@AGUPUBLICATIONS

Geophysical Research Letters

RESEARCH LETTER

10.1002/2015GL064456

Key Points:

- Penguin distribution tied to upwelling in Galápagos cold pool
- Galápagos cold pool intensifying and expanding northward
- Implications for ongoing and futures conservation measures

Correspondence to:

K. B. Karnauskas, kristopher.karnauskas@colorado.edu

Citation:

Karnauskas, K. B., S. Jenouvrier, C. W. Brown, and R. Murtugudde (2015), Strong sea surface cooling in the eastern equatorial Pacific and implications for Galápagos Penguin conservation, *Geophys. Res. Lett.*, *42*, 6432–6437 doi:10.1002/2015GL064456.

Received 5 MAY 2015 Accepted 14 JUL 2015 Accepted article online 29 JUL 2015 Published online 6 AUG 2015

Strong sea surface cooling in the eastern equatorial Pacific and implications for Galápagos Penguin conservation

K. B. Karnauskas¹, S. Jenouvrier^{2,3}, C. W. Brown⁴, and R. Murtugudde⁵

¹Cooperative Institute for Research in Environmental Sciences & Department of Atmospheric and Oceanic Sciences, University of Colorado, Boulder, Colorado, ²Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA, ³Centre d'Etudes Biologiques de Chizé, CNRS and Université de La Rochelle, Villiers-en-Bois, France, ⁴Center for Satellite Applications and Research, NOAA, College Park, Maryland, USA, ⁵Earth System Science Interdisciplinary Center, University of Maryland, College Park, Maryland, USA

Abstract The Galápagos is a flourishing yet fragile ecosystem whose health is particularly sensitive to regional and global climate variations. The distribution of several species, including the Galápagos Penguin, is intimately tied to upwelling of cold, nutrient-rich water along the western shores of the archipelago. Here we show, using reliable, high-resolution sea surface temperature observations, that the Galápagos cold pool has been intensifying and expanding northward since 1982. The linear cooling trend of 0.8°C/33 yr is likely the result of long-term changes in equatorial ocean circulation previously identified. Moreover, the northward expansion of the cold pool is dynamically consistent with a slackening of the cross-equatorial component of the regional trade winds—leading to an equatorward shift of the mean position of the Equatorial Undercurrent. The implied change in strength and distribution of upwelling has important implications for ongoing and future conservation measures in the Galápagos.

1. Introduction

Past and future trends in the coupled ocean-atmosphere system of the tropical Pacific are the subject of a broad ranging investigation among the climate dynamics community [see *Collins et al.*, 2010, and references therein]. Perhaps nowhere are the expressions of those dynamics more vivid—both in terms of key physical quantities as well the biological, chemical, and ecological response—than the Galápagos Archipelago [*Karnauskas et al.*, 2014]. Because the Galápagos straddles the equator in the eastern Pacific, its mean oceanographic environment is shaped by the relatively weaker wind-driven (Ekman) upwelling that extends along the equator across most of the basin and is coupled to the Walker circulation [*Bjerknes*, 1969], intense local upwelling due to the upward deflection of the Equatorial Undercurrent (EUC) by the islands themselves, and a confluence of surface currents and countercurrents originating in both hemispheres. As such, and purely by accident of geography, the Galápagos is a remarkably well-suited environment for animals traditionally associated with higher-latitude climates such as the Galápagos Penguin, *Spheniscus mendiculus*, and the Galápagos Fur Seal, *Arctocephalus galapagoensis*, both of which are endangered and acutely sensitive to seasonal, interannual, and possibly longer-term variability in ocean circulation including anthropogenically forced trends. In addition to being the northernmost colony of penguins on the planet, the Galápagos Penguin is the rarest and most critically endangered penguin species [*BirdLife-International*, 2012].

Sea surface temperature (SST) is a readily observable quantity that integrates the aforementioned physical processes, while also serving as an important ecological constraint for species of seabirds and marine mammals, because they depend critically on food from the ocean for reproductive effort and survival. However, at only ~100 km in horizontal scale, the Galápagos and its influence on ocean circulation [*Karnauskas et al.*, 2007, 2010] are difficult for most gridded instrumental data sets to capture and even more so for many ocean and climate models to properly resolve [*Karnauskas et al.*, 2012]. Very high resolution infrared satellite missions such as Moderate Resolution Imaging Spectroradiometer and microwave instruments such as the Tropical Rainfall Measuring Mission Microwave Imager have the necessary spatial resolution but with relatively short temporal records. This paper employs the NOAA National Centers for Environmental Prediction (NCEP) Optimal Interpolation version 2 (Olv2)-gridded SST data set, with a 0.25° spatial resolution, global coverage, daily temporal resolution, and presently spans 33 complete years from 1982 to 2014. The NCEP Olv2 product optimally combines satellite and in situ (ship and buoy) observations

©2015. American Geophysical Union. All Rights Reserved.

Geophysical Research Letters



Figure 1. Ocean climatology and penguin distribution in the Galápagos region. (a) Annual mean SST from 1982 to 2014 at 0.25° resolution (colors; °C) [*Reynolds et al.*, 2002] with the distribution of the Galápagos Penguins (heavy black lines) [*BirdLife-International*, 2012] including the region in which 67% of Galápagos Penguins live (heavy green line) [*Vargas et al.*, 2005] and two regions over which area average time series are computed (dashed black lines). The box marked SST_W extends to 100°W/260°E. (b) Mean daily seasonal cycles of SST in the SST_W region (red) and SST_G region (blue). (c) Mean daily seasonal cycle of Equatorial Undercurrent (EUC) transport at 95°W [*Johnson et al.*, 2002].

to produce a complete, well-validated observational data set of suitable quality and consistency for climate studies [*Reynolds et al.*, 2002]. The relationship between SST (and by extension upwelling) and the distribution and population of Galápagos Penguins is explored here, with a focus on multidecadal trends and their context within the broader coupled ocean-atmosphere system.

2. Data and Methods

Sea surface temperature (SST) data from the NOAA National Centers for Environmental Prediction (NCEP) Optimal Interpolation version 2 (Olv2)-gridded SST data set [*Reynolds et al.*, 2002] were downloaded from the NOAA Earth System Research Laboratory (ESRL) Physical Sciences Division (PSD)-gridded climate data set archive (http://www.esrl.noaa.gov/psd/data/gridded/). The NCEP Olv2 high-resolution data set has a 0.25° spatial resolution, global coverage, daily temporal resolution, and spans September 1981 through the present. Prior to analysis, the daily SST data were subject to a 31 day centered running mean to reduce high-frequency noise in estimates of time means and trends.

Near-surface (10 m) meridional wind data from the NCEP/National Center for Atmospheric Research (NCAR) Reanalysis [Kalnay et al., 1996] were also downloaded from the NOAA/ESRL/PSD archive and have a 1.9° spatial resolution, global coverage, monthly temporal resolution, and span 1948 to the present.

Estimates of statistical significance are based on the *effective* degrees of freedom, accounting for serial autocorrelation of the time series [*Leith*, 1973].

3. Results

The eastward flowing EUC is constrained to the equator by the Coriolis force, while the cross-equatorial (northward) component of the wind stress displaces the EUC by ~0.5° south of the equator in the eastern equatorial Pacific [*Charney and Spiegel*, 1971; *Johnson et al.*, 2002; *Kessler et al.*, 1998; *Philander and Delecluse*, 1983]. Isabela and Fernandina Islands in the western Galápagos Archipelago, being situated between 1.1°S and 0.2°N, thus deflect a substantial volume of cold, nutrient-rich EUC water upward. This topographic upwelling results in an intense cold pool with annual mean SST adjacent to Isabela and Fernandina of 22°C–23°C (Figures 1a and 1b), representing a local deviation (δ SST) of ~1°C relative to neighboring waters (Figure 1*c*; see caption for definition of δ SST). Seasonally, the intensity of the Galápagos cold pool varies with the strength of the EUC (Figures 1c and 1d); during boreal spring, the EUC at 95°W reaches 30 sverdrup [*Johnson et al.*, 2002], at which point the cold pool is over 1°C cooler than its surroundings.

Geophysical Research Letters



Figure 2. Equatorial Pacific SST trends. (a) Linear SST trend from 1982 to 2014 (°C/33 yr) including, for reference, the 23°C isotherm from the annual mean SST in Figure 1a (dashed black line) and penguin distribution as in Figure 1a. (b) Zonal profiles of SST trend at each latitude between 1°S and 1°N (every 0.25°).

Galápagos Penguins feed on pelagic schooling fish prevalent in upwelling environments [*Boersma et al.*, 2013], and their distribution closely coincides with the main upwelling area of the archipelago (Figure 1a) [*BirdLife-International*, 2012; *Boersma*, 1978]. Approximately 95% of the Galápagos Penguins are found in the westernmost islands of Isabela and Fernandina [*Boersma*, 1977; *Vargas et al.*, 2006], which is likely a result of the nutrients brought to the surface by topographic upwelling of the EUC and subsequent enhancement of biological productivity. Specifically, a 2005 survey showed that 67% of the Galápagos Penguins are found along the southern bulge of Isabela, precisely in line with the coldest SST and most intense upwelling [*Vargas et al.*, 2005]. Similarly, the Galápagos Fur Seal is predominantly found on the western side of Isabela, where rocky shores provide ideal breeding grounds in addition to the productive upwelling pool [*Aurioles and Trillmich*, 2008].

There has been a pronounced cooling trend in SST near the Galápagos from 1982 to 2014 (Figure 2a). The largest trend, which appears along the northern edge of the Galápagos cold pool, is -0.8° C over the 33 year record. The SST trend along the western shores of Isabela and Fernandina Islands—the predominant location of penguins in the Galápagos—is in fact the strongest trend (of either sign) anywhere in the equatorial Pacific over this period (Figure 2b). The basin-scale trends in equatorial SST reveal a warming trend in the western Pacific warm pool (up to 0.6° C) and a cooling trend in the eastern Pacific cold tongue (~ 0.3° C), punctuated by the 0.8° C trend at the Galápagos. The basin-scale trends over this period are consistent with (albeit larger than) trends since 1880 based on a range of gridded instrumental data sets [*Cane et al.*, 1997; *Compo and Sardeshmukh*, 2010; *Karnauskas et al.*, 2009; *Kumar et al.*, 2010; *L'heureux et al.*, 2013; *Solomon and Newman*, 2012; *Zhang et al.*, 2010]. The spatial structure of the cooling trend within the Galápagos region is indicative of a northward expansion of the cold pool, which is likely a result of a strengthening and equatorward (northward) shift of the EUC and consequently a northward expansion of the upwelling area in which Galápagos Penguins can thrive. This SST-based indication of a strengthening EUC in recent decades is highly consistent with a recent analysis of trends in equatorial ocean circulation also beginning in the late 19th century [*Drenkard and Karnauskas*, 2014].

Previously published census data on Galápagos Penguins [see *Boersma et al.*, 2013, and references therein] indicate an increasing trend in the penguin population over the same period (Figure 3a). These population data have previously been compared to local SST measurements to show the precipitous declines in





AGU Geophysical Research Letters



Figure 4. (a) Time series of SST_W (red) and SST_G (blue) with a 5 year running mean. (b) Time series of δSST with an annual running mean (black line) and linear trend (red line). (c) Linear trend of δSST as a function of calendar day where the error bars represent 95% confidence limits. (d) Mean October position of the 22°C isotherm from 1982 to 1997 (blue line) and from 1998 to 2014 (red line) and penguin distribution as in Figure 1a.

population following major El Niño events (e.g., 1997/1998 [see also *Boersma*, 1978, 1998; *Vargas et al.*, 2006, 2007]). Penguin population collapses during or following major El Niño events is understandable from an oceanographic perspective. The EUC is known to weaken substantially and even disappear altogether during such events [*Firing et al.*, 1983], with dramatic consequences for the entire food web from schooling fish to penguins [*Boersma*, 1978, 1998; *Boersma et al.*, 2013], fur seals [*Aurioles and Trillmich*, 2008], marine iguanas [*Nelson et al.*, 2004], and other marine predators. However, the interannual variability and trend in penguin population appear more closely related to δ SST (i.e., change in local SST relative to its surroundings, a robust indicator of EUC, and topographic upwelling) than local SST itself (Figures 3b and 3c), further underscoring the critical role of topographic upwelling-driven productivity for the viability of the Galápagos Penguin population [*Boersma*, 1998; *Vargas et al.*, 2007].

The trend in δ SST is quite linear and is statistically significant at the 95% confidence level over the analysis period (Figures 4a and 4b). The resulting effective number of degrees of freedom of the δ SST time series shown in Figure 4b is 12. More importantly, the linear trend is comparable to the amplitude of interannual variability. It is often the case in the tropical Pacific that anomalies associated with El Niño–Southern Oscillation (ENSO) dwarf lower-frequency variability or trends. However, the linear trend is sufficiently strong that the amplitude of each successive El Niño since 1982 was weaker in terms of short-term δ SST changes— and presumably also in the reduction of EUC strength and topographic upwelling—than the previous (comparing, for example, the 1982/1983 and 1997/1997 events, which were nearly identical climatic events by standard indices such as Niño3.4).

Computing the linear trend of δ SST as a function of season reveals that the cooling and northward extension of the Galápagos cold pool is preferentially occurring between July and December, when the δ SST trend is ~1°C/33 yr (Figure 4c). Previously published ecological studies have suggested that Galápagos Penguins breed when SST is between 15°C and 22°C and typically between May and December [*Boersma*, 1978]. Using October as an example, the seasonality and spatial structure of the SST trend is such that the

AGU Geophysical Research Letters



Figure 5. Trends in cross-equatorial wind. (a) Linear trend in August–November 10 m meridional wind (m/s/33 yr) [Kalnay et al., 1996] including, for reference, the 23°C isotherm from the annual mean SST in Figure 1a (heavy black line). (b) Time series of area average August–November 10 m meridional wind over the dashed box shown in Figure 5a with linear trend (red line).

intersection of the 22°C isotherm with the Galápagos is 35 km (0.333°) further north in the second half of the record than the first half (Figure 4d), with likely consequences for the distribution pattern of the Galápagos Penguin and other cold-water species.

Finally, the physical mechanism for the equatorward shift of the EUC is briefly considered using 10 m meridional wind data from the NCEP/NCAR Reanalysis [Kalnay et al., 1996]. As mentioned above, the timemean EUC is centered slightly south of the equator due to the cross-equatorial (southerly) component of the wind stress in the eastern equatorial Pacific. Over the same time period analyzed above, there is a robust weakening of the southerly component of the trade winds in the ~1000 km wide stretch immediately west of the Galápagos (Figure 5), which is consistent with an equatorward relaxation of the EUC position and expansion of the Galápagos cold pool. The dynamics governing the EUC's latitudinal dependence on—and the sensitivity of the local SST response to—the wind stress in the eastern equatorial Pacific, including meridional amplitude and spatial structure, clearly warrant further investigation.

4. Discussion

Food web dynamics, population dynamics, viability, and shifts in the distribution of marine sentinel species such as the Galápagos Penguin are far more complicated than a simple dependence on SST. However, the SST pattern in the Galápagos region—and penguin distribution—is to first order described by the cold pool fed by topographic upwelling. We have used 33 years of reliable SST observations to reveal a strong cooling trend in the Galápagos cold pool, indicative of an intensification and equatorward shift of the EUC and upwelling along the western shores of the Isabela and Fernandina Islands. Such results, particularly the increasing EUC strength, are consistent with longer-term historical trends in circulation including their seasonality [*Drenkard and Karnauskas*, 2014] as well as future projections by global climate models to the end of the 21st century in response to anthropogenic radiative forcing [*Karnauskas and Cohen*, 2012; *Luo et al.*, 2009; *Sen Gupta et al.*, 2012].

If the northern sector of these islands is indeed becoming a more suitable foraging habitat for penguins and other species associated with cold water, such as fur seals, in terms of upwelling, SST, and productivity, then there are important implications for ongoing and future conservation measures such as repopulation initiatives and marine protected area (MPA) design. For example, penguin populations in Elizabeth Bay (0.6°S, near the midsection of Isabela) diminished in the 1970s and early 1980s due to the introduction of rats, declining nest sites, and a major El Niño event [*Boersma*, 1977], while the population along the southern bulge of Isabela increased [*Vargas et al.*, 2006]. Rat eradication and habitat restoration projects have reportedly found hope for increasing the penguin population [*Boersma et al.*, 2013], and Elizabeth Bay has been recommended for MPA status [*Galápagos Conservancy*, 2015]. Scaling up such efforts, particularly in the central and northern sectors of Fernandina and Isabela including Elizabeth Bay, might have particularly high chances of success as the heart of the nutrient-rich Galápagos cold pool also intensifies and expands northward. Despite the data limitations, this is a clear example of the local impacts of global trends. Much attention has been focused on the impact of trade wind and SST changes on the global warming hiatus [*England et al.*, 2014; *Kosaka and Xie*, 2013], but the regional specificity of environmental and ecological responses will be critical to understand for deciphering the overall impacts of global trends.

This is an outstanding case study underscoring the need to focus on local and regional impacts of global climate variability and change and the associated ecological responses in the face of grave concerns about the inexorable loss of species and biodiversity. Global warming impacts are inherently local. The daunting challenges of understanding the tropical Pacific response to global warming cannot be overemphasized, but the local dynamics and ecological response playing out in the Galápagos is a cautionary tail in understanding other seemingly obvious biophysical interactions—a timely reminder that nature makes the rules and biology finds the loopholes.

References

Aurioles, D., and F. Trillmich (2008), Arctocephalus galapagoensis, The IUCN Red List of Threatened Species(2014.3).

BirdLife-International (2012), Spheniscus mendiculus, The IUCN Red List of Threatened Species(Version 2014.3).

Bjerknes, J. (1969), Atmospheric teleconnections from the Equatorial Pacific1, Mon. Weather Rev., 97(3), 163–172.

Boersma, P. D. (1977), An ecological and behavioral study of the Galápagos Penguin, Living Bird, 15, 43–93.

Boersma, P. D. (1978), Breeding patterns of Galápagos Penguins as an indicator of oceanographic conditions, Science, 200, 1481–1483.

Boersma, P. D. (1998), Population trends of the Galápagos Penguin: Impacts of El Niño and La Niña, Condor, 100(2), 245–253.

Boersma, P. D., A. Steinfurth, G. Merlen, G. Jiménez–Uzcátegui, F. Vargas, and P. G. Parker (2013), Galápagos Penguin (Spheniscus mendiculus), in *Penguins Natural History and Conservation*, edited by P. G. Borboroglu and P. D. Boersma, 360 pp., Univ. of Washington Press, Seattle, Wash. [Available at www.washington.edu/uwpress/search/books/BORPEN.html.]

Cane, M. A., A. C. Clement, A. Kaplan, Y. Kushnir, D. Pozdnyakov, R. Seager, S. E. Zebiak, and R. Murtugudde (1997), Twentieth-century sea surface temperature trends, *Science*, 275(5302), 957–960.

Charney, J. G., and S. L. Spiegel (1971), The structure of wind-driven equatorial currents in homogeneous oceans, *J. Phys. Oceanogr.*, 1, 149–160. Collins, M., et al. (2010), The impact of global warming on the tropical Pacific Ocean and El Niño, *Nat. Geosci.*, 3(6), 391–397. Compo, G. P., and P. D. Sardeshmukh (2010), Removing ENSO-related variations from the climate record, *J. Clim.*, 23, 1957–1978.

Drenkard, E. J., and K. B. Karnauskas (2014), Strengthening of the Pacific Equatorial Undercurrent in the SODA reanalysis: Mechanisms, ocean dynamics, and implications, J. Clim., 27(6), 2405–2416.

England, M. H., S. McGregor, P. Spence, G. A. Meehl, A. Timmermann, W. J. Cai, A. Sen Gupta, M. J. McPhaden, A. Purich, and A. Santoso (2014), Recent intensification of wind-driven circulation in the Pacific and the ongoing warming hiatus, *Nat. Clim. Change*, 4(3), 222–227.

Firing, E., R. Lukas, J. Sadler, and K. Wyrtki (1983), Equatorial Undercurrent disappears during 1982–1983 El Niño, *Science*, 222(4628), 1121–1123. Galápagos Conservancy (2015), Ecosystem restoration: Increasing the Galápagos Penguin population. [Available at www.galapagos.org/ conservation/increasing-the-galapagos-penguin-population/.]

Johnson, G. C., B. M. Sloyan, W. S. Kessler, and K. E. McTaggart (2002), Direct measurements of upper ocean currents and water properties across the tropical Pacific during the 1990s, *Prog. Oceanogr.*, 52(1), 31–61.

Kalnay, E., et al. (1996), The NCEP/NCAR 40-year reanalysis project, Bull. Am. Meteorol. Soc., 77(3), 437-471.

Karnauskas, K. B., and A. L. Cohen (2012), Equatorial refuge amid tropical warming, Nat. Clim. Change, 2(7), 530-534.

Karnauskas, K. B., R. Murtugudde, and A. J. Busalacchi (2007), The effect of the Galápagos Islands on the equatorial Pacific cold tongue, J. Phys. Oceanogr., 37(5), 1266–1281.

Karnauskas, K. B., R. Seager, A. Kaplan, Y. Kushnir, and M. A. Cane (2009), Observed strengthening of the zonal sea surface temperature gradient across the equatorial Pacific Ocean, J. Clim., 22(16), 4316–4321.

Karnauskas, K. B., R. Murtugudde, and A. J. Busalacchi (2010), Observing the Galápagos-EUC interaction: Insights and challenges, J. Phys. Oceanogr., 40(12), 2768–2777.

Karnauskas, K. B., G. C. Johnson, and R. Murtugudde (2012), An equatorial ocean bottleneck in global climate models, J. Clim., 25(1), 343–349. Karnauskas, K. B., R. Murtugudde, and W. B. Owens (2014), Climate and the global reach of the Galápagos Archipelago, in The Galápagos: A

Natural Laboratory for the Earth Sciences, edited by K. S. Harpp et al., John Wiley, Hoboken, N. J., doi:10.1002/9781118852538.ch11. Kessler, W. S., L. M. Rothstein, and D. K. Chen (1998), The annual cycle of SST in the eastern tropical Pacific, diagnosed in an ocean GCM,

J. Clim., 11(5), 777–799.

Kosaka, Y., and S. P. Xie (2013), Recent global-warming hiatus tied to equatorial Pacific surface cooling, *Nature*, *501*(7467), 403–407.
Kumar, A., B. Jha, and M. L'Heureux (2010), Are tropical SST trends changing the global teleconnection during La Niña?, *Geophys Res Lett*, *37*, L12702, doi:10.1029/2010GL043394.

Leith, C. E. (1973), The standard error of time-averaged estimates of climatic means, J. Appl. Meteorol. Climatol., 12, 1066–1069.

L'heureux, M. L., S. Lee, and B. Lyon (2013), Recent multidecadal strengthening of the Walker circulation across the tropical Pacific, Nat. Clim. Change, 3(6), 571–576.

Luo, Y. Y., L. M. Rothstein, and R. H. Zhang (2009), Response of Pacific subtropical-tropical thermocline water pathways and transports to global warming, *Geophys Res Lett*, *36*, L04601, doi:10.1029/2008GL036705.

Nelson, K., H. Snell, and M. Wikelsi (2004), Amblyrhynchus cristatus, The IUCN Red List of Threatened Species (Version 2014.3).

Philander, S. G. H., and P. Delecluse (1983), Coastal currents in low latitudes (with application to the Somali and El Niño Currents), Deep-Sea Res., 30(8), 887–902.

Reynolds, R. W., N. A. Rayner, T. M. Smith, D. C. Stokes, and W. Q. Wang (2002), An improved in situ and satellite SST analysis for climate, J. Clim., 15(13), 1609–1625.

Sen Gupta, A., A. Ganachaud, S. McGregor, J. N. Brown, and L. Muir (2012), Drivers of the projected changes to the Pacific Ocean equatorial circulation, *Geophys. Res. Lett.*, 39, L09605, doi:10.1029/2012GL051447.

Solomon, A., and M. Newman (2012), Reconciling disparate twentieth-century Indo-Pacific Ocean temperature trends in the instrumental record, *Nat. Clim. Change*, 2(9), 691–699.

Vargas, F. H., S. Harrison, S. Rea, and D. W. Macdonald (2006), Biological effects of El Niño on the Galápagos Penguin, Biol. Conserv., 127(1), 107–114.
Vargas, F. H., R. C. Lacy, P. J. Johnson, A. Steinfurth, R. J. M. Crawford, P. D. Boersma, and D. W. Macdonald (2007), Modelling the effect of El Niño on the persistence of small populations: The Galápagos Penguin as a case study, Biol. Conserv., 137(1), 138–148.

Vargas, H., C. Lougheed, and H. Snell (2005), Population size and trends of the Galápagos Penguin Spheniscus mendiculus, *Ibis*, 147(2), 367–374.
Zhang, W. J., J. P. Li, and X. Zhao (2010), Sea surface temperature cooling mode in the Pacific cold tongue, *J. Geophys. Res.*, 115, C12042, doi:10.1029/2010JC006501.

Acknowledgments

K.B.K. acknowledges support from the Alfred P. Sloan Foundation, the James E. and Barbara V. Moltz Fellowship administered by the Woods Hole Oceanographic Institution (WHOI) Ocean and Climate Change Institute (OCCI), and the National Science Foundation (NSF) Physical Oceanography program (grant OCE-1233282), S.J. acknowledges support from WHOI. C.W.B. was supported by the NOAA Center for Satellite Applications and Research. The authors are very grateful for the tremendous effort by many to collect the ecological data published in Boersma et al. [2013]. All data sets are publicly available (see section 2) and/or freely available upon request.

The Editor thanks an anonymous reviewer for assisting in the evaluation of this paper.