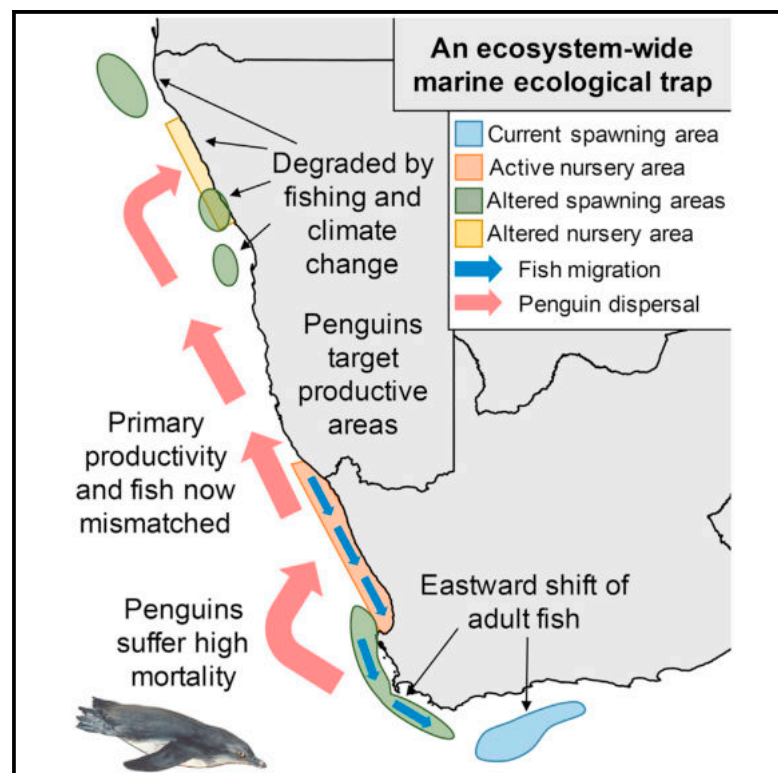# Metapopulation Tracking Juvenile Penguins Reveals an Ecosystem-wide Ecological Trap

Graphical Abstract

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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.

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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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
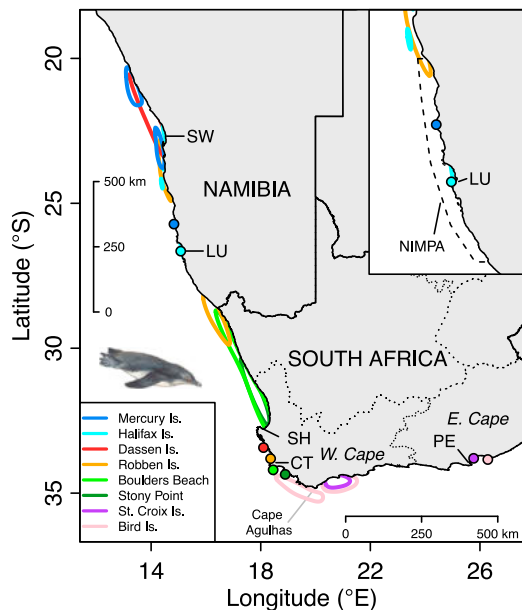
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Figure 1. Core Foraging Areas of the 54 Juvenile Penguins
Colony-specific colors show study colonies (filled circles) and associated 50% volume contours (colored polygons). SW, Swakopmund; LU, Lüderitz; SH, St. Helena Bay; CT, Cape Town; PE, Port Elizabeth; 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
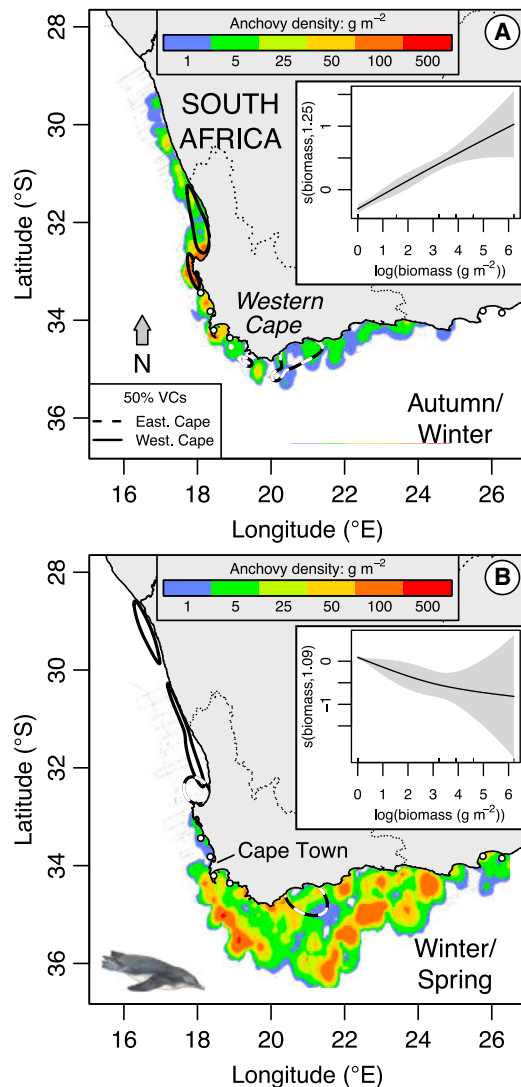
Figure 2. Penguin Foraging Areas and Prey Availability in South Africa

(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.

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.

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
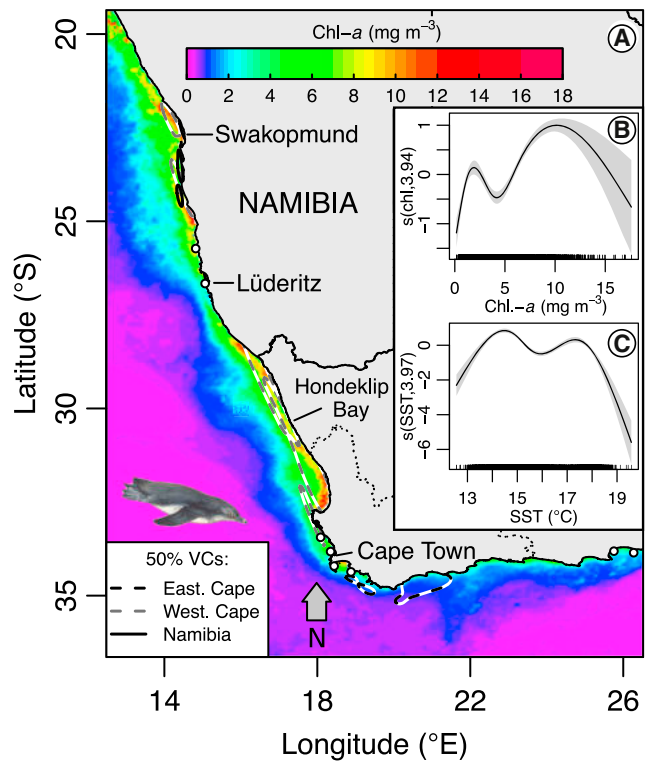
[21, 33], and understanding how individuals that survive to adulthood avoid degraded habitats is an important avenue for future research.

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
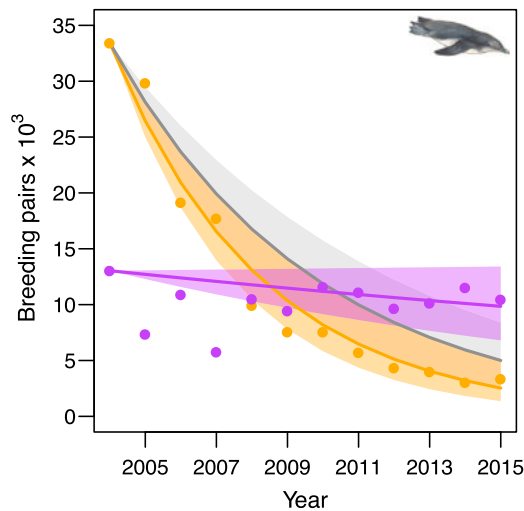
Figure 4. African Penguin Population Projections 2004–2015
Observed (circles) and modeled (lines) populations in the Eastern Cape (purple: $\phi_a = 0.88$, $\phi_j = 0.51$, $F = 0.56$); the Western Cape under scenario 1 (orange: $\phi_a = 0.74$, $\phi_j = 0.19$, $F = 0.67$), where juvenile penguins forage 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 ($\lambda = 0.79$, 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 ($\lambda = 0.84$; 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 $\hat{R}$ 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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Supplemental Information

Metapopulation Tracking Juvenile Penguins

Reveals an Ecosystem-wide Ecological Trap

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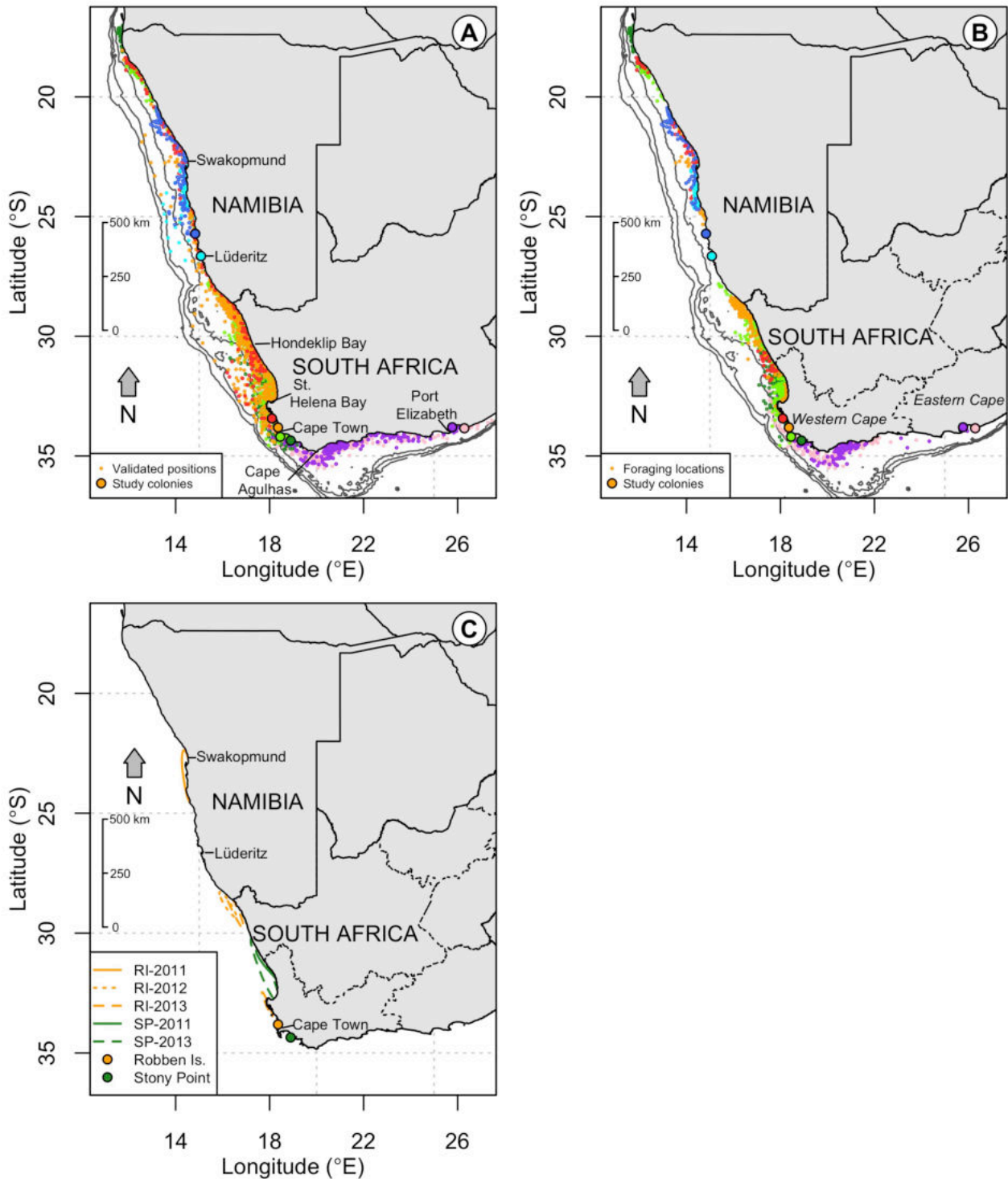
Figure S1, *related to Figure 1.* **All validated positions, foraging locations and annual consistency of core foraging locations.**
(A) All validated positions (from the state-space model), (B) all validated foraging locations for all 54 tracked juvenile African penguins *Spheniscus demersus* in relation to the 200, 500 and 1000 m isobaths (grey lines) and (C) the core foraging areas (50% volume contours) for penguins tracked from Robben Island (orange) in 2011, 2012 and 2013 and Stony Point (green) in 2011 and 2013. The study colonies are shown as black-outlined, solid-colored dots, in colony-specific colors, which also show the foraging locations and core foraging areas for each study colony. From north to south-east: Mercury Island (blue), Halifax Island (cyan), Dassen Island (red), Robben Island (orange), Boulders Beach (light green), Stony Point (dark green), St. Croix Island (purple), Bird Island (pink).
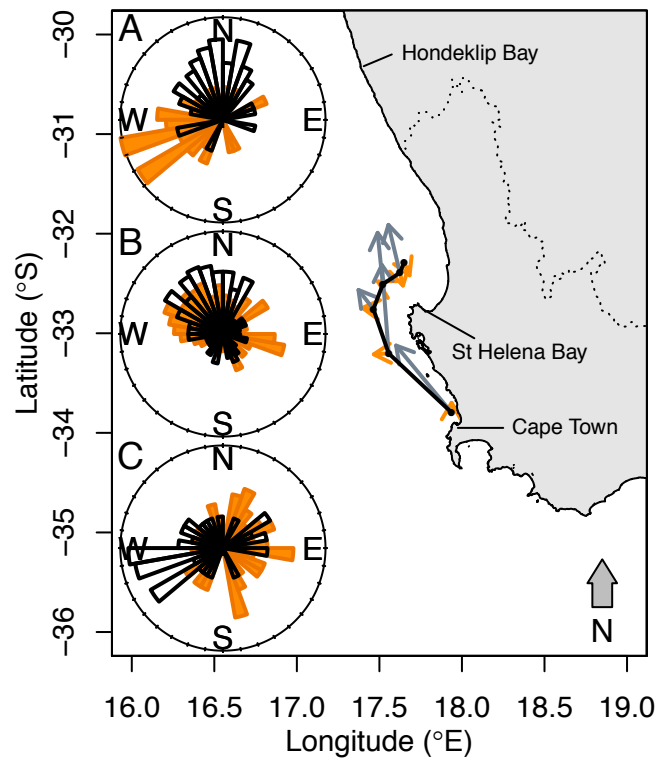
Figure S2, *related to Figure 1 and Figure 3*. **Initial dispersal and ocean current results.**
An example of the current velocities (orange arrows), penguin's track (black dots and lines) and corresponding heading velocities (grey arrows) for a juvenile penguin tracked from Robben Island and circular histograms in which length of bars is proportional to the number of track segments (black) and current directions (orange) oriented within 10° bins for birds from the (A) Namibian, (B) Western Cape and (C) Eastern Cape colonies. The track and current directions were not correlated in any of the three regions, suggesting active dispersal, leading to active selection of habitat linked to high primary productivity.
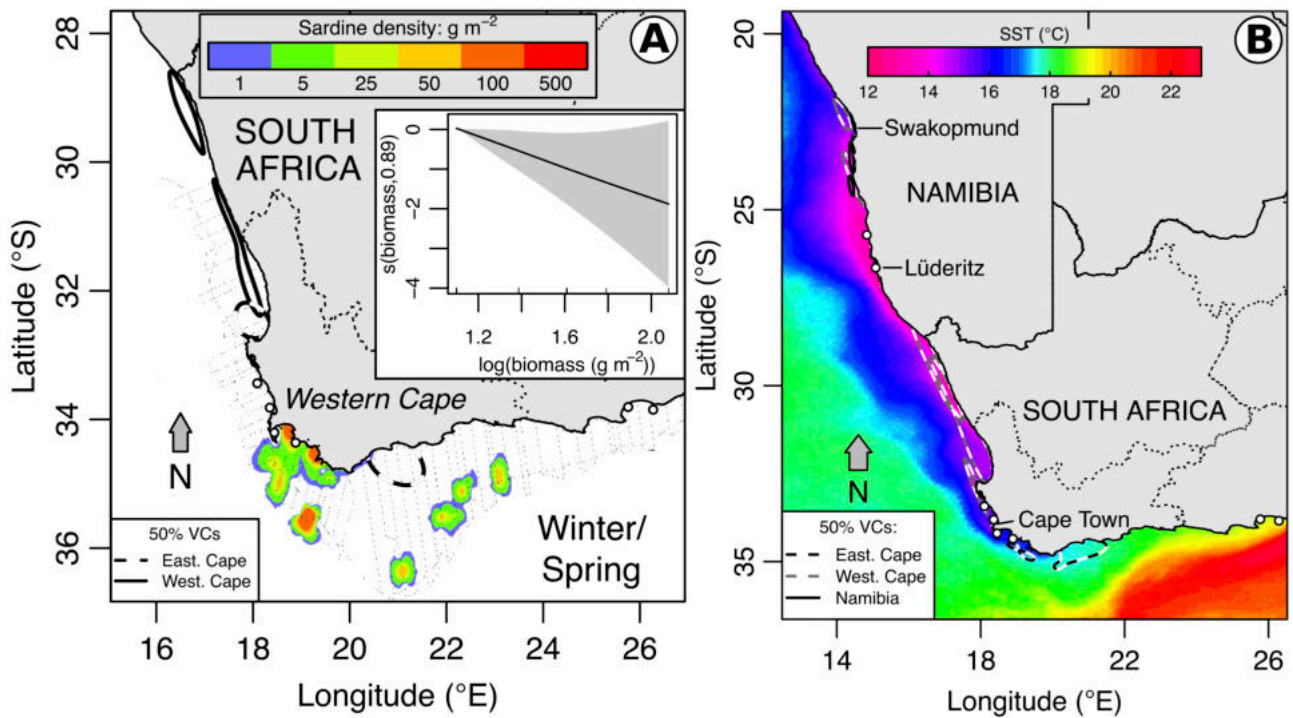
Figure S3, *related to Figure 2 and 3.* **Additional habitat modeling results.**

Left: core foraging areas (50% VCs) for 25 juvenile penguins tracked between 1 August and 21 November 2013 from the two Eastern Cape colonies (dashed black and white contours) and four Western Cape colonies (solid black contours) in relation to the adult sardine biomass (excluding age 0 fish; g m^{-2}) in South Africa during November 2013. The hydro-acoustic survey transects are shown as thin grey lines and the study colonies as white circles (locations in Figure 1). The insert shows the modeled habitat selection function with 95% confidence intervals (grey shaded area) linking the foraging locations from 35 penguins at sea in South Africa between 1 August and 6 December in 2011, 2012 and 2013 to sardine spawner biomass.

Right: Core foraging areas (50% volume contours) for 43 juveniles tracked between March and November 2013 from St. Croix and Bird islands (dashed black and white contours); Boulders Beach, Stony Point, Robben Island and Dassen Island (dashed grey and white contours); and Halifax and Mercury islands (solid black contours) in relation to mean sea surface temperatures (SST; °C) from March to November 2013. Core areas for the two Western Cape colonies north of Cape Town and the two south of Cape Town are calculated separately.

Table S1, *related to Figure 1*. Full list of all 54 juvenile African penguins tracked and their summary data.

No.	PTT ID	Year	Breeding colony	Breeding region	Release mass (g)	First date at sea	Last transmission date	Days transmitting	Status
1	105335	2011	Robben Island (RI)	WC	3220	26 Jun 2011	23 Jul 2011	27	H
2	105336	2011	Robben Island (RI)	WC	3180	19 Jul 2011	25 Oct 2011	98	H
3	105337	2011	Robben Island (RI)	WC	3040	26 Jul 2011	25 Oct 2011	91	H
4	105338	2011	Stony Point (SP)	WC	2950	13 Sep 2011	06 Dec 2011	84	H
5	105339	2011	Stony Point (SP)	WC	3200	13 Sep 2011	23 Sep 2011	10	H
6	119178	2012	Robben Island (RI)	WC	3130	12 Jun 2012	18 Sep 2012	98	W
7	119179	2012	Robben Island (RI)	WC	3020	12 Jun 2012	16 Sep 2012	96	W
8	119180	2012	Robben Island (RI)	WC	3290	12 Jun 2012	24 Aug 2012	73	W
9	119181	2012	Robben Island (RI)	WC	3100	19 Jul 2012	06 Oct 2012	79	H
10	119182	2012	Robben Island (RI)	WC	3250	19 Jul 2012	24 Aug 2012	36	H
11	119183	2012	Robben Island (RI)	WC	3150	19 Jul 2012	15 Aug 2012	27	H
12	119333	2013	Mercury Island (MI)	N	3050	15 Mar 2013	25 Mar 2013	10	W
13	119334	2013	Mercury Island (MI)	N	2925	19 Mar 2013	24 May 2013	66	W
14	119335	2013	Mercury Island (MI)	N	2975	19 Mar 2013	17 Apr 2013	29	W
15	119337	2013	Mercury Island (MI)	N	3100	15 Mar 2013	28 Mar 2013	13	W
16	119338	2013	Mercury Island (MI)	N	3000	19 Mar 2013	25 Mar 2013	6	W
17	119315	2013	Halifax Island (HI)	N	3120	06 Mar 2013	04 Apr 2013	29	W
18	119319	2013	Halifax Island (HI)	N	3040	06 Mar 2013	16 Apr 2013	41	W
19	119323	2013	Halifax Island (HI)	N	3060	06 Mar 2013	14 Apr 2013	39	W
20	119324	2013	Halifax Island (HI)	N	3020	06 Mar 2013	16 Apr 2013	41	W

Table S1. Cont.

No.	PTT ID	Year	Breeding colony	Breeding region	Release mass (g)	First date at sea	Last transmission date	Days transmitting	Status
21	119326	2013	Halifax Island (HI)	N	3480	06 Mar 2013	24 Apr 2013	49	W
22	123188	2013	Dassen Island (DI)	WC	3115	07 Jul 2013	24 Sep 2013	79	W
23	123189	2013	Dassen Island (DI)	WC	3035	06 Jul 2013	04 Aug 2013	29	W
24	123190	2013	Dassen Island (DI)	WC	2925	03 Jul 2013	23 Aug 2013	51	W
25	123191	2013	Dassen Island (DI)	WC	3135	07 Jul 2013	06 Sep 2013	61	W
26	118229	2013	Robben Island (RI)	WC	3040	28 Jun 2013	22 Jul 2013	24	W
27	118230	2013	Robben Island (RI)	WC	2920	28 Jun 2013	12 Jul 2013	14	W
28	118231	2013	Robben Island (RI)	WC	3135	05 Jul 2013	31 Jul 2013	26	W
29	118232	2013	Robben Island (RI)	WC	3120	05 Jul 2013	25 Sep 2013	82	W
30	118233	2013	Robben Island (RI)	WC	3450	05 Jul 2013	04 Sep 2013	61	W
31	118234	2013	Boulders Beach (BB)	WC	3220	27 Jun 2013	27 Aug 2013	61	W
32	118235	2013	Boulders Beach (BB)	WC	3180	08 Aug 2013	21 Oct 2013	74	H
33	118236	2013	Boulders Beach (BB)	WC	3000	08 Aug 2013	21 Oct 2013	74	H
34	118237	2013	Boulders Beach (BB)	WC	2980	08 Aug 2013	22 Oct 2013	75	H
35	123193	2013	Boulders Beach (BB)	WC	3040	27 Jun 2013	21 Aug 2013	55	W
36	123194	2013	Boulders Beach (BB)	WC	3320	27 Jun 2013	29 Aug 2013	63	W
37	118238	2013	Stony Point (SP)	WC	3040	20 Aug 2013	28 Aug 2013	8	H
38	118239	2013	Stony Point (SP)	WC	3020	20 Aug 2013	21 Nov 2013	93	H
39	118240	2013	Stony Point (SP)	WC	3120	20 Aug 2013	19 Oct 2013	60	H
40	123183	2013	Stony Point (SP)	WC	3020	20 Jun 2013	23 Jun 2013	3	W

Table S1. Cont.

No.	PTT No.	Year	Breeding colony	Breeding region	Release mass (g)	First date at sea	Last transmission date	Days transmitting	Status
41	123184	2013	Stony Point (SP)	WC	3280	20 Jun 2013	18 Aug 2013	59	W
42	123185	2013	Stony Point (SP)	WC	3060	20 Jun 2013	08 Sep 2013	80	W
43	123186	2013	Stony Point (SP)	WC	2980	20 Jun 2013	25 Aug 2013	66	W
44	123187	2013	Stony Point (SP)	WC	2950	20 Jun 2013	02 Jul 2013	12	W
45	126540	2013	St. Croix Island (SC)	EC	3300	30 May 2013	10 Aug 2013	72	W
46	126541	2013	St. Croix Island (SC)	EC	3600	29 May 2013	29 Aug 2013	92	W
47	126542	2013	St. Croix Island (SC)	EC	3350	27 May 2013	05 Jun 2013	9	W
48	126543	2013	St. Croix Island (SC)	EC	3200	29 May 2013	01 Aug 2013	64	W
49	126544	2013	St. Croix Island (SC)	EC	3100	25 May 2013	24 Jul 2013	60	W
50	126535	2013	Bird Island (BI)	EC	3030	05 Jun 2013	10 Aug 2013	66	W
51	126536	2013	Bird Island (BI)	EC	3120	03 Jun 2013	07 Aug 2013	65	W
52	126537	2013	Bird Island (BI)	EC	2950	27 May 2013	15 Aug 2013	80	W
53	126538	2013	Bird Island (BI)	EC	3030	25 May 2013	14 Aug 2013	81	W
54	126539	2013	Bird Island (BI)	EC	2980	02 Jun 2013	19 Aug 2013	78	W

Abbreviations: PTT = Platform Terminal Transmitter, WC = Western Cape province, N = Namibia, EC = Eastern Cape, W = wild (completely parent-reared) juvenile, H = juvenile partially hand-reared by SANCCOB. See Supplemental Experimental Procedures and [S1] for more details. The number of days transmitting excludes days for which birds were at SANCCOB or remained in the nest.

Table S2, *related to Figure 4*. Demographic parameters used in the population projection models and their sources.

Region/scenario	Parameter	Parameter value	Source
Eastern Cape	Adult survival[1] (ϕ_a)	0.88[2]	[S2,S3]
	Juvenile survival (ϕ_j)	0.51 (SD = 0.11)[2]	[S2,S3]
	Mean clutch size (*E*)	1.86	[S4,S5]
	Egg survival (ϕ_e)	0.47	[S6][3]
	Chick survival (ϕ_c)	0.51	[S6][3]
	Clutches per annum (*C*)	1.27	[S4,S5]
	Fecundity (*F*)[4]	0.566	
	Assumed sex ratio	1:1	[S7]
	Starting populations[5]:		
	Juveniles	1,642	-
	Immature 1	2,000	-
	Immature 2	2,000	-
	Immature 3	2,000	-
	Adults (breeders)	13,039	[S8]
Western Cape Scenario 1	Adult survival[1] (ϕ_a)	0.743	[S7,S9]
	Juvenile survival (ϕ_j)	0.194 (SD = 0.117)	[S9]
	Mean clutch size (*E*)	1.86	[S4,S5]
	Egg survival (ϕ_e)	0.55	[S4,S7]
	Chick survival (ϕ_c)	0.52	[S7][6]
	Clutches per annum (*C*)	1.27	[S4,S5]
	Fecundity (*F*)[4]	0.676	($E \times \phi_e \times \phi_c \times C$)
	Assumed sex ratio	1:1	[S7]
	Starting populations[5]:		
	Juveniles	2060	-
	Immature 1	2000	-
	Immature 2	2000	-
	Immature 3	2000	-
	Adults (breeders)	33,425	[S10]
Western Cape Scenario 2	Adult survival[1] (ϕ_a)	0.743	[S7,S9]
	Juvenile survival (ϕ_j)	0.497 (SD = 0.175)	[S9]
	Mean clutch size (*E*)	1.86	[S4,S5]
	Egg survival (ϕ_e)	0.55	[S4,S7]
	Chick survival (ϕ_c)	0.52	[S7][5]
	Clutches per annum (*C*)	1.27	[S4,S5]
	Fecundity (*F*)[4]	0.676	($E \times \phi_e \times \phi_c \times C$)
	Assumed sex ratio	1:1	[S7]
	Starting populations[5]:		
	Juveniles	4875	-
	Immature 1	2000	-
	Immature 2	2000	-
	Immature 3	2000	-
	Adults (breeders)	33,425	[S10]

Notes: 1. Annual survival in the three immature and the one breeding adult states was equal as no difference has been detected in a recent multistate capture-mark-recapture (CMR) analysis for this species [S9]. 2. These are estimated based on previous modeling studies that (*inter alia*) assessed the demographic parameters required to keep an African penguin population stable (in equilibrium) over time. The only estimate available for annual adult survival in the Eastern Cape was 0.9 [S11], but this was not based on CMR analyses. 3. Based on the mean of annual values from all nest types on Bird Island, Eastern Cape, between 2009 and 2012 reported in Lei *et al*. [S6]. 4. The model/scenario specific fecundity (*F*) = $E \times \phi_e \times \phi_c \times C$ for each model, following Sherley et al. [S7]. 5. The starting population for the adult state is the number of breeding pairs counted in the 2004 annual census; the starting populations for the other states were approximated based on the stable stage distribution at convergence. 6. Based on the mean of annual values at Robben Island between 2001 and 2013 reported in Sherley et al. [S7].

SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Instrumentation and data collection

We tracked 54 post-fledging, juvenile African penguins from eight colonies in Namibia and South Africa (Figure 1, Figure S1 and Table S1):

- Mercury Island (MI, blue), Namibia (25°43'S, 14°50'E), five birds in 2013;

- Halifax Island (HI, cyan), Namibia (26°37'S, 15°04'E), five birds in 2013;

- Dassen Island (DI, red), Western Cape province, South Africa (33°25'S 18°05'E), four birds in 2013;

- Robben Island (RI, orange), Western Cape province, South Africa (33°48'S, 18°22'E), three birds in 2011, six in 2012 and five in 2013.

- Boulders Beach (BB, light green), Simon's Town, Western Cape province, South Africa (34°11'S, 18°27'E), six birds in 2013;

- Stony Point (SP, dark green), Betty's Bay, Western Cape province, South Africa (34°22'S, 18°53'E), two birds in 2011 and eight in 2013;

- St. Croix Island (SC, purple), Eastern Cape province, South Africa (33°47'S 25°46'E), five birds in 2013;

- Bird Island (BI, pink), Eastern Cape province, South Africa (33°50'S, 26°17'E), five birds in 2013.

Of these, 14 were hand-reared juveniles (5 in 2011, 3 in 2012, 6 in 2013; Table S1) orphaned or abandoned before they were ready to fledge and reared by a specialist rehabilitation center in Cape Town [S1,S12]. Each year, a number of African penguin chicks are abandoned because they are no longer being provisioned prior to independence. Abandonment is usually assessed on the basis of repeated measurements using a chick condition index [S13] and differs from the temporary abandonment that occurs naturally during the post-guard phase [S1]. These chicks are hand-reared until ready to fledge. They are then released following blood, waterproofing and body condition evaluations [S1,S14]. The rearing and release of abandoned chicks forms part of conservation management actions under the national African Penguin Biodiversity Management Plan [S15] and monitoring takes place to inform future conservation translocations of African penguins aimed at creating new breeding colonies in areas where the marine habitat is less degraded [S1]. These juveniles survive and recruit as well as wild birds S. For these reasons, and because the potential for deleterious effects of PTTs on penguins [S17] meant that we needed to balance knowledge acquisition with ethical and conservation concerns, we selected hand-reared chicks (rather than chicks fledged naturally at a breeding colony) for the first PTT deployments in 2011 [S12] and then compared wild-reared (WRJ) and hand-reared juveniles (HRJ) in 2012. In total, five HRJ were tracked from Robben Island and Stony Point in 2011 [S12], three were tracked from Robben Island in 2012 and six were tracked from Stony Point and Boulders Beach in 2013 (Table S1).

We compared the initial behavior of the 14 hand-reared juveniles (HRJ) during their first 5 days at sea to that of the 19 wild-reared juveniles (WRJ) tracked from the four breeding colonies in the Western Cape province and there was no evidence that they differed: neither their mean (± SD) track velocities (WRJ = 60.7 ± 35.7,

HRJ = 52.9 ± 33.8 cm s^{-1}, permutations test: p = 0.16) nor the mean heading velocities (WRJ = 61.1 ± 35.3, HRJ = 55.3 ± 35.7 cm s^{-1}, permutations test: p = 0.31) differed significantly. In addition, the initial directions of their tracks (circular ANOVA: $F_{(1,163)}$ = 0.079, p = 0.78) and headings (circular ANOVA: $F_{(1,161)}$ = 0.16, p = 0.69) were not significantly different. Furthermore, the penguins targeted waters with chlorophyll-a concentration ~11 mg m^{-3} whether the hand-reared chicks were included (GAMM: edf = 3.94, χ^2 = 281.6, p < 0.001) or excluded (edf = 3.90, χ^2 = 178.8, p < 0.001) from the habitat modelling, and preferred Sea Surface Temperatures between ~14.5 and ~17.5 °C whether the hand-reared chicks were included (edf = 3.96, χ^2 = 231.1, p < 0.001) or not (edf = 3.97, χ^2 = 254.3, p < 0.001). Similarly, when we refit the GAMMs modelling habitat selection based forage fish abundance with each bird's status (HRJ vs. WRJ) included as a fixed effect, there was no evidence that HRJ unduly influenced the modeled mismatch with sardine spawner biomass (smooth term: edf = 0.89, χ^2 = 4.88, p = 0.03, status main effect: z = −0.40, p = 0.69) or anchovy spawner biomass (smooth term: edf = 1.09, χ^2 = 14.22, p < 0.001, status main effect: z = 0.07, p = 0.95). Only WRJ were at sea between 25 May and 31 July 2012 and 2013, so it was not necessary to refit the model using anchovy recruit biomass. See below for details on these statistical methods.

For both HRJ and WRJ, we also only selected chicks for deployment if they were in full fledging plumage (all secondary down lost) and exceeded the mean fledging mass at Robben Island in 2004 (2830 g). This was a year of above average chick growth and chick body condition [S13,S18]. All but two of the birds selected also exceeded 2928 g, the upper quartile of 263 fledging mass measurements made at Robben Island between 2010 and 2014 (RBS, unpubl. data).

The KiwiSat® 202 (60 × 27 × 17 mm, 32 g; Sirtrack) satellite transmitters, or Platform Terminal Transmitters (PTTs) were attached to each penguin using Tesa® tape (4651, 18 x 50 mm), cyanoacrylate glue (Loctite® 401) and plastic cable ties. The PTTs were placed centrally on the back, caudal to the flippers, as far aft as possible so the birds could walk unimpeded by the antenna, but still preen [S12]. At Dassen, St. Croix and Bird islands, birds were returned to nests and went to sea within 6.4 ± 4.1 days. At Boulders Beach, Stony Point, and Halifax, Mercury and Robben islands we kept the fledglings overnight in holding facilities and released them the following morning, close to landings used by commuting penguins.

State-space modeling and kernel smoothing
Location data with specified levels of accuracy were obtained from the ARGOS system (www.argos-system.org). Low quality positions (location classes A, B, or Z) were excluded before further analysis. Not all devices transmitted on each day of their duty-cycle, so positions were not equally spaced in time. We therefore analyzed each trip with a non-linear state-space model (SSM) using the *bsam* R library (v. 0.43.1) [S19], three Monte Carlo Markov Chains of 100,000 iterations, a burn-in of 50,000 samples and thinning by 10 to eliminate auto-correlation.

SSMs, such as those implemented by the *bsam* library, combine a hypothetical mechanistic model of animal movements (called a process model) with an observation model, to obtain a probability of obtaining a particular observation, conditional on the animal's true position, termed the animal's state [S20]. This can include an animal's mode of movement (foraging or transiting) as well as its position. We used the 'fitSSM' function in the *bsam* library for R [S19] to implement a hierarchical, first-difference, correlated random walk, switching model (hDCRWS) [S21] with a daily time-step. We assessed the quality of the SSM fit for each individual track by visually inspecting them for obvious problems like poor fits to the data and unrealistic estimated movements [S22] and visually assessed the plots of the chains to determine convergence of the MCMC algorithm.

We used this model to infer animal positions for times when there are no observations and identify each position as one being in either the transiting (= 1) or foraging (= 2) state for each iteration of the model, with the overall probability for which state each position was in then determined by the mean of all iterations [S23,S24]. We then defined all positions classified as being in the foraging state (mean state > 1.5) as validated 'foraging locations' and considered all positions from the SSM for further analyses. Finally, prior to using the positions and foraging locations for kernel smoothing or habitat selection functions (HSFs), we discarded any positions that fell on land, using map data available from the Global Administrative Areas database (http://www.gadm.org).

We mapped all position from the SSM (Figure S1A) and validated foraging locations (Figure S1B), then used kernel smoothing to determine the core foraging areas (Figure 1). We used the 'kde' and 'Hscv' functions from the *ks* library (v. 1.9.4) in R (v. 3.1.2) [S25], with a multivariate normal density and bandwidths determined by unconstrained smoothed cross validation to smooth the validated foraging locations (e.g. Figure 1).

Initial dispersal and ocean currents

To assess whether the initial dispersal of the juvenile penguins was active or passive, we compared each penguins' movements during their first five days at sea to the total surface current velocity field (sum of the geostrophic and Ekman surface components) obtained from the GEKCO2 integrated product [S26]. We calculated the penguins' track velocities (v_t, cm s^{-1}) and direction (degrees) between successive positions using a straight line distance over a cylindrical equal area projection and determined the penguins' heading velocities (v_h), which expresses active movement as: $v_h = v_t - v_c$ (Figure S2) [S27]. We used circular statistics (*circular* R library, v. 0.4-7) to analyze the direction data and permutation tests to compare the velocity data (*perm* R library, v. 1.0-0.0, 10,000 iterations).

Both the direction of the currents (circular ANOVA: $F_{(2,254)}$ = 70.87, p < 0.001) and the penguins' track directions (circular ANOVA: $F_{(2,254)}$ = 27.81, p < 0.001) differed significantly between the three regions (Namibia, Western Cape and Eastern Cape; Figure S3). Thus we assessed each of the correlations between the penguins' tracks and the currents separately for each region in turn (see main results). In addition, we

compared both the birds' heading velocities and the current velocities between the three breeding regions. The heading velocities did not differ (permutations test: p = 0.32), while the currents were nearly twice as fast in the Western Cape (14.3 ± 7.4 cm s^{-1}) and almost three times as fast in the Eastern Cape (22.4 cm ± 10.2 cm s^{-1}) as they were in Namibia (7.8 ± 4.5 cm s^{-1}; permutations test: p < 0.001). This adds additional support that the birds were swimming actively during their first five days at sea and not simply drifting passively in the current.

Habitat Selection Functions (HSFs).

Seabirds often show marked associations with particular habitat features that should indicate aggregations of their prey [S24,S28,S29] and we explored whether the penguins actively targeted areas of high chlorophyll-*a* (chl-*a*) concentrations and low sea surface temperature (SST) using habitat selection functions (HSFs). We used monthly mean MODIS-Aqua chlorophyll-*a* concentrations and sea surface temperature (SST) on 4 km^2 grids (from NASA's Goddard Space Flight Centre), to construct a mean across the Benguela ecosystem for March to November 2013. This period covered the 2013 tracking and was of sufficient duration to obscure shorter-term, higher frequency variability.

HSFs compare the habitat used to that available via a logistic-regression based approach by creating pseudo-absence data to control for habitat that was available to the animals but unused [S30]. The method uses a binomial response, with data belonging to the tracking dataset scored as 1 and the pseudo-absence data as 0. A large number (e.g. thousands) of randomly selected pseudo-absences is recommended with regression-based approaches [S31] and we used generalized additive mixed models (GAMMs) from the *gamm4* R library (v. 0.2-3), with binomial error assumptions, to model the HSFs. We therefore generated 5 pseudo-absence locations for each foraging location (giving 6390 in total) by selecting positions randomly from the population's 95% VC using a uniform spatial Poisson process [S28]. The value of each environmental covariate (SST, chl-*a* or prey biomass, see below) at each foraging location and pseudo-absence location was then extracted.

Prior to modeling we examined the correlations between the chlorophyll-*a* and SST variables. The two were strongly negatively correlated (r_s = −0.78, p < 0.001). Since correlation greater than r_s > 0.4 is considered problematic for HSFs by some [S28] and |r| > 0.7 has been found to be a good indicator for when collinearity begins to severely distort model estimation [S32], we modeled penguins' responses to chlorophyll-*a* and SST with two separate models. We took the Bayesian view that both variables were components of the world, and therefore should be presented, rather than using any form of model selection, which can anyway be problematic with tracking datasets [S30], to determine which variable was more important. For the GAMMs, we specified a random intercept for each bird, used cubic regression splines with shrinkage and specified an upper limit of five on the effective degrees of freedom to prevent over-fitting [S28]. In GAMM plots, y-axes show partial model residuals, or relative population-level habitat preferences [S30].

Data on the spatial availability of the penguins' main prey in South Africa were obtained from maps of sardine and anchovy distributions (e.g. Figure S3), generated by interpolation (linear Kriging) of 10 nautical mile-integrated fish density data from hydro-acoustic surveys [S33]. Maps were provided by the South African Department of Agriculture, Forestry and Fisheries (DAFF) and georeferenced in Quantum GIS (v. 2.8.2). Surveys in May 2011, 2012 and 2013 between the border with Namibia and Cape St Francis (34°11'S, 24°50'E) provided the distribution of recruit (age 0) anchovy, the key prey for chick-rearing [S34]. These surveys were taken to represent prey availability during the late (austral) autumn and early winter, the period during which most penguins fledge in South Africa [S8], and compared to foraging locations for 5 penguin at sea in South Africa between 12 June and 31 July 2012 and 27 penguins at sea in South Africa between 25 May and 31 July 2013. Survey in November 2011, 2012 and 2013 (late-spring) between Hondeklip Bay (30°19'S, 17°16'E) and Port Alfred (33°36'S, 26°53'E) provided the distribution of adult sardine and anchovy biomass (excluding age 0 juveniles), an energy-rich prey important for adult and first year survival [S3,S9]. The distributions of these adult fish were compared with the foraging positions for 4 penguins at sea in South Africa between 01 August and 06 December 2011, 6 penguins at sea in South Africa between 01 August and 06 October 2012 and 25 penguins at sea in South Africa between 01 August and 21 November 2013. Similar hydro-acoustic survey data do not exist for Namibia and we recognize that the South African surveys only provide short temporal windows on forage fish distributions. We applied to same process as above to model HSFs relating to prey availability, but restricting the data to birds at sea at the appropriate times outlined above and using the natural logarithm of the fish biomass as explanatory variables (each in its own model).

Bayesian Projection Modeling

To examine the potential consequences of juvenile penguins foraging in degraded habitat, we constructed a demographic model with one juvenile, three immature adult and one breeding adult states [S7]. We informed our model with and compared it to census data collected between 2004 and 2015 for Robben and Dassen islands [S7,S8] for the Western Cape scenarios, and for Bird and St. Croix islands [S8] for the Eastern Cape scenario. Adult survival (ϕ_a) and fecundity (F) were deterministic, while juvenile survival (ϕ_j) was stochastic using observed means ± SDs. For the Western Cape, we ran two scenarios for juvenile survival from Robben and Dassen Island based on observed survival rates over two time periods [S9], before the observed eastward shift in sardine and anchovy in South Africa (1994/95 to 2000/01) and after the observed eastward shift in sardine and anchovy (2001/02 to 2011/12). Because the annual values were poorly estimated in many years [S9], we used the mean and standard deviations from only those years where the standard error associated with the annual juvenile survival estimate was < 0.11. For the first time period, the estimates used were from Dassen Island for 1994/95 to 2000/01 inclusive and from Robben Island in 1994/95, 1997/98 and 1998/99. For the second time period, the estimates used were from Dassen Island in 2009/10 and 2010/11, and from Robben Island for 2001/02 to 2003/04 inclusive, 2007/08, 2009/10 and 2010/11. This resulted in $\phi_j = 0.194$ (SD = 0.117) as the mean observed after 2001, which we used for scenario 1 to represent juveniles encountering an ecological trap in their foraging habitat (see Table S2) and $\phi_j = 0.497$ (SD = 0.175) as the

observed mean prior to 2001 [S9] (see Table S2), which we used for scenario 2. For the Eastern Cape, $F =$ 0.56 [S6] while $\phi_a = 0.88$ and $\phi_j = 0.51$ (SD = 0.11) were set to values used to represent an equilibrium state for this species [S3] as robust, recent estimates from capture-mark recapture analyses were not available.

We ran the models using three MCMC chains of 100,000 samples (burn-in of 10,000, no thinning) in the JAGS software (v. 4.1.0), called from the *jagsUI* R library (v. 1.3.7). The model was run for $t = 12$ years (thus, simulating the population trajectory from 2004 to 2015) and the population growth rate (λ) was calculated using $t = 6$ to $t = 12$ to ensure convergence at the stable-age distribution. This mean λ value ($\pm$ 95% CI) was then used to predict modeled populations for 2004 to 2015 ($\pm$ 95% CIs) for comparison to the observed population trajectory [S7,S8]. We used a beta prior distribution for ϕ_j and binomial and Poisson distributions to map the number of individuals in each of the five states from year t to $t + 1$ [S35]. The full set of parameter values is given in Table S2. These were based on previous models of African penguin demographics [S3,S9]. We present posterior means $\pm$ 95% credible intervals.

A SCHEMATIC REPRESENTATION OF HOW THE ECOLOGICAL TRAP OPERATES

Figure S4, below, is a schematic diagram showing how the ecological trap operates. All references to arrows, letters or numbered locations in parentheses below – e.g. (1) – are to Figure S4 unless otherwise specified.
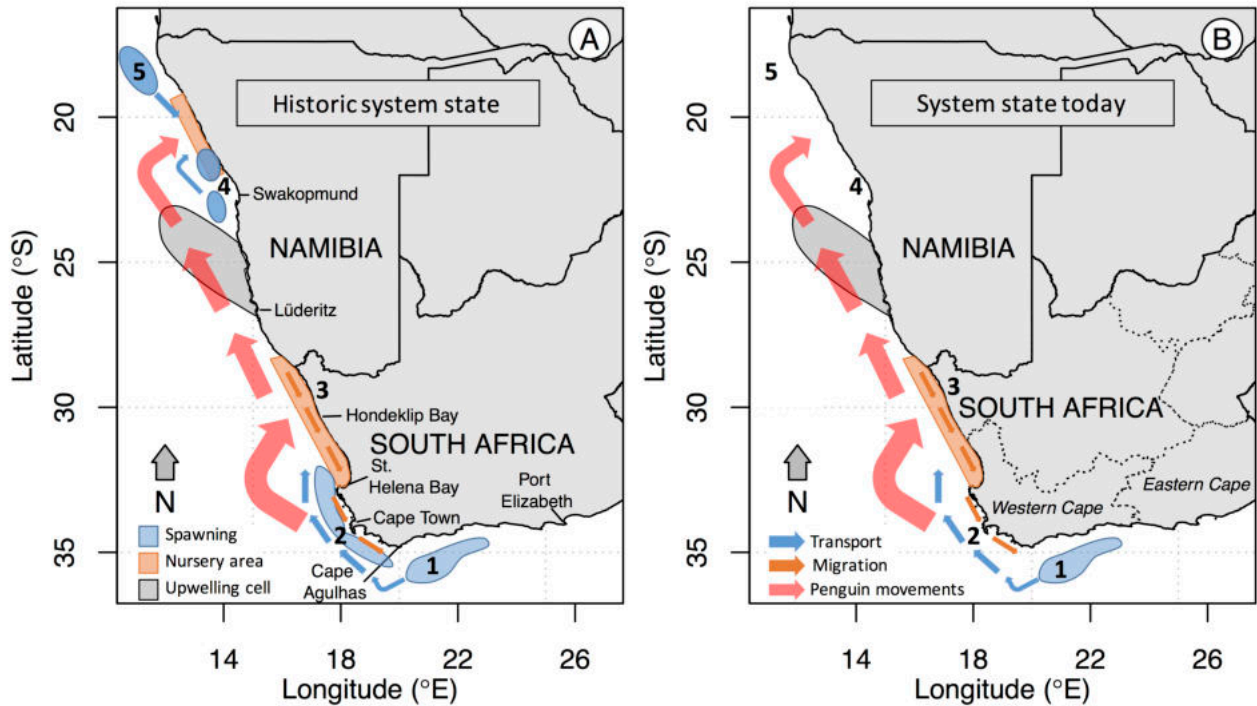

Figure S4, *related to Figure 2 and 3*. **A schematic diagram of the ecological trap.**

Blue polygons represent sardine and anchovy (forage fish) spawning areas, orange polygons forage fish nursery grounds and the grey polygon is the Lüderitz upwelling cell. Blue arrows show transport of forage fish eggs and larvae on ocean currents, orange arrows the southward migration of forage fish recruits along the west coast and red arrows the hypothetical movements of juvenile penguins from Western Cape breeding colonies. Spawning areas are (1) the Central and Eastern Agulhas Bank, (2) the Western Agulhas Bank, (3) the west coast nursery area, (4) the Central Namibia nursery and spawning area, and (5) the Angola-Benguela Front spawning area. Figure based on Hutchings et al. [S36].

Under the historic system state (A) sardine and anchovy in the southern Benguela (south of the Lüderitz upwelling cell) spawned on the Agulhas Bank (1 and 2), predominately on the Western Agulhas Bank, between Cape Agulhas and Cape Town – the southern portion of (2). In some years, sardine also spawned between 31°S and 35°S on the west coast, represented by the northern portion of (2) and anchovy on the Central and Eastern Agulhas Bank (1) [S36]. Spawning peaks in the Austral spring and summer (November and December) and adult penguins in South Africa molt around this time (the timing of spawning has not altered). After spawning, some adult forage fish moved onto the west coast and adult sardine were apparently abundant around St Helena Bay until the late-1950s [S37]. For example ~180 000 tonnes were caught in just St Helena Bay in both 1952 and 1953 [S37]; sardine catches for the whole southern Benguela have rarely exceeded that since 1985 [S37,S38].

The eggs produced by spawning fish on the Agulhas Bank are transported by currents to an offshore area of the west coast (blue arrows). The eggs develop into pre-recruits, which move shoreward to the west coast nursery ground (3). During the Austral autumn and winter, the recruit sardine and anchovy migrate back south to the Agulhas Bank (orange arrows). By the winter period when most juvenile penguins are fledging from South African colonies (approximately May to July), recruit forage fish are abundant between the Orange River (the border with Namibia) and the Eastern Agulhas Bank (Figure 3, main text and Figure S3). For penguins fledging from Western Cape colonies at this time, the west coast nursery ground (3) provides profitable initial foraging habitat (Figure 3, main text).

As the austral winter progresses sardine and anchovy recruits migrate south to the Agulhas Bank (orange arrows) to spawn [S36], such that by November they are once again scare on South Africa's west coast (Figure 3, main text and Figure S3). Historically, moving through the Lüderitz upwelling cell and into Namibia towards the end of winter would have brought juvenile penguins to additional profitable foraging areas. Sardine spawning peaks during September–October (austral spring) in the Central Namibia spawning area (4) and around November (mid-summer) at the Angola-Benguela Front spawning area (5). Finally, during December–March (late summer) warm water from the Angolan Current pushes southwards, pushing eggs and larvae into the central Namibia nursery ground (4) [S36]. Thus, by moving from (3) to (5), juveniles from the Western Cape would have been able to access forage fish for at least a year post-fledging. In addition, at this time of year, most juvenile penguins fledge from Namibian colonies and our results showed that they also moved to forage in this nursery area (Figure 1, main text and Figure S1).

Today (B), although sardine and anchovy have shifted to spawning predominately on the Central and Eastern Agulhas Bank (1), the west coast continues to serve as a nursery ground [S36,S37] and appears to remains attractive to juveniles as initial foraging habitat (Figure 3, main text), triggering initial, active northward movements post-fledging (Figure S3). However, fishing and climate change mean sardine are now scarce in St Helena Bay [S37], fewer spawners use the west coast [S38–S40] and sardine stocks have collapsed in Namibia to be replaced ecologically by goby and jellyfish [S41]. Juvenile penguins attracted by environmental cues to move from (3) to (4) and (5) suffer high mortality and thus fall into an ecological trap.

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