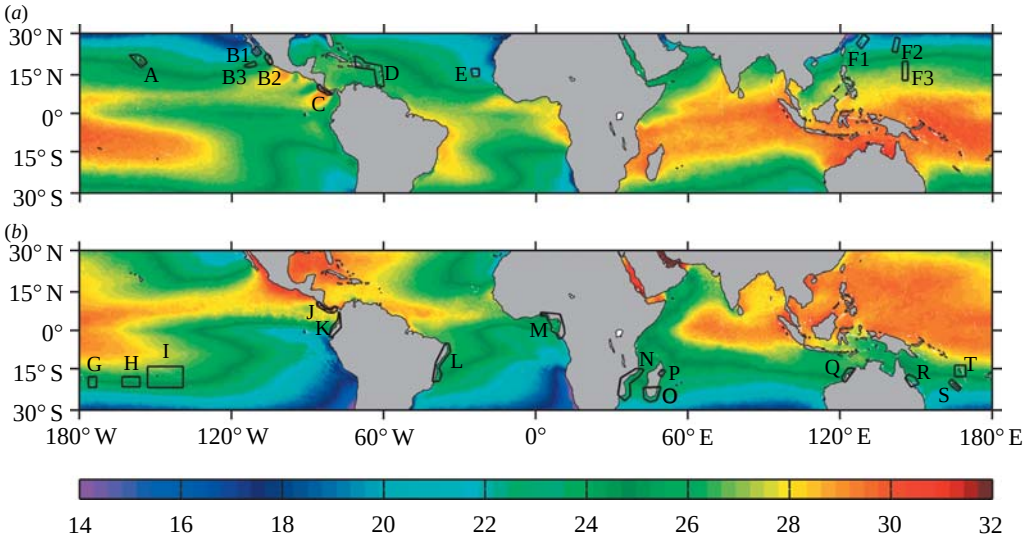

Figure 2. Worldwide distribution of wintering areas (black polygons) for (*a*) 10 Northern (A–F) and (*b*) 14 Southern (G–T) Hemisphere humpback whale populations (see electronic supplementary material for sources), overlaid on climatological SST for February and August, respectively. Letter codes bear no relationship to Southern Hemisphere stock designations by the IWC.

and singing males) were indicative of an area used for calving and mating. This area is probably an extension of the wintering area off Ecuador and Colombia (figure 1). The combined extent of these wintering areas (figure 2) may be a result of whales migrating further north to Central America due to space limitation or other density-dependent process.

Another unique aspect of this area is the spatial overlap with whales from the Northern Hemisphere. The work we have conducted off Central America during the boreal winter season (December–April) since 1996 indicates that this is also a wintering area for eastern North Pacific humpback whales migrating from feeding areas off California (Calambokidis *et al.* 2000). In fact, anecdotal whale sightings have been reported monthly off Central America (Rasmussen 2006), although the population identity of animals seen during the non-peak occurrence months remains undetermined. Eastern North and South Pacific populations share genetic traits indicating a trans-equatorial exchange, probably off Central America (Medrano-González *et al.* 2001).

The climatological August SST in the Central American wintering area is 28°C (electronic supplementary material). Temperatures between 24 and 28°C were reported at other humpback whale wintering areas (Dawbin 1966; Herman & Antinoja 1977; Whitehead & Moore 1982), consistent with our global SST analysis (figure 2; electronic supplementary material). Coastal upwelling and cold tongue development during the austral winter result in cool surface waters extending from the South American coast into the eastern equatorial Pacific, such that SSTs greater than 24°C only occur north of the equator (figures 1 and 2). This implies that humpback whales in the eastern South Pacific need to migrate farther north to wintering areas off Ecuador, Colombia and Central America. This pattern is observed again off the western coast of Africa, where an anomalously northerly wintering area for eastern South Atlantic humpback whales (Findlay *et al.* 1994; Walsh *et al.* 2000; Van Waerebeek *et al.* 2001) coincides with the occurrence of coastal upwelling and an equatorial cold tongue (figure 2). Thus, while the availability of suitable reproductive habitat at the wintering areas is important at the fine scale (e.g. Ersts & Rosenbaum 2003; Félix & Haase 2005), water temperature influences their distribution at the basin scale.

Our analysis shows that worldwide humpback whale wintering areas are found in warm coastal waters irrespective of latitude. In the ongoing debate on the reasons for migration, this result supports previous ideas linking temperature at the wintering areas to energetic strategies without the need to invoke killer whale avoidance. Clapham (2001) suggests that, as in some terrestrial mammals, energy conserved during offspring development can be devoted to growth, leading to larger size and increased reproductive success in adulthood. Thus, the temperature regime at the wintering areas, regardless of distance to the feeding areas, probably constitutes a major selective force driving humpback whale migration.

Funding was provided by the Homeland Foundation and the National Fish and Wildlife Foundation. Photographs were contributed by K. Robertson Chater and I. McWhirter. DMP was supported by award no. N00014-05-1-0045 from the US Office of Naval Research, National Oceanographic Partnership Program. Helpful comments were provided by P. J. Clapham, J. T. Harvey, R. L. Brownell, S. J. Bograd and an anonymous reviewer.

Allen, J. M., Stevick, P. T., & Carlson, C. 2006 The Antarctic Humpback Whale Catalogue: description and summary. Paper SC/A06/HW58 presented to the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, Hobart, Tasmania 4–7 April 2006. [Paper available from the International Whaling Commission, Cambridge, UK.]

Baker, C. S. & Herman, L. M. 1984 Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Can. J. Zool.* **62**, 1922–1937.

Brodie, P. F. 1975 Cetacean energetics, an overview of intraspecific size variation. *Ecology* **56**, 152–161. (doi:10.2307/1935307)

Calambokidis, J. *et al.* 2000 Migratory destinations of humpback whales that feed off California, Oregon and Washington. *Mar. Ecol. Prog. Ser.* **192**, 295–304.

Clapham, P. 2001 Why do baleen whales migrate? A response to Corkeron and Connor. *Mar. Mamm. Sci.* **17**, 432–436. (doi:10.1111/j.1748-7692.2001.tb01289.x)

Clapham, P. J. & Mead, J. G. 1999 *Megaptera novaeangliae*. *Mamm. Spec.* **604**, 1–9. (doi:10.2307/3504352)

Corkeron, P. J. & Connor, R. C. 1999 Why do baleen whales migrate? *Mar. Mamm. Sci.* **15**, 1228–1245. (doi:10.1111/j.1748-7692.1999.tb00887.x)

Dawbin, W. H. 1966 The seasonal migratory cycle of humpback whales. In *Whales, dolphins and porpoises* (ed. K. S. Norris), pp. 145–170. Berkeley, CA: University of California Press.

Ersts, P. J. & Rosenbaum, H. C. 2003 Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *J. Zool. Lond.* **260**, 337–345. (doi:10.1017/S0952836903003807)

Evans, P. G. H. 1987 *The natural history of whales and dolphins*. London, UK: Christopher Helm.

Félix, F. & Haase, B. 2001 The humpback whale off the coast of Ecuador, population parameters and behavior. *Rev. Biol. Mar. Oceanogr.* **36**, 61–74.

Félix, F. & Haase, B. 2005 Distribution of humpback whales along the coast of Ecuador and management implications. *J. Cetacean Res. Manage.* 7, 21–31.

Findlay, K. P., Best, P. B., Peddemors, V. M. & Gove, D. 1994 The distribution and abundance of humpback whales on their southern and central Mozambique winter grounds. *Rep. Int. Whal. Comm.* **44**, 311–320.

Flórez-González, L., Capella, A. J., Haase, B., Bravo, G. A., Félix, F. & Gerrodette, T. 1998 Changes in winter destinations and the northernmost record of Southeastern Pacific humpback whales. *Mar. Mamm. Sci.* **14**, 189–196. (doi:10.1111/j.1748-7692.1998.tb00707.x)

Herman, L. M. & Antinoja, R. C. 1977 Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst.* **29**, 59–85.

Katona, S. K. & Whitehead, H. P. 1981 Identifying humpback whales using their natural markings. *Polar Rec.* **20**, 439–444.

Mackintosh, N. A. 1942 The southern stocks of whalebone whales. *Discov. Rep.* **22**, 197–300.

Matthews, L. H. 1937 The humpback whale, *Megaptera nodosa*. *Discov. Rep.* **17**, 7–92.

Medrano-González, L. *et al.* 2001 Trans-oceanic population genetic structure of humpback whales in the North and South Pacific. *Mem. Qld. Mus.* **47**, 465–479.

Mikhalev, Y. A. 1997 Humpback whales *Megaptera novaeangliae* in the Arabian sea. *Mar. Ecol. Prog. Ser.* **149**, 13–21.

Norris, K. S. 1967 Some observations on the migration and orientation of marine mammals. In *Animal orientation and migration* (ed. R. M. Storm), pp. 101–125. Corvallis, OR: Oregon State University Press.

Rasmussen, K. 2006 Comparison of two distinct populations of humpback whales (*Megaptera novaeangliae*) off Pacific Central America. MS thesis, Moss Landing Marine Laboratories, San Francisco State University, San Francisco, CA, p. 90.

Stone, G. S., Flórez-González, L. & Katona, S. 1990 Whale migration record. *Nature* **346**, 705. (doi:10.1038/346705a0)

Tyack, P. & Whitehead, H. 1983 Male competition in large groups of wintering humpback whales. *Behaviour* **83**, 132–154.

Van Waerebeek, K., Tchibozo, S., Montcho, J., Nobime, G., Sohouhoue, P. & Dossou, C. 2001 The Bight of Benin, a North Atlantic breeding ground of a Southern Hemisphere humpback whale population, likely related to Gabon and Angola substocks. Paper SC/53/IA21 presented to the IWC Scientific Committee, July 2001, London (Unpublished). [Paper available from the International Whaling Commission Cambridge, UK.]

Walsh, P. D., Fay, J. M., Gulick, S. & Sounguet, G. P. 2000 Humpback whale activity near Cap Lopez, Gabon. *J. Cetacean Res. Manage.* **2**, 63–67.

Whitehead, H. P. & Moore, M. J. 1982 Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* **60**, 2203–2211.

Winn, H. E. & Winn, L. K. 1978 The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar. Biol.* **47**, 97–114. (doi:10.1007/BF00395631)

Electronic supplementary material for:

doi:10.1098/rsbl.2007.0067

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

By: K. Rasmussen, D. M. Palacios, J. Calambokidis, M. T. Saborío, L. Dalla Rosa, E. R. Secchi, G. H. Steiger, J. M. Allen, and G. S. Stone

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.

REFERENCES

Chittleborough, R. G. 1958 The breeding cycle of the female humpback whales, *Megaptera nodosa* (Bonnaterrre). *Aus. J. Mar. Freshwater Res*. 9, 1-18.

Clapham, P. J. & Mead, J. G. 1999 *Megaptera novaeangliae*. *Mamm. Spec*. 604, 1-9.

Félix, F., Palacios, D. M., Caballero, S., Haase, B. & Falconí, J. 2006 The 2005 Galápagos Humpback Whale Expedition: a first attempt to assess and characterize the population in the archipelago. Paper SC/A06/HW15 presented to the IWC Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, Hobart, Tasmania, 4–7 April 2006.

[Paper available from the Office of the International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK].

Hazevoet, C. J. & Wenzel, F. W. 2000 Whales and dolphins (Mammalia, Cetacea) of the Cape Verde Islands, with special reference to the humpback whale *Megaptera novaeangliae* (Borowski, 1781). *Contr. Zool.* 69, 197-211.

Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S. K., Martin, A. R., Reeves, R. R., Seton, R., Stevick, P. T. & Wenzel, F. W. 2003 Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *J. Cetacean Res. Manage.* 5, 125-129.

Mikhalev, Y. A. 1997 Humpback whales *Megaptera novaeangliae* in the Arabian Sea. *Mar. Ecol. Prog. Ser*. 149, 13-21.

Mori, K., Sato, F., Yamaguchi, M., Suganuma, H. & Ueyanagi, S. 1998 Distribution, migration and local movements of humpback whale (*Megaptera novaeangliae*) in the adjacent waters of the Ogasawara (Bonin) Islands, Japan. *J. School of Mar. Sci. and Tech*. 45, 197-213.

Ohizumi, H., Matsuishi, T. & Kishino, H. 2002 Winter sightings of humpback and Bryde's whales in tropical waters of the western and central North Pacific. *Aquat. Mamm.* 28, 73-77.

Reiner, F., Dos Santos, M. E. & Wenzel, F. W. 1996 Cetaceans of the Cape Verde Archipelago. *Mar. Mamm. Sci.* 12, 434-443.

Urban-R, J. & Aguayo-L, A. 1987 Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae*, in the Mexican Pacific. *Mar. Mamm. Sci.* 3, 333-344.

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

[1]Herman, L. M. & Antinoja, R. C. 1977 Humpback whales in the Hawaiian breeding waters: population and pod characteristics. *Sci. Rep. Whales Res. Inst.* 29, 59-85.

[2]Baker, C. S. & Herman, L. M. 1981 Migration and local movement of humpback whales (*Megaptera novaeangliae*) through Hawaiian waters. *Can. J. Zool.* 59, 460-469.
[3]Urban-R, J. & Aguayo-L, A. 1987 Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae*, in the Mexican Pacific. *Mar. Mamm. Sci.* 3, 333-344.
[4]Rasmussen, K. 2006. Comparison of two distinct populations of humpback whales (*Megaptera novaeangliae*) off Pacific Central America. M.S. Thesis, Moss Landing Marine Laboratories, San Francisco State University, San Francisco, CA. 90 pp.
[5]Whitehead, H. & Moore, M. J. 1982 Distribution and movements of West Indian humpback whales in winter. *Can. J. Zool.* 60, 2203-2211.
[6]Winn, H. E., Edel, R. K. & Taruski, A. G. 1975 Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. *J. Fish. Res. Board Can.* 32, 499-506.
[7]Reiner, F., Dos Santos, M. E. & Wenzel, F. W. 1996 Cetaceans of the Cape Verde Archipelago. *Mar. Mamm. Sci.* 12, 434-443.
[8]Hazevoet, C. J. & Wenzel, F. W. 2000 Whales and dolphins (Mammalia, Cetacea) of the Cape Verde Islands, with special reference to the humpback whale *Megaptera novaeangliae* (Borowski, 1781). *Contr. Zool.* 69, 197-211.
[9]Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S. K., Martin, A. R., Reeves, R. R., Seton, R., Stevick, P. T. & Wenzel, F. W. 2003 Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *J. Cetacean Res. Manage.* 5, 125-129.
[10]Nishiwaki, N. 1959 Humpback whales in Ryukyuan waters. *Sci. Rep. Whales Res. Inst.* 14, 49-87.
[11]Nishiwaki, N. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling Results. In *Whales, dolphins and porpoises* (ed. K. S. Norris), pp 171-191. Berkeley: University of California Press.
[12]Rice, D. 1974 Whales and whale research in the eastern North Pacific. In *The whale problem* (ed. W.E. Schevill), pp. 170-195. Cambridge: Harvard University Press.
[13]Darling, J. D. & Mori, K. 1993 Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. *Can. J. Zool.* 71, 325-333.
[14]Omura, H. 1950. Whales in the adjacent waters of Japan. *Sci. Rep. Whales Res. Inst.* 4, 27-113.
[15]Mori, K., Sato, F., Yamaguchi, M., Suganuma, H. & Ueyanagi, S. 1998 Distribution, migration and local movements of humpback whale (*Megaptera novaeangliae*) in the adjacent waters of the Ogasawara (Bonin) Islands, Japan. *J. School of Mar. Sci. Tech.* 45, 197-213.
[16]Ohizumi, H., Matsuishi, T. & Kishino, H. 2002 Winter sightings of humpback and Bryde's whales in tropical waters of the western and central North Pacific. *Aquat. Mamm.* 28, 73-77.
[17]Garrigue, C., Greaves, J. & Chambellant, M. 2002 Characteristics of the New Caledonian humpback whale population. *Mem. Qld. Mus.* 47, 539-546.
[18]Garrigue, C., Dodemont, R., Steel, D. & Baker, C. S. 2004 Organismal and 'gametic'capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Mar. Ecol. Prog. Ser.* 274, 251-262.
[19]Hauser, N., Peckham, H. & Clapham, P. 2000 Humpback whales in the southern Cook Islands, South Pacific. *J. Cetacean Res. Manage.* 2, 159-164.
[20]Gannier, A. 2004 The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquat. Mamm.* 30, 227-336.

[21]Clarke, R. 1962 Whale observation and whale marking off the coast of Chile in 1958 and from Ecuador towards and beyond the Galápagos Islands in 1959. *Norsk Hvalfangsttid.* 51, 265-87.
[22]Flórez-González, L. 1991 Humpback whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: population and pod characteristics. *Mem. Qld. Mus.* 30, 291-295.
[23]Flórez-González, L., Capella-A., J., Haase, B., Bravo, G. A., Félix, F. & Gerrodette, T. 1998 Changes in winter destinations and the northernmost record of Southeastern Pacific humpback whales. *Mar. Mamm. Sci.* 14, 189-196.
[24]Scheidat, M., Castro, C., Denkinger, J., González, J. & Adelung, D. 2000 A breeding area for humpback whales (*Megaptera novaeangliae*) off Ecuador. *J. Cetacean Res. Manage.* 2, 165-171.
[25]Félix, F. & Haase, B. 2001 The humpback whale off the coast of Ecuador, population parameters and behavior. *Rev. Biol. Mar. Ocean.* 36, 61-74.
[26]Siciliano, S. 1995. Report of the Scientific Committee, Annex E. Report of the Sub-Committee on Southern Hemisphere Baleen Whales, Appendix 6. Preliminary report on the occurrence and photo-identification of humpback whales in Brazil. *Rep. int. Whal. Commn*. 45:138-40.
[27]Martins, C. C. A., Morete, M. E., Engel, M. H., Freitas, A. C., Secchi, E. R. & Kinas, P. G. 2001 Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Mem. Qld. Mus.* 47, 563-570.
[28]Zerbini, A. N., Andriolo, A., Rocha, J., Simoes-Lopes, P. C., Siciliano, S., Pizzorno, J. L., Waite, J. M., De Master, D. P. & Van Blaricom, G. R. 2004 Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off northeastern Brazil. *J. Cetacean Res. Manage.* 6, 101-107.
[29]Findlay, K. P., Best, P. B., Peddemors, V. M. & Gove, D. 1994 The distribution and abundance of humpback whales on their southern and central Mozambique winter grounds. *Rep. int. Whal. Commn.* 44, 311-320.
[30]Darling, J. D. & Sousa-Lima R. S. 2005 Songs indicate interaction between humpback whale populations in the western and eastern South Atlantic Ocean. *Mar. Mamm. Sci.* 21,557-566.
[31]Van Waerebeek, K., Tchibozo, S., Montcho, J., Nobime, G., Sohou, Z., Sehouhoue, P. and Dossou, C. 2001. The Bight of Benin, a North Atlantic breeding ground of a Southern Hemisphere humpback whale population, likely related to Gabon and Angola substocks. Paper SC/53/IA21 presented to the IWC Scientific Committee, July 2001, London (unpublished) [Paper available from the Office of the International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB4 9NP, UK].
[32]Walsh, P. D., Fay, J. M., Gulick, S. & Sounguet, G. P. 2000 Humpback whale activity near Cap Lopez, Gabon. *J. Cetacean Res. Manage.* 2, 63-67.
[33]Best, P. 1994 The distribution and abundance of humpback whales off southern Madagascar, August-September 1994. *Rep. int. Whal. Commn.* Paper SC/47/SH15.
[34]Rosenbaum, H. C., Walsh, P. D., Razafindrakoto, Y., Vely, M. & DeSalle, R. 1997 First description of a humpback whale wintering ground in Baie d'Antongil, Madagascar. *Cons. Biol.* 11, 312-314.
[35]Ersts, P. J. & Rosenbaum, H. C. 2003 Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *J. Zool.* 260, 337-345.
[36]Chittleborough, R. G. 1954. Aerial observations on the humpback whales, with notes on other species. *Aust. J. Mar. Fresh. Fish.* 4, 219-226.

[37]Dawbin, W. H. & Gill, P. C., 1991 humpback whales songs along the coast of Western Australia and some comparison with east coast songs. *Mem. Qld. Mus.* 30, 249-254.
[38]Jenner, K. C. S. & Jenner, M. N. 1994 A preliminary population estimate of the group IV breeding stock of humpback whales off Western Australia. *Rep. int. Whal. Commn* 44, 303-307.
[39]Jenner, K. C. S. & Jenner, M. N. & McCabe, K. A. 2001 Geographical and temporal movements of humpback whales in Western Australian waters. *Aus. Petrol. Prod. Expl. Assoc. J.* 41, 749-765.
[40]Paterson, R. & Paterson, P. 1984 A study of the past and present status of humpback whales in east Australian waters. *Biol. Cons.* 29, 321-343.
[41]Simmons, M. L. & Marsh, H. 1986 Sightings of humpback whales in Great Barrier Reef waters. *Sci. Rep. Whales Res. Inst.* 37, 31-46.
[42]Paterson, R. A. 1991 The migration of humpback whales *Megaptera novaeangliae* in east Australian waters. *Mem. Qld. Mus.* 30, 333-341.
[43]Garrigue, C. & Gill, P. C. 1994 Observations of humpback whales *Megaptera novaeangliae* in New Caledonian waters during 1991-1993. *Biol. Cons.* 70, 211-218.

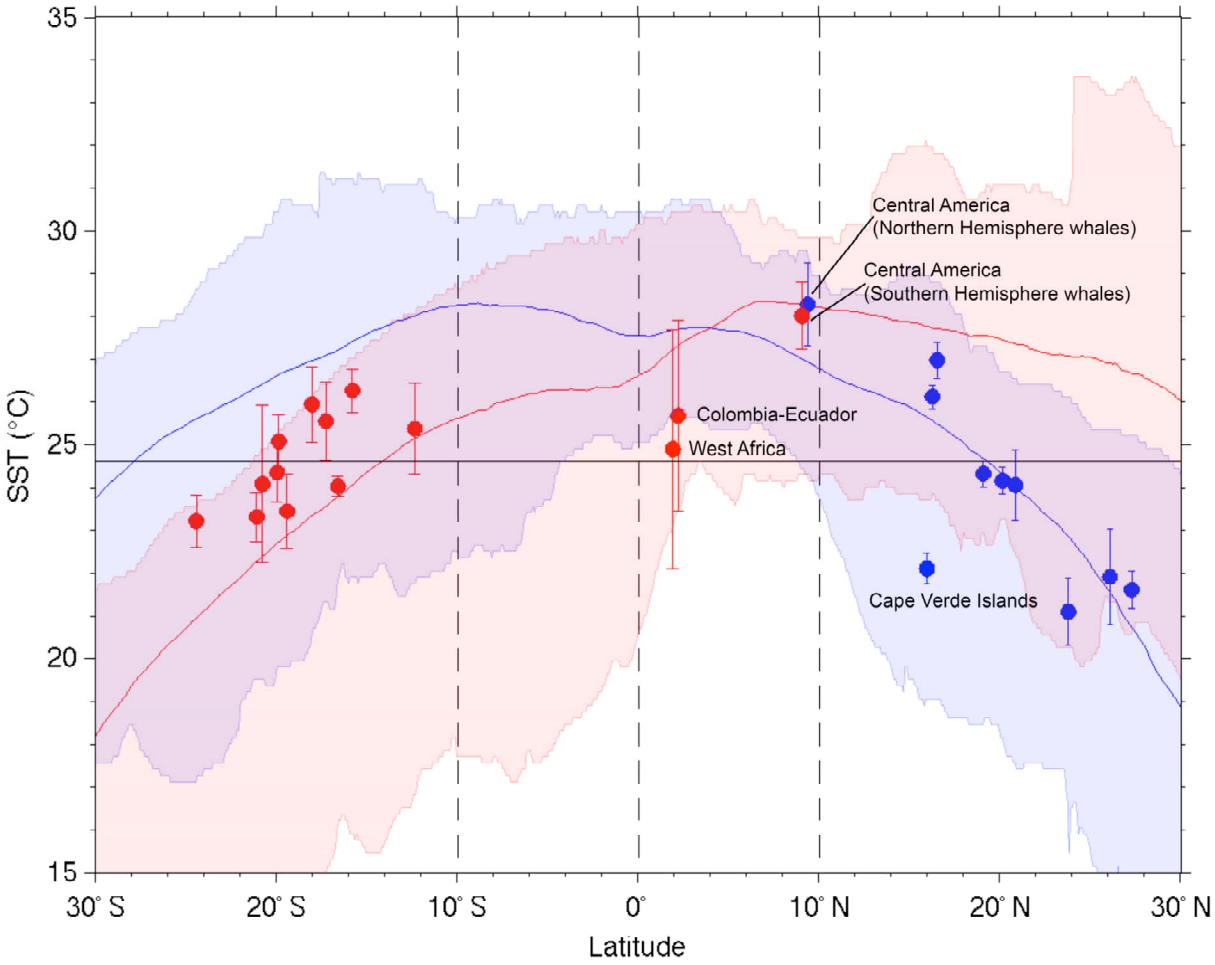

Figure A1. Mean latitude vs. mean SST at the wintering areas for Northern (blue circles) and Southern (red circles) Hemisphere humpback whale populations. Error bars are the standard deviations reported in table A1, and are a measure of the spatial variability of SST within each wintering area. Shaded 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.