subtracting each judge's rating of the typical American from his or her rating of the typical compatriot for each NCS item. Assuming that cultures agree on the typical American, this procedure in effect subtracts the bias plus a constant and leaves a potentially better estimate of national character. We standardized the differences as $T$ scores, using difference score normative values from the worldwide sample, excluding the United States. The difference scores were highly correlated with NCS scores ($rs$ = 0.65 to 0.91, $P$ < 0.001) and provided essentially the same results. ICCs between difference scores and NEO-PI-R observer ratings ranged from −0.44 for England to 0.48 for Lebanon (median, 0.03). ICCs between differences scores and NEO-PI-R self-reports ranged from −0.47 for Russia to 0.53 for Poland (median, 0.01). For the five factors, correlations with observer ratings across cultures ranged from 0.08 to 0.23, and those with self-reports ranged from −0.37 to 0.23. These results suggest that the lack of correspondence between NEO-PI-R and NCS profiles is not simply due to different standards of evaluation in different cultures. A different issue concerns the reference-group effect (28), according to which self-reports and observer ratings of individuals are implicitly made by reference to the distribution of scores in the rater's culture. Such an effect would tend to make aggregate personality scores uniform for all cultures, and the failure to find correlations with NCS factors would be due to a lack of variation in aggregate NEO-PI-R means. However, NEO-PI-R means in fact vary systematically across cultures and show strong correlations across methods and with other culture-level variables (12, 14). Thus, the reference-group effect cannot explain the failure to find correlations with NCS scales.

28. S. J. Heine, D. R. Lehman, K. P. Peng, J. Greenholtz, *J. Pers. Soc. Psychol.* **82**, 903 (2002).
29. F. van de Vijver, K. Leung, *J. Pers.* **69**, 1007 (2001).
30. D. L. Hamilton, T. L. Rose, *J. Pers. Soc. Psychol.* **39**, 832 (1980).
31. T. W. Adorno, E. Frenkel-Brunswik, D. J. Levinson, R. N. Sanford, *The Authoritarian Personality* [Norton, New York, 1969 (original work published 1950)].
32. F. H. Allport, *The Nature of Prejudice* (Houghton Mifflin, New York, 1954).
33. R.R.M. receives royalties from the Revised NEO Personality Inventory. This research was supported in part by the Intramural Research Program of NIH, National Institute on Aging. Czech participation was supported by grant 406/01/1507 from the Grant Agency of the Czech Republic and is related to research plan AV AV0Z0250504 of the Institute of Psychology, Academy of Sciences of the Czech Republic. S.G.'s participation was supported by the Turkish Academy of Sciences. Burkinabè and French Swiss participation was supported by a grant from the Swiss National Science Foundation to J.R. The data collection in Hong Kong was supported by Research Grants Council Direct Allocation Grants (DAG02/03.HSS14 and DAG03/04.HSS14) awarded to M.Y. Data collection in Malaysia was supported by Univesiti Kebangsaan Malaysia Fundamental Research Grant 11JD/015/2003 awarded to K.A.M. Portions of these data were presented at the 113th Convention of the American Psychological Association, August 2005, Washington, DC. For helpful comments on the manuscript, we thank Y. H. Poortinga; for their assistance on this project we thank F. Abal, L. de Almeida, S. Baumann, H. Biggs, D. Bion, A. Butković, C. Y. Carrasquillo, H. W. Carvalho, S. Catty, C.-S. Chan, A. Curbelo, P. Duffill, L. Etcheverry, L. Firpo, J. Gonzalez, A. Gramberg, H. Harrow, H. Imuta, R. Ismail, R. Kamis, S. Kannan, N. Messoulam, F. Molina, M. Montarroyos Calegaro, S. Mosquera, J. C. Munene, V. Najzrova, C. Nathanson, D. Padilla, C. N. Scollon, S. B. Sigurdardottir, A. da Silva Bez, M. Takayama, T. W. Teasdale, L. N. Van Heugten, F. Vera, and J. Villamil.

# Transoceanic Migration, Spatial Dynamics, and Population Linkages of White Sharks

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The large-scale spatial dynamics and population structure of marine top predators are poorly known. We present electronic tag and photographic identification data showing a complex suite of behavioral patterns in white sharks. These include coastal return migrations and the fastest known transoceanic return migration among swimming fauna, which provide direct evidence of a link between widely separated populations in South Africa and Australia. Transoceanic return migration involved a return to the original capture location, dives to depths of 980 meters, and the tolerance of water temperatures as low as 3.4°C. These findings contradict previous ideas that female white sharks do not make transoceanic migrations, and they suggest natal homing behavior.

Great white sharks (*Carcharodon carcharias*) occupy the apex of most marine food webs in which they occur. Their major centers of abundance are in the coastal waters of California–Baja California, Australia–New Zealand, South Africa, and, formerly, the Mediterranean Sea (*1–3*). Management and conservation of this threatened species (*4, 5*) have been limited, partly because its space utilization and migrations and the linkages between populations were poorly understood and difficult to research until the development of sophisticated telemetry instruments and high-resolution genetic markers for the species (*6–9*). Long believed to primarily be shelf inhabitants, white sharks are now known to be more pelagic and to travel from California to Hawaii (*6*). Males are assumed to move between distant populations, whereas females have been assumed to be nonroving and philopatric (*9*).

We tagged white sharks off the Western Cape of South Africa between June 2002 and November 2003 with pop-up archival satellite-transmitting (PAT) tags ($n$ = 25), near-real-time satellite tags (from here onward, "satellite tags") ($n$ = 7), and acoustic tags ($n$ = 25) in order to study their spatial dynamics (table S1). Using high-resolution photographic identification techniques, we have recorded the daily presence or absence of individual white sharks off Gansbaai (34°39′S, 019°24′E; Western Cape) since October 1997 (*10*).

Electronic tagging and photographic identification records reveal complex spatial dynamics in white sharks, which we categorized into four behavioral patterns: rapid transoceanic return migrations, frequent long-distance coastal return migrations, smaller-scale patrolling, and site fidelity. A white shark performed a previously unknown fast transoceanic return migration spanning the entire Indian Ocean, swimming coast-to-coast from South Africa to Australia and back. This ~380-cm total length (TL; measured as a straight line from the tip of the snout to the end of the upper caudal lobe) female shark (number P12), PAT-tagged on 7 November 2003 off Gansbaai, traveled in 99 days to a location 2 km from shore and 37 km south of the Exmouth Gulf in Western Australia (22°01′05″S, 113°53′13″E; Fig. 1A). This shark's course of ~11,100 km (*11*) entailed a counterclockwise displacement of more than 750 km off the southern tip of Africa, followed by a remarkably direct path toward northwestern Australia, indicating that white sharks do not need oceanic islands as gateways for transoceanic migrations, as previously hypothesized (*12*). Shark P12 traveled at a minimum speed of 4.7 km hour$^{-1}$ during its migration to Australia (*13*), which is the fastest sustained long-distance speed known among sharks (*14–17*) and comparable to

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**Fig. 1.** Transoceanic migration of a white shark from South Africa to northwestern Australia and possible first leg of a second transoceanic-migrating shark. (**A**) Positions of (dots) and track followed by (black line) shark P12 during coastal and transoceanic movement; geolocation-estimated positions were corrected using SST data to derive positions shown (*11*). The first leg of another possible transoceanic migration to Australia (or an offshore movement toward the northeast coast of South Africa) is shown by the pop-up location of the PAT tag from shark P3 (blue line and square). Tagging and pop-up dates were as follows: for P12, 7 November 2003 and 28 February 2004; for P3, 14 April 2003 and 25 December 2003. SST is an average composite at 4 km resolution for daily Moderate Resolution Imaging Spectroradiometer data from 23 November 2003 to 28 February 2004. Southwest Indian Ridge shown as white depth contours (100 to 2000 m). The scale bar represents 5000 km; the white arrow marks the tag deployment location. (**B**) Differential time-at-depth patterns during the coastal and oceanic legs of shark P12's trip, showing a bimodal pattern with a strong preference for the depths of 0.0 to 0.5 m and 500 to 750 m during transoceanic travel. (**C**) Minimum (black line and squares) and maximum (bright blue line) depths and minimum temperature (orange dots) visited during the coastal and oceanic phases of movement; all data are in 6-hour periods.
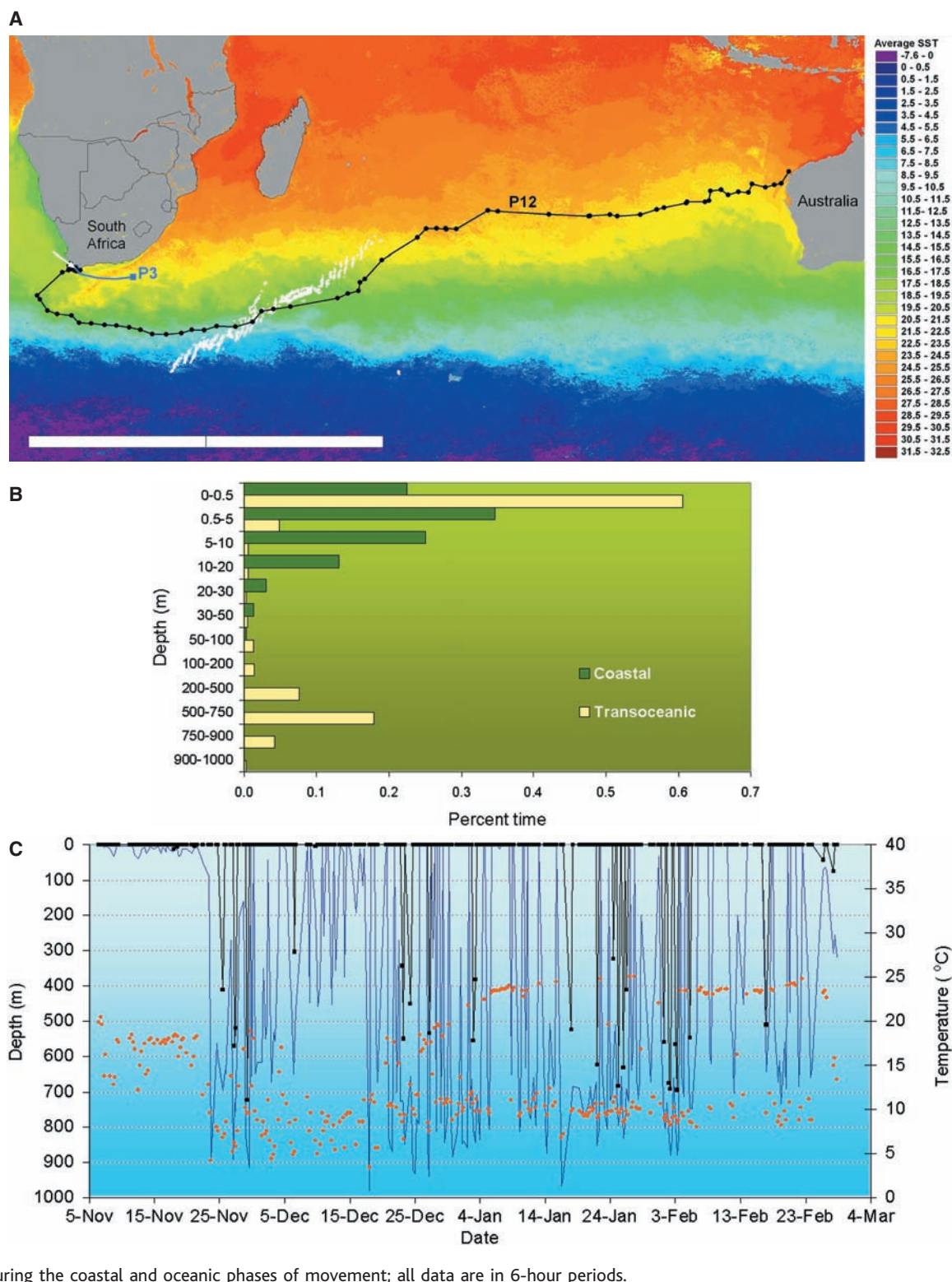
that of some of the fastest-swimming tunas (*18*, *19*). Records obtained through photographic identification revealed the return of P12 from Australia back to its original tagging site on 20 August 2004 (Fig. 2 and fig. S1), evidencing site fidelity and an outstanding navigational ability. Shark P12 performed the fastest transoceanic return migration recorded among marine fauna (*14*, *20*), taking just under 9 months to complete a circuit of more than 20,000 km. Logged records from the photographic identification study show that P12 is a seasonal visitor (from June to December) to the Gansbaai area (table S2). It has been recorded during 38 different days spanning 1999–2004, suggesting that it is a South African shark and that its transoceanic return migration could be common. A second PAT-tagged shark (unsexed, ~200- to 230-cm TL; number P3) traveled to an offshore location 242 km SE of Port Elizabeth, where its tag detached on 26 December 2003, in what might have been the first leg of a migration toward Australia (Fig. 1A).

**Fig. 2.** Photographic identification records of shark P12 at tagging (7 November 2003) and upon return to the tagging location at Gansbaai (20 August 2004) after its transoceanic migration to Western Australia. (**A**) Trailing edge of the first dorsal fin, showing a unique notch pattern allowing identification; the white lines connect corresponding notches in both photographs. (**B**) Right side of the first dorsal fin, with magnified details (left insets) showing a unique black pigmentation pattern aiding identification.
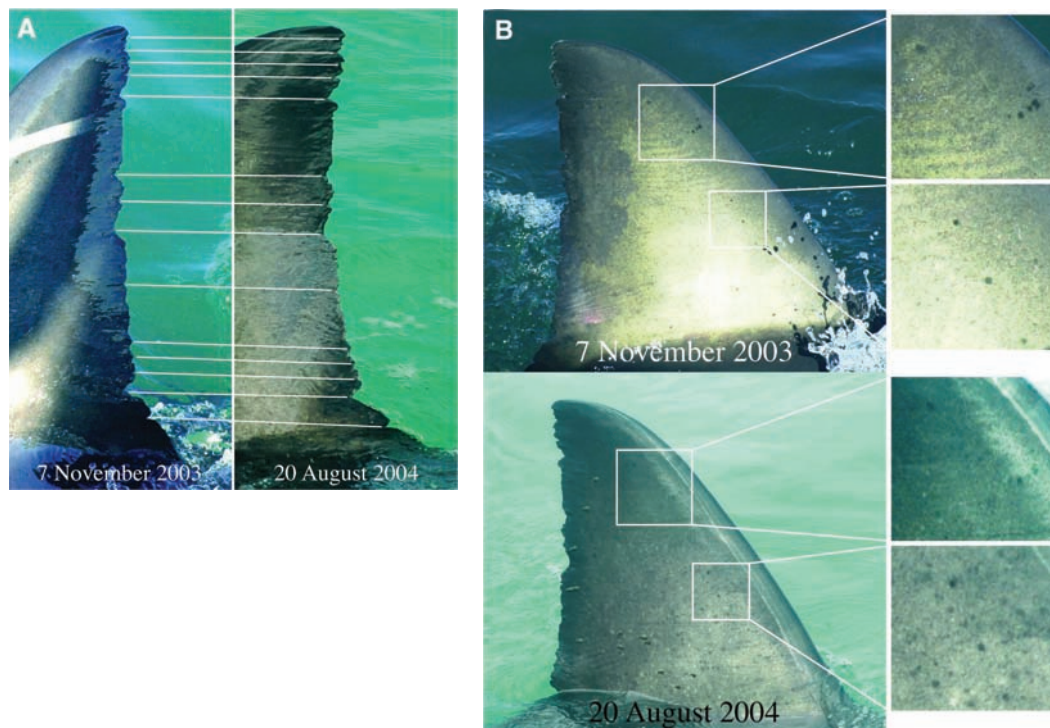


Transoceanic return migration is previously unknown in white sharks and only suspected in other chondrichthyans. Our results provide direct evidence of a physical link between two of the most important and widely separated white shark populations, and they confirm philopatry in white sharks. They also prove that female white sharks are capable of transoceanic migrations and indicate that the sex-biased dispersal of this species (9) is not necessarily based on differences in the proclivity of either sex to undertake transoceanic migrations, but is probably attributable to differences in how these migrants become reproductively integrated into the "recipient" population. In light of our data, the transmission of nuclear, and not mitochondrial, genetic material between South Africa and Australia (9) could be explained if (i) both sexes make transoceanic migrations, but only males reproduce in the recipient population, and/or (ii) females make transoceanic migrations and mate with males from the recipient population, only to return to their original location to give birth. Indeed, the migration of P12 from South Africa to Australia corresponds to what is thought to be the mating season in this region (21). An eventual return of this shark to give birth in South Africa would prove natal homing in white sharks, as has been suggested for other shark species (22, 23), and would support recent theories about the similarity of reproductive strategies among a wide range of marine taxa (24).

The mechanisms used by P12 to navigate to Australia and back remain unknown; aside from a few shallow seamounts on the South-west Indian and Ninety East Ridges, there are no other topographic features that could be used for orientation on the route it followed (Fig. 1A). We analyzed the satellite-transmitted summary data to reveal the diving pattern of P12 and found that during eastward transoceanic migration, it made frequent deep dives, reaching record maximum depths (980 m) (25), experienced record ambient temperatures of 3.4°C, and spent 18% of the time at depths of 500 to 750 m (Fig. 1, B and C). This shark spent considerably more time (61%) just below the surface (0.0 to 0.5 m) while in oceanic waters than when in coastal waters (23%), swimming most of the time (66%) above 5 m during this trip. A strong preference for surface swimming during oceanic travel is a behavioral pattern previously unreported in white sharks (1, 2, 6, 26). We speculate that, like many other vertebrates (14), white sharks could be using visual stimuli such as celestial cues as an important navigational mechanism in addition to, or instead of, following gradients in Earth's magnetic field as is commonly accepted behavior for sharks (27).

Great white sharks undertake long-distance return migrations along the South African coast with relative frequency, as revealed by the tracking of satellite tags and by PAT tag pop-up locations (Fig. 3 and fig. S2). They travel from high-abundance sites in the Western Cape (28, 29) to waters as far as >2000 km away off kwaZulu-Natal and beyond, using underwater routes along the continental shelf, then return to their original tagging sites off the Western Cape after 4 to 6 months. A 284-cm TL female (S1) was fitted with a satellite tag in Mossel Bay (34°08′S, 22°07′E) on 24 May 2003 and completed the first tracked long-distance return migration for a chondrichthyan, moving in 65 days to waters northeast of Delagoa Bay (Mozambique) and outside the South African Economic Exclusive Zone, where white sharks are legally protected (Fig. 3). S1 returned to Mossel Bay 162 days after being tagged, and was photographed with its transmitter still attached. Shark S2, a 310-cm TL female double-tagged with satellite and acoustic tags in Mossel Bay on 31 May 2003, was tracked for 46 days to the Tugela Bank, then recorded by our acoustic-tag bottom monitors back in Mossel Bay 123 days after being tagged (Fig. 3). In total, 25% of tagged sharks that yielded information moved from the Western Cape to kwaZulu-Natal and beyond, and 12.5% showed return migrations (Fig. 3 and fig. S2). The high proportion of immature white sharks (table S1, Fig. 3, and fig. S2) moving to the rich environment of the Tugela Bank (30, 31) suggests that these long-distance coastal return migrations might be feeding-related events.

Records obtained from satellite and PAT tags reflect additional spatial dynamics patterns in white sharks, including smaller-scale patrolling behavior and site fidelity (Fig. 3 and figs. S3 and S4). These patterns and the return migrations described above suggest a wider and more complex range of behavioral patterns in white sharks than was previously thought to exist. The discovery of a trans–Indian Ocean return-migrating white shark after a relatively low tagging effort, in addition to its periodic absence from Gansbaai as evidenced through photographic records, implies that the Australian and South African pop-
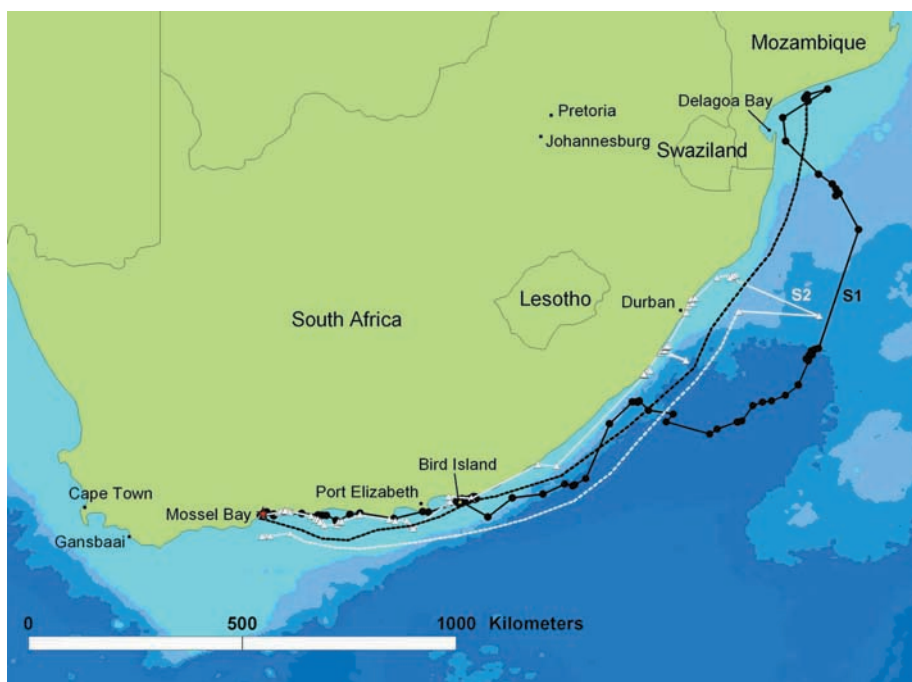
**Fig. 3.** Northeastward long-distance return migrations of South African white sharks. The figure shows the tracks of two satellite-tagged sharks showing long-distance return migrations and crossing to Mozambique. Shark S1 (black trace) left Mossel Bay after tagging (24 May 2004); moved rapidly to Bird Island, residing within a limited area (385 km²) for 27 days; and continued northeast along the shelf edge, then in oceanic waters beyond the Agulhas Current, reaching Mozambique 65 days after tagging. Transmissions ceased 11 days later, to resume on Bird Island 62 days later, then at the original tagging location on 2 November 2003. Shark S2 (white trace), tagged on 31 May 2003 with satellite and acoustic tags, traveled steadily along the coast to the Tugela Bank in 37 days, where it ceased transmitting 9 days later and was recorded by acoustic bottom receivers back in Mossel Bay on 1 October 2004. The red star indicates the tagging location; the dashed line indicates projected movement during long periods without transmissions.

ulations maintain a physical link within a single generation and that this return migration might be more common than is presently known.

Our studies show that we do not have a full understanding of the ways in which identified populations are connected. The movement of a female to a region of Australia known for the presence of Australian white sharks and its return to South Africa, in conjunction with previous genetic studies, implies that earlier hypotheses about sex-biased dispersal might need to be modified. Males are currently considered to be the ones who move between populations (9), but our data suggest that the connectivity between populations could be facilitated also or exclusively by females. The return of females mating in Australia to give birth in South Africa would be consistent with genetic analyses; the finding of a rare male of South African "origin" in Australia (9) might reflect equally rare birthing in Australia by South African females.

The discoveries presented here and our lack of evidence of sex- or size-related patterns of space utilization in white sharks underscore the need for additional research. Multidisciplinary studies integrating population genetic analyses and electronic tagging, as well as the development of improved monitoring instruments, should be encouraged.

Long-distance and transoceanic migrations expose great whites to increased risk of mortality as they leave domestically protected waters in South Africa/Australia and travel into neighboring or remote countries, sometimes located across entire ocean basins. An increasing global demand for shark products (32), coupled with our findings, suggests that global protective measures, such as the recent listing of the white shark in CITES Appendix 2 (CITES, Convention on International Trade in Endangered Species of Wild Fauna and Flora), are warranted to ensure the effectiveness of local protective legislation currently in place in a handful of countries.

## References and Notes

1. A. P. Klimley, D. G. Ainley, Eds., *Great White Sharks: The Biology of Carcharodon carcharias* (Academic Press, San Diego, CA, 1996).
2. L. J. V. Compagno, *Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Vol. 2. Bullhead, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes No. 1* (Food and Agriculture Organization of the United Nations, Rome, 2001).
3. A. Soldo, I. Jardas, *Periodicum Biologorum* **104**, 195 (2002).
4. L. J. V. Compagno, M. A. Marks, I. K. Fergusson, *Environ. Biol. Fish* **50**, 61 (1997).
5. C. Hilton-Taylor, Compiler, *2002 IUCN Red List of Threatened Species* (IUCN, Gland, Switzerland, 2000).
6. A. M. Boustany *et al.*, *Nature* **415**, 35 (2002).
7. B. A. Block, H. Dewar, C. Farwell, E. D. Prince, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 9384 (1998).
8. R. L. Johnson *et al.*, paper presented at the meeting on Conservation Research of Great White Sharks, New York, 20 to 22 January 2004 (Wildlife Conservation Society, New York, 2004).
9. A. T. Pardini *et al.*, *Nature* **412**, 139 (2001).
10. Materials and methods are available as supporting material on *Science* Online.
11. The positions estimated from archived light-level data using geolocation algorithms provided by the manufacturer of the tags were corrected using satellite sea surface temperature (SST) data with the method described in the supporting online material.
12. G. Cliff, L. J. V. Compagno, M. J. Smale, R. P. Van Der Elst, S. P. Wintner, *S. Afr. J. Sci.* **96**, 365 (2000).
13. The widely accepted definition of migration is "the act of moving from one spatial unit to another" (*14*). This definition is general enough to be applicable to all animal taxa, independently of spatiotemporal scales, and includes at its core individual migration.
14. R. R. Baker, *Migration: Paths Through Time and Space* (Hodder and Stoughton, London, 1982).
15. S. A. Eckert, B. S. Stewart, *Environ. Biol. Fish* **60**, 299 (2001).
16. N. E. Kohler, P. A. Turner, *Environ. Biol. Fish.* **60**, 191 (2001).
17. I. G. Priede, *Fish. Res.* **2**, 201 (1984).
18. B. A. Block *et al.*, *Science* **293**, 1310 (2001).
19. T. Itoh, S. Tsuji, A. Nitta, *Fish. Bull. (Wash. D.C.)* **101**, 514 (2003).
20. D. Inagake *et al.*, *Bull. Nat. Res. Inst. Far Seas Fish* **38**, 53 (2001).
21. M. P. Francis, in (*1*), pp. 157–172.
22. R. E. Hueter, M. R. Huepel, E. J. Heist, D. B. Keeney, *J. Northw. Atl. Fish. Sci.* **35**, 239 (2005).
23. K. A. Feldheim, S. H. Gruber, M. V. Ashley, *Proc. R. Soc. London Ser. B* **269**, 1655 (2002).
24. P. Cury, *Can. J. Fish. Aquat. Sci.* **51**, 1664 (1994).
25. Previous reports of record diving depths of 1280 m for white sharks (*2*) are based on the capture of one specimen in a longline set at that depth; however, to our knowledge, there is no evidence that the shark was caught at 1280 m as opposed to anywhere else along the water column.
26. F. G. Carey *et al.*, *Copeia* **2**, 254 (1982).
27. T. P. Quinn, *Trends Ecol. Evol.* **9**, 277 (1994).
28. L. J. V. Compagno, D. A. Ebert, M. J. Smale, *Guide to the Sharks and Rays of Southern Africa* (Struik, Cape Town, South Africa, 1989).
29. R. L. Johnson, thesis, University of Pretoria, South Africa (2003).
30. S. T. Fennessy, *S. Afr. J. Mar. Sci.* **14**, 263 (1994).
31. S. T. Fennessy, *S. Afr. J. Mar. Sci.* **14**, 287 (1994).
32. S. C. Clarke, thesis, University of London, UK (2003).
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