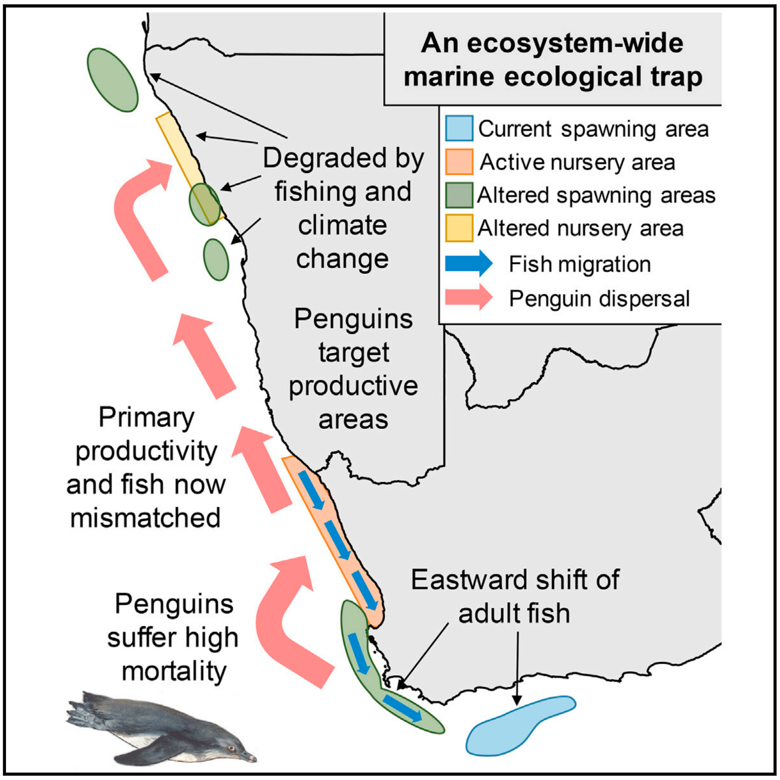
Report

Current Biology

Metapopulation Tracking Juvenile Penguins Reveals an Ecosystem-wide Ecological Trap

Graphical Abstract



Highlights

- Whether climate change and fisheries drive marine ecological traps is unknown
- Postnatal African penguins target habitat cues associated with high prey abundance
- Overfishing and climate change mean that penguins feed where forage fish are now scarce
- Population-level effects of this forage fish depletion confirm an ecological trap

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In Brief

Sherley et al. show how dispersing juvenile penguins move across a large marine ecosystem, targeting cues to high prey abundance. Doing so induces high mortality because fishing and climate change have degraded fish stocks. The resultant population-level impact offers the first evidence that forage fish depletion can drive marine ecological traps.

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Metapopulation Tracking Juvenile Penguins Reveals an Ecosystem-wide Ecological Trap

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SUMMARY

Climate change and fisheries are transforming the oceans, but we lack a complete understanding of their ecological impact [1–3]. Environmental degradation can cause maladaptive habitat selection, inducing ecological traps with profound consequences for biodiversity [4–6]. However, whether ecological traps operate in marine systems is unclear [7]. Large marine vertebrates may be vulnerable to ecological traps [6], but their broad-scale movements and complex life histories obscure the population-level consequences of habitat selection [8, 9]. We satellite tracked postnatal dispersal in African penguins (*Spheniscus demersus*) from eight sites across their breeding range to test whether they have become ecologically trapped in the degraded Benguela ecosystem. Bayesian state-space and habitat models show that penguins traversed thousands of square kilometers to areas of low sea surface temperatures (14.5°C–17.5°C) and high chlorophyll-*a* (~11 mg m^{-3}). These were once reliable cues for prey-rich waters, but climate change and industrial fishing have depleted forage fish stocks in this system [10, 11]. Juvenile penguin survival is low in populations selecting degraded areas, and Bayesian projection models suggest that breeding numbers are ~50% lower than if non-impacted habitats were used, revealing the extent and effect of a marine ecological trap for the first time. These cascading impacts of localized forage fish depletion—unobserved in studies on adults—were only elucidated via broad-scale movement and demographic data on juveniles. Our results support suspending fishing when prey biomass drops below critical thresholds [12, 13] and suggest that mitigation of marine ecological traps will require matching conservation action to the scale of ecological processes [14].

RESULTS AND DISCUSSION

Ecological traps occur when environmental change causes organisms to mistakenly select habitats that have lower fitness relative to the available alternatives [5, 15], but their significance in marine biodiversity loss is unknown [7]. In the Benguela ecosystem, fishing and climate change have rapidly reduced forage fish abundance, with the potential to create an ecological trap. Overfishing in Namibia precipitated a regime shift whereby sardines (*Sardinops sagax*) have now been replaced by low-energy gobies (*Sufflogobius bibarbatus*) and jellyfish [11]. Off South Africa, localized overfishing in the 1950s reduced adult sardine abundance [16], while environmental changes (increased temperatures and changes in salinity) and fishing pressure in the mid-1990s and 2000s shifted sardine and anchovy (*Engraulis encrasicolus*) spawning aggregations eastward [17]. Together, these changes reduced adult forage fish availability west of Cape Agulhas [10], triggering an ~80% decline in the Western Cape penguin population [18, 19]. African penguins (*Spheniscus demersus*), like many large marine vertebrates, are long-lived and most likely refine their foraging skills over many years [20, 21]. The changes in this system may therefore put inexperienced juveniles at risk of falling into an ecological trap.

Postnatal Dispersal and Forage Fish-Penguin Mismatch

We satellite tracked the dispersal of 54 juvenile African penguins for ~3,000 days during 2011–2013, from eight colonies holding ~87% of the global population and spanning this Endangered species' three breeding regions (Namibia and the Western

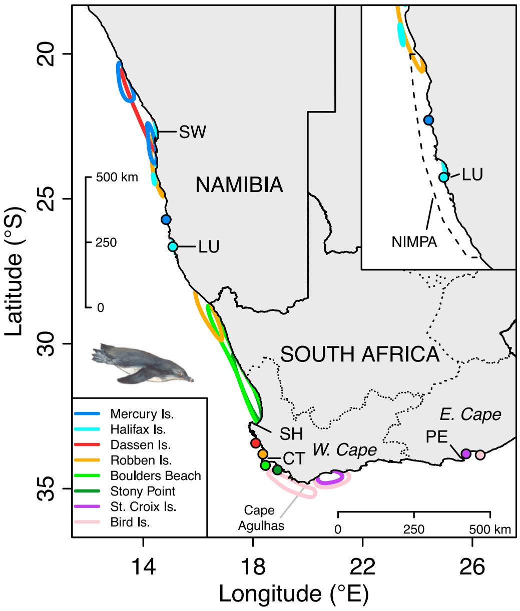

Figure 1. Core Foraging Areas of the 54 Juvenile Penguins

Colony-specific colors show study colonies (filled circles) and associated 50% volume contours (colored polygons). SW, Swakopmund; LU, Lüderitz; SH, St. Helena Bay; CT, Cape Town; PE, Port Elizabeth; NIMPA, Namibian Islands' Marine Protected Area. See also Figure S1 and Table S1.

Cape and Eastern Cape provinces of South Africa; Figure 1; Table S1) [22]. Juveniles dispersed westward or northward, consistently across years (Figures 1, S1, and S2). They occupied three core foraging areas around (1) Swakopmund, Namibia; (2) South Africa's west coast, north of St. Helena Bay; and (3) Cape Agulhas, South Africa (Figure 1). Before forage fish stocks were altered in this system, these areas were all important nursery and spawning areas for the penguins' prey, sardines and anchovies [16, 22, 23].

In light of the environmental changes that have occurred, only penguins dispersing from the Eastern Cape foraged in areas with high-density aggregations of energy-rich forage fish (Figures 2 and S3). Although juvenile penguins from both the Western and Eastern Cape colonies foraged where anchovy recruits were abundant shortly after fledging (austral autumn and winter, May to July; Figure 2A; generalized additive mixed model [GAMM]: estimated degrees of freedom [edf] = 1.25, χ^2 = 67.07, $p < 0.001$), these young sardines and anchovies migrate south to spawn around Cape Agulhas as the winter progresses [23] (Figure S4). The juvenile penguins did not, however, track this southward movement (Figure 2). Instead, they moved north to areas where adult sardines were formerly abundant in the spring (St. Helena Bay and Namibia) but are now scarce; as a consequence, the foraging locations of birds at sea from South African colonies in late winter and early spring were more likely than expected by chance to be devoid of adult anchovies (Figure 2B; GAMM: edf = 1.09, χ^2 = 14.26, $p < 0.001$) or sardines in November (Figure S3; GAMM: edf = 0.89, χ^2 = 4.81, p = 0.03). Similarly, penguins fledging from Namibian colonies—and those from all four Western Cape colonies that moved into Namibia (Figures 1 and S1)—would not have encountered high forage fish biomass during their dispersal since sardine stocks have collapsed in the northern Benguela [11].

Selection of Degraded Habitat—Evidence for an Ecological Trap

In an unaltered ecosystem, the dispersal patterns observed in all three regions would most likely have been adaptive. As their foraging proficiency improves, juvenile penguins should switch from feeding on slow-swimming recruits to feeding on energy-rich adult fish [20]. In the past, all of the juvenile penguins would have been well placed to do this; their selected habitats would have matched spatially and temporally with forage fish recruits immediately after fledging and then high-energy adult sardines shortly thereafter (Figure S4). For example, sardine spawning around Swakopmund traditionally peaked during September and October [23], just as forage fish recruits move away from South Africa's west coast (Figure 2).

Today, however, the scarcity of sardines (in particular) off western South Africa is linked to low adult and juvenile penguin survival at Robben and Dassen islands [18, 24], while low juvenile survival seems to be limiting growth of the Namibian penguin population [25]. Our results indicate that this high first-year mortality is mediated through the maladaptive selection of attractive, but now degraded, foraging habitat (Figures 2 and 3). First, the observed dispersal movements were active, not passive: the current directions and penguin movements were not correlated in Namibia ($r_{43} = -0.12$, $p = 0.31$), the Western Cape ($r_{161} = -0.13$, $p = 0.10$), or the Eastern Cape ($r_{47} = 0.21$, $p = 0.18$; Figure S2) and the birds' heading velocities (mean ± SD = 56.7 ± 34.2 cm s^{-1}) were significantly faster than current speeds (14.7 ± 8.8 cm s^{-1}; permutations test: $p < 0.001$), indicating directional swimming. Second, juvenile penguins selected cool waters with high primary productivity, preferring chlorophyll-*a* concentrations of ~11 mg m^{-3} (Figures 3A and 3B; GAMM: edf = 3.94, χ^2 = 281.6, $p < 0.001$) and sea surface temperatures (SSTs) between ~14.5 and ~17.5°C (Figure 3C; GAMM: edf = 3.96, χ^2 = 231.1, $p < 0.001$), while avoiding the lower productivity of the Lüderitz upwelling cell and warmer waters east of 22°E (Figures 3 and S3). High primary productivity should correspond to high forage fish abundance, but the two are now mismatched in the Benguela ecosystem [10, 23]; consequently, the penguins mistakenly selected depauperate foraging areas (Figures 2 and 3).

Although several mechanisms could underpin this active habitat selection, social information from experienced birds appears to be unlikely; adults move to different areas [26, 27], actively exclude juveniles from foraging groups [28], and do not appear to have become trapped in this way. In turn, although there may be innate control in the departure direction, endogenous "rules of thumb" cannot generally explain convergence on specific areas alone [29]. Instead, penguins seem to use contemporaneous environmental cues to select habitats consistent with high productivity. Similar targeted movements have been observed in juvenile king penguins (*Aptenodytes patagonicus*), and attraction to volatiles such as dimethyl sulfide (DMS) may be key [30]. DMS production is high where primary consumers graze phytoplankton [31], which in turn attracts forage fish [23] and apex predators, including penguins [31, 32]. Thus, under a natural system state, DMS should offer a cue to waters

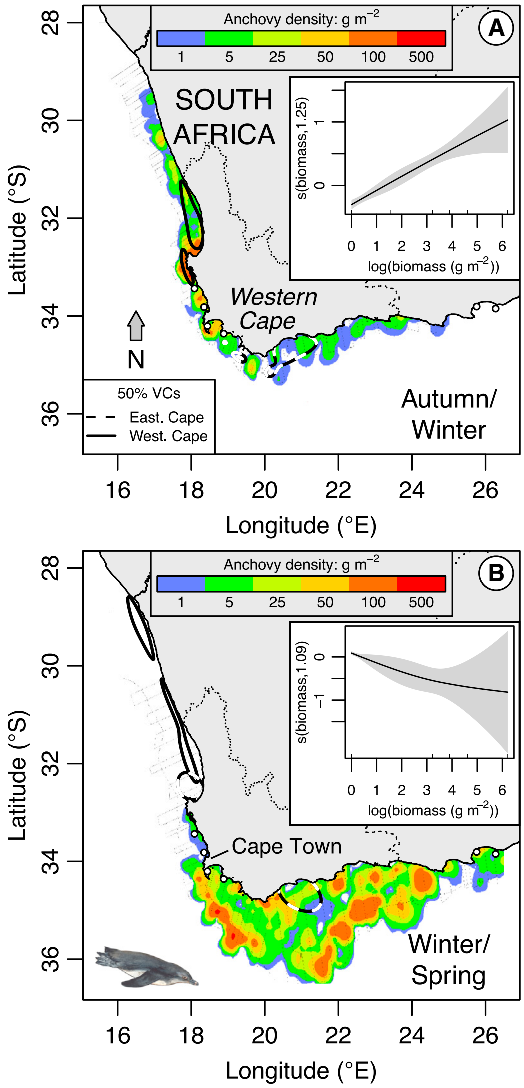

Figure 2. Penguin Foraging Areas and Prey Availability in South Africa

(A) Core foraging areas (50% volume contours, VCs) for 27 juvenile penguins at sea May 25–July 31, 2013, from the two Eastern Cape colonies (dashed black and white contours) and four Western Cape colonies (solid black contours) in relation to the distribution of recruit anchovy (age 0 fish) in May 2013.

(B) As in (A), but for 25 penguins at sea August 1–November 21, 2013, and related to adult anchovy biomass (excluding age 0 fish) in November 2013.

Inserts show the modeled habitat selection functions with 95% confidence intervals (gray shaded area) relating penguin foraging locations to (A) anchovy recruit distributions in 2012 and 2013 and (B) anchovy spawner distributions in 2011, 2012, and 2013 (B). See the Experimental Procedures for details. Hydroacoustic survey transects are shown as thin gray lines and the study colonies as white circles (see Figure 1). See also Figures S3 and S4.

rich in forage fish. Productivity and zooplankton distributions remain intact off Namibia and the Western Cape, but anthropogenic actions have depleted forage fish availability [10], leading these birds into an ecological trap (Figure S4). In contrast, post-breeding adults orientate toward suitable foraging habitat on the central or eastern Agulhas Bank [26]. Marine vertebrates may learn to locate reliable foraging areas over many years [21, 33], and understanding how individuals that survive to adulthood avoid degraded habitats is an important avenue for future research.

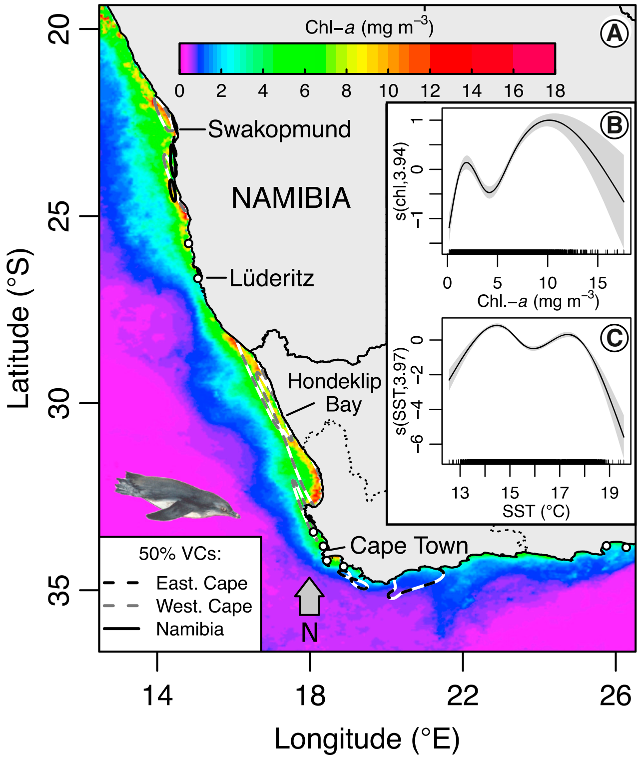

Figure 3. Penguin Foraging Areas and Oceanographic Conditions, March–November 2013

(A) Core foraging areas and mean chlorophyll-*a* concentrations (mg m^{-3}). 50% volume contours (VCs) are for birds from the Eastern Cape (dashed black and white contours), the Western Cape (dashed gray and white contours, calculated separately for the colonies north and south of Cape Town), and Namibia (solid black contours). Colonies shown as white circles (see Figure 1).

(B) Modeled habitat selection function for chlorophyll-*a* with 95% confidence intervals (gray shaded area). The y axes show partial model residuals or relative population-level habitat preferences.

(C) Modeled habitat selection function for sea surface temperature (SST), as in (B).

See also Figures S2–S4.

Consequences for Metapopulation Dynamics and Conservation

Marine vertebrates are long-lived, mobile animals that select habitats using cues with spatial or temporal lags [8]. Our results suggest that young, inexperienced individuals may be at particular risk from ecological traps [6, 21]. The impacts of heightened juvenile mortality could be severe; immature dispersal is crucial to gene flow, compensatory recruitment, and the demographic process as a whole and thus plays a key role in adaptability to change [34, 35]. To assess the demographic effect of the observed ecological trap on the South African penguin population, we used stochastic Bayesian projection models to reproduce recent declines (Figure 4). For the Eastern Cape, we set mean juvenile survival (ϕ_j) = 0.51, a value used to represent an equilibrium state for this species [24], as dispersing juveniles

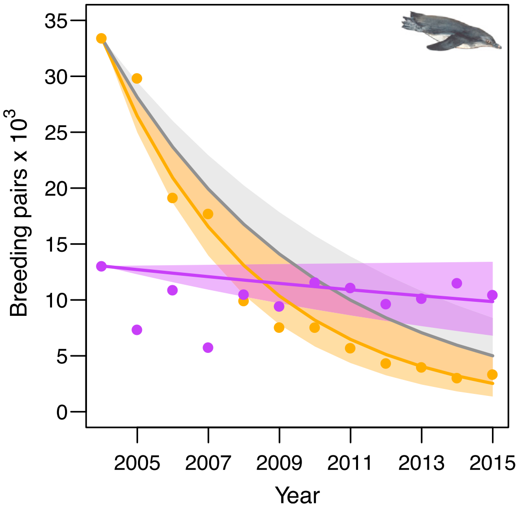

Figure 4. African Penguin Population Projections 2004–2015

Observed (circles) and modeled (lines) populations in the Eastern Cape (purple: $\phi_a = 0.88$, $\phi_j = 0.51$, $F = 0.56$); the Western Cape under scenario 1 (orange: $\phi_a = 0.74$, $\phi_j = 0.19$, $F = 0.67$), where juvenile penguins forage in degraded habitat; and the Western Cape population under scenario 2 (gray: $\phi_a = 0.74$, $\phi_j = 0.50$, $F = 0.67$), where juveniles hypothetically avoid trap habitat. Shaded areas indicate Bayesian 95% credible intervals. See also Table S2.

would have good access to forage fish resources (Figure 2). Accordingly, the modeled growth rate (λ) of 0.98 (95% Bayesian credible intervals: 0.94–1.00) matched the observed slow decline (Figure 4). For the Western Cape, we modeled population change both in the presence of the ecological trap, with juveniles assumed to feed where adult forage fish were scarce (scenario 1), and in its absence, where juveniles hypothetically avoid trap habitats and access forage fish all year (scenario 2). Under scenario 1, we set $\phi_j = 0.19$ (SD = 0.12), based on survival rates observed post-2001 and the shift of forage fish spawners [18]; the model tracked the observed population decline (λ = 0.79, 0.75–0.84), and the 2015 population was predicted as 2,531 pairs. Under scenario 2, we set $\phi_j = 0.50$ (SD = 0.18), the mean observed prior to 2001 [18] (and similar to the Eastern Cape value). The population declined much less steeply (λ = 0.84; 0.79–0.88), and the predicted 2015 population of 5,026 pairs was 98.6% higher than under scenario 1 (Figure 4).

Although the variability in the observed survival rates adds some uncertainty to the projections, these models reveal the important implications that ecological traps could have at the population-level by lowering juvenile survival (Figure 4). Moreover, our tracking data indicate that traps may be difficult to detect for highly mobile species if they arise from degradation of habitat distant from breeding sites [6, 15]. Under normal source-sink dynamics, natal dispersal away from poor habitat contributes to metapopulation persistence. If, however, heightened mortality results from juveniles foraging in degraded habitat, fewer individuals would survive to recruit into source populations. In turn, if natal fidelity is strong, surviving individuals would continue to select impaired environments, driving local population extirpation (e.g., Figure 4) and reducing resilience to future change [6]. Under these circumstances, conservation efforts targeted at components of a metapopulation, like breeding sites, would be insufficient for species survival [8, 14, 19].

In the marine environment, much conservation emphasis is placed on marine protected areas (MPAs). However, perhaps <10% of marine species have >5% of their range protected [36], and conservation action at anything less than seascape scales is unlikely to protect most marine megafauna [14, 36, 37]. In southern Africa, the 10,000 km^2 Namibian Islands' MPA (Figure 1) was declared to protect Namibia's breeding seabirds, but it does not protect the spawning or nursery grounds where juvenile penguins forage, and sardines are still fished for socio-economic reasons [38]. Similarly, fishing for sardines has continued off western South Africa for the last decade despite concerns that fishing contributed to their altered distribution [17] and biomass being consistently below a critical threshold for penguin survival [18, 39]. Unsurprisingly, purse-seine closures around seabird colonies are unable to fully offset the mortality of non-breeding animals linked to prey availability over seascape scales [19]. More broadly, these results demonstrate the wide-reaching deleterious impacts that regime shifts and localized overfishing can have on threatened marine predators, highlighting the importance of conservation action on the appropriate ecological scales [8, 14, 37].

Conclusions

Forage fish play key trophic roles in many marine ecosystems and support some of the world's largest fisheries, which in turn can contribute to stock collapses [13]. Here we show, for the first time, how such a forage fish stock collapse, driven by fisheries and climate change, can induce an ecological trap in the marine environment. This ecological trap was only made apparent by studying juveniles, and the dispersive phases of most marine predators are poorly studied [9], so similar traps could be operating undetected elsewhere. Traps of this nature, operating across large marine ecosystems, may prove difficult to mitigate. Spatial protection will provide some resilience [19, 37], but predator populations are most sensitive to broad-scale depletion by fisheries when forage fish biomass is low [39, 40]. Suspending fishing when forage fish populations fall below critical ecological thresholds can reduce the chances of crossing ecosystem tipping points and help protect dependent predators [40], with minimal losses to fisheries [12, 13]. Juveniles may have limited capacity to adapt their initial dispersal behavior, making them vulnerable to forage fish depletion; impacts on predator populations could be severe. With future climate change being likely to exacerbate matters [2], management actions that alleviate and, ultimately, remove fishing pressure at low biomass should be implemented to ensure the sustainability of ecosystems dependent on forage fish.

EXPERIMENTAL PROCEDURES

Instrumentation and Data Collection

We tracked 43 birds in 2013, six in 2012, and five in 2011 (Table S1) using platform terminal transmitters (PTTs), selecting individuals exceeding 2,830 g [27]. Fourteen were partially hand reared; for these, we attached PTTs 5.2 ± 4.8 (mean ± SD) days before release, and each bird swam in a pool with the device for ~1 hr on ≥2 days to ensure that they could maneuver and dive successfully [27]. The remaining birds were either returned to their nests and went to sea within 6.4 ± 4.1 days or were kept overnight in holding facilities and then released close to landings used by commuting penguins. The two types of juveniles did not differ in their behavior or habitat selection (see the Supplemental Experimental Procedures for details). The PTTs transmitted every 45 s between 0100 and 0459 hr GMT every 2 days in 2011 and 1 day in 2012 and 2013 (see Table S1 for individual tracking durations). Device attachment and study protocols were approved by the South African Department of Environmental Affairs (RES2011/57, RES2012/75, and RES2013/30), the Western Cape Provincial Conservation authority, CapeNature (0035-AAA008-00005 and AAA007-00067-0056), the Scientific Services branch of South African National Parks Authority, and the University of Cape Town's Animal Experimentation Committee (2011/V2/RS+LU and 2013/R2011/V2).

State-Space Modeling and Kernel Smoothing

We excluded low-quality locations (class A, B, or Z) and then analyzed location data for each trip using a Bayesian state-space model (SSM) to infer an even spread of position estimates in time and assign each one as either a transiting or foraging location based on turning angles and speeds [41]. We then mapped the foraging locations using kernel smoothing, taking the 50% volume contours (VCs) as core foraging areas [27, 42] (see the Supplemental Experimental Procedures).

Initial Dispersal and Ocean Currents

To rule out passive dispersal, we calculated the current velocity ($\mathbf{v_c}$),

$$\mathbf{v_c} = \sqrt{U^2 + V^2}, \qquad \text{(Equation 1)}$$

and direction (δ),

$$\delta = \tan^{-1}\left(\frac{U}{V}\right) \times \frac{180}{\pi}, \qquad \text{(Equation 2)}$$

(U is the zonal and V the meridional component) at the sea surface for each bird's locations over their first 5 days from the SSM and compared these to the penguins' velocity ($\mathbf{v_t}$; cm s^{-1}), direction (degrees), and heading ($\mathbf{v_h} = \mathbf{v_t} - \mathbf{v_c}$; Figure S2) using circular statistics and permutation tests (see the Supplemental Experimental Procedures).

Habitat Selection Functions

We used habitat selection functions based on binomial GAMMs, with foraging locations (=1), five associated random pseudo-absence positions (=0), and bird identity as a random effect, to explore the conditions characterizing foraging [43]. Distribution maps of sardine and anchovy biomass in South Africa during 2011, 2012, and 2013 were obtained from hydro-acoustic surveys. Surveys in May of recruit (age 0) biomass gave prey availability in (austral) autumn and early winter (when most penguins fledge), which we compared to all the validated foraging locations for 32 penguins at sea in South Africa between May 25 and July 31 in 2012 and 2013. Surveys in November gave adult sardine and anchovy biomass, energy-rich prey important for adult and first-year survival [18, 24], which we compared to all foraging locations for 35 penguins at sea in South Africa between August 1 and December 6 in 2011, 2012, and 2013 (see the Supplemental Experimental Procedures). Prey data were not available for Namibia. Finally, we used monthly mean MODIS-Aqua data from each month between March and November 2013 to construct maps of the mean chlorophyll-*a* concentrations (Chl-*a*) and SSTs across this time period on 4 km^2 grids for the Benguela ecosystem (see the Supplemental Experimental Procedures for details).

Bayesian Projection Modeling

Our demographic model structure and parameter values (Table S2) were based on previous models of African penguin demographics [19, 24]. Adult survival ($\phi_a = 0.74$) and fecundity ($F = 0.68$) were deterministic to allow for clear comparisons between different scenarios for juvenile survival (ϕ_j). Because ϕ_j is variable over time and parameter uncertainty is therefore high, we modeled it as stochastic using observed means and SDs (Table S2). For the Western Cape, under scenario 1, $\phi_j = 0.19$ (SD = 0.12), the mean observed after 2001 [18]. For scenario 2, $\phi_j = 0.50$ (SD = 0.18) the observed mean prior to 2001 [18]. For the Eastern Cape, $F = 0.56$, $\phi_a = 0.88$, and $\phi_j = 0.51$ (SD = 0.11) [24]. We modeled means ± 95% Bayesian credible intervals using three Markov chain Monte Carlo (MCMC) chains (100,000 samples, burn-in of 10,000, no thinning), confirmed unambiguous model convergence using Gelman-Rubin diagnostics (all $\widehat{R}$ values < 1.01), and compared the population projections to census data from 2004 to 2015 [19, 22] (see the Supplemental Experimental Procedures for details).

ACCESSION NUMBERS

The tracking data reported in this paper have been uploaded to BirdLife International's Seabird Tracking Database and are available at http://seabirdtracking.org/mapper/contributor.php?contributor_id=927.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four figures, and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.12.054.

AUTHOR CONTRIBUTIONS

Conceptualization, R.B.S. and L.G.U.; Methodology, R.B.S., J-P.R., A.B.M., and S.C.V.; Investigation, R.B.S., K.L., and B.M.D.; Formal Analysis, R.B.S., T.L., and K.L.S.; Writing – Original Draft, R.B.S.; Writing – Review & Editing, R.B.S., S.C.V., J-P.R., T.L., K.L.S., and K.L.; Funding Acquisition, R.B.S., L.G.U., and A.B.M.; Resources, A.B.M. and J-P.R.; Supervision, R.B.S., L.G.U., and S.C.V.

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