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Incidental and intentional catch threatens Galápagos waved albatross

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ABSTRACT

As large, long-lived seabirds with delayed and slow reproduction, albatrosses have low intrinsic mortality rates and are especially vulnerable to extinction from extrinsic sources of mortality such as fishery bycatch. Leg-band recovery information for waved albatrosses revealed mortality from both incidental catch and intentional catch for human consumption. Annual adult survival in 1999–2005, estimated from capture-mark-recapture data, was lower than historical estimates. This recent increase in adult mortality probably contributed to recent and dramatic shrinkage of the breeding population; periodic matrix models confirm that population growth rate is most sensitive to changes in adult survival. Banding data and recovery information also suggest that capture by fisheries is male-biased, which should reduce fecundity in this species with obligate bi-parental care. This new documentation of bycatch, harvesting, and associated demographic consequences provides reason for serious concern about the persistence of the single breeding population of the waved albatross.

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1. Introduction

Albatrosses belong to the bird family most threatened by extinction, and mortality in fisheries has been linked to numerous albatross population declines (Croxall et al., 2005). Long-lived species with slow annual reproductive rates and low intrinsic mortality are especially vulnerable to increased mortality from extrinsic sources (Wooler et al., 1992;

Holdaway and Jacomb, 2000). Fishery interactions threaten albatross species in subantarctic, subarctic, and subtropical oceans due to adult mortality as bycatch (Croxall and Gales, 1998). Satellite tracking studies identified the tropical Peruvian Upwelling as the principal foraging site of waved albatrosses (*Phoebastria irrorata*; Anderson et al., 2003). Until recently, this species was somewhat unusual in the apparent absence of threat from fisheries, since fleets near the

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Peruvian upwelling comprise small artisanal boats with a few fishermen deploying handmade gear, and because near their breeding grounds in the Galápagos Islands waved albatrosses do not display the boat-following behavior that makes some species more vulnerable to bycatch (Anderson and Cruz, 1998).

Essentially the entire population of waved albatrosses breeds on Isla Española, Galápagos (Harris, 1973; Anderson et al., 2002). Recent population estimates suggested a marked decline in breeding population size between 1994 and 2001 (Anderson et al., 2002). When we reported population estimates in 2002, we noted the possibility that the high breeding failure during the El Niño-southern oscillation (ENSO) warm event in 1992–93 caused an atypically large number of adults to attempt to breed in 1994. Data collected after the 2002 ENSO event have led us to reject that possibility. The Oceanic Niño Index indicated anomalously warm sea surface temperatures during the 2002 breeding season and prior to the 2003 season (Climate Prediction Center website, National Weather Service), and the number of clutches initiated in our study area in 2003 (145) was nearly identical to the mean number of initiations in the 2 years preceding the ENSO event when sea surface temperatures were anomalously cold (141.5; unpub. data). The large estimate of the breeding population size in 1994 thus probably was influenced little by the preceding ENSO event, and indicates a substantial change in population size in the 7 years after 1994.

In long-lived species with slow annual reproduction and late maturity, population growth rate is expected to be most sensitive to changes in adult survival. Here we use capture-mark-recapture (CMR) analyses to estimate adult survival and a matrix model approach to assess sensitivity of population growth to various demographic parameters including adult survival. Vital rates to which population growth rate (λ) has lower sensitivity are predicted to have larger variation in response to environmental stochasticity than parameters such as survival to which λ is presumed to be more sensitive (Pfister, 1998). In the case of ENSO warm events, Pacific seabirds have demonstrated both reduced breeding success (Rechten, 1986; Anderson, 1989; Boersma, 1998; Huyvaert et al., 2006) and reduced survival (Doherty et al., 2004). Determining the effects of variable adult survival and reproductive success on the population growth rate of these species requires incorporation of the periodic effect of ENSO events, rather than a deterministic calculation of λ . We used a stage-based periodic Leslie matrix model analysis incorporating environmental fluctuation, to allow the vital rates of long-lived animals to be analyzed within distinct demographic stages.

Another demographic influence on vital rates, and thus population growth, is the sex ratio of the population. In a seabird with bi-parental care, reproductive success will be restricted by numbers of the limiting sex. When biased sex ratio in the adult population is the result of differential extrinsic mortality, this discrepancy can reduce fecundity (Mills and Ryan, 2005). Alternatively, in wandering albatrosses (*Diomedea exulans*), a male-biased sex ratio was determined to have minimal effect on fecundity, since earlier mortality in females was a result of relatively greater reproductive effort and occurred at an older age, when most birds had passed their reproductive prime (Weimerskirch et al., 2005). Identifying

possible sex bias in adult mortality could determine if the effective population size is lower due to a reduction in numbers of one sex in this obligately bi-parental seabird.

Here we evaluate new evidence of substantial mortality of waved albatrosses in fisheries located in the Peruvian upwelling and inspect overlap of albatross foraging range with distribution of observed fishing trips. We also examine the influence that environmental heterogeneity may have on vital rates and incorporate increased mortality in our discussion of the influence of a stochastic environment on albatross vital rates. In light of these findings, the effects of fishery mortality on adult survival raise new concerns about the stability of the single breeding population of waved albatrosses.

2. Methods

2.1. Banding and surveys

To evaluate fishery mortality as a possible cause of population decline, we estimated annual survival rates from yearly resight surveys conducted since 1999 for several hundred leg-banded adult waved albatrosses at their breeding site on Isla Española, Galápagos. These estimates were then compared with the average survival rate detected during the 1960s by Harris's mark-recapture data. Following the methods of Huyvaert et al. (2006), we banded any unbanded birds at the beginning of the 1999–2005 breeding seasons in an oblong study area $\sim 3500 \text{ m}^2$ at Punta Cevallos. Daily resight data were collected prior to dusk, approximately 1800–1830, when attendance in colony is highest. Resight data included sightings of banded birds within a buffer zone of approximately 250 m^2 , an area where adult albatrosses frequently congregated, including some of those banded within the study area. We also began surveying 37 major fishing communities widely distributed throughout the coast of Perú in, 2003 and collecting band recovery information in eight of these ports. To monitor the incidental or intentional take of seabirds we also placed onboard observers on 30 trips made by artisanal longline and gillnet fishing vessels operating out of the ports of Salaverry and Callao, Perú beginning in October 2004. GPS locations of longline and gillnet deployment on these trips were recorded by observers and compared to GPS locations of five foraging albatrosses making long trips to the Peruvian coast from mid-May to early July 2004 (method of GPS deployment on albatrosses is reported in Awkerman et al., 2005) using ArcView Geographic Information System (Version 3.2, Environmental Systems Research Institute). Waved albatrosses forage near the Peruvian coast throughout much of the year (Anderson et al., 2003).

In May–July 2004, we also banded an additional 2539 adult albatrosses to increase the resolution of survival estimates based on the initial surveys. All birds banded during this period, early in the breeding season, were presumed to be experienced adults rather than inexperienced young adults or juveniles (Harris, 1973, unpub. data). Additional birds ($N = 365$) were banded in November 2004 but not seen during May–July 2004 and were therefore assumed to be young adults (Harris, 1973). During 2000–2004, 514 chicks were banded prior to fledgling and constitute the maximum banded juvenile population at sea.

2.2. Mark-resight analysis

By applying Cormack–Jolly–Seber (CJS) open-population capture–recapture methods (Lebreton et al., 1992; Burnham and Anderson, 2002) implemented in Program MARK (Pradel and Lebreton, 1999; Cooch and White, 2005), we analyzed resight histories of 497 birds banded between 1999 and 2005 to estimate survival probabilities of adult waved albatrosses. Robust design multistate mark–recapture analyses to account for temporary emigration (Kendall and Nichols, 2002) yielded similar conclusions (unpub. results), but we used survival estimates from CJS analyses here, because waved albatross life history is more similar to an annual breeder than that of other large albatross species, with only a small percentage of the breeding population failing to return to the colony each year. Our CJS candidate model set consisted of survival (ϕ) and resight/recapture (p) probability parameters that could remain constant (\cdot), vary with year (t), vary by sex (g), or include variation from the mild 2002 ENSO warm event (E). We used Akaike's information criterion (AIC) for model selection and ranking (Burnham and Anderson, 2002). In practice, we used QAICc, a version of AIC adjusted for overdispersion and sample size, incorporating adjustment of the variance inflation factor based on estimates of median $c\text{-hat}$ ($\hat{c} = 1.54$; Cooch and White, 2005). Models with the lowest QAICc values are assumed to better explain variation in the data. By model averaging the top ranking models, we calculated estimates of adult survival and resight/recapture probabilities.

2.3. Periodic Leslie matrix model

To understand the effects of reduced adult survival and associated factors on population growth, we constructed a life table which consisted of four stages: (1) chicks (in their first year post-hatching); (2) juveniles (age 1–5); (3) inexperienced breeders (age 6–8), and (4) experienced breeders (age 9–50). Waved albatrosses are known to live to at least 38 years (Douglas and Fernández, 1997), and we expect that the typical albatross lifespan of 60 years (Tickell, 2000) is possible although sufficient banding information does not exist to confirm this. We used a typical maximum lifespan of 50 years for our final life stage. Juveniles and inexperienced breeders were assumed to survive at the same rate estimated for experienced adults based on the results of Harris (1973), and this rate was drawn from our CMR analyses. Matrices were calculated for both non-ENSO and mild ENSO warm event years from the stage-based life tables. Following the methods of Caswell (2001), we calculated a periodic matrix product for varying lengths of ENSO cycle (2–7 years based on Cane, 1983; Trenberth, 1997; Doherty et al., 2004) with ENSO parameter estimates for one annual phase and non-ENSO parameter estimates for the remaining annual phases, such that the periodic matrix (A) is the product of M matrices, B_1, \dots, B_M . Adult survival estimates used were from our CMR analyses, and reproductive success was based on Harris's (1973) estimate of fledging success (0.23), which was similar to our own observations in non-ENSO years. During the 2002–2003 breeding season the lower reproductive success that we observed (0.08) was used in the ENSO matrix. We assumed no density-dependent regulation in demographic

rates, because existing data are insufficient to construct a reliable model of such effects, and a declining population would reduce any density-dependent feedback. We calculated the elasticities, or proportional sensitivities, of the dominant eigenvalue of the matrix product to parameters in both the non-ENSO and ENSO matrices.

3. Results

3.1. Band recovery and observer program

In the year following the banding of 2539 birds in May–July 2004, fishermen reported capturing 0.95% of these birds in artisanal gillnets and on longlines and acknowledged catching some intentionally for consumption. This percentage constitutes a minimum estimate of fishery mortality, because some catches may not have been reported, and we collected band recovery data at only eight of the ports. Bycatch in international tuna fisheries, known to overlap with waved albatrosses (Anderson et al., 1998), are also excluded from this capture rate. Because these birds were banded early in the breeding season, all 24 were assumed to be experienced adults. During this time only one banded juvenile and one banded young adult were recovered, suggesting that fishery mortality affects primarily breeding adults. Interviews with fishermen suggested that albatross harvest is not a novelty; however, we have no quantitative information on harvest history. Our on-board observer program to quantify capture rate reported no albatross catch on eight trips from Callao, and of 22 observed trips from Salaverry, no albatrosses were caught on 19 trips, one boat caught one waved albatross, one boat caught two, and one boat caught nine, suggesting great variability in catch rate among vessels. In all 12 cases of capture during observed trips, albatrosses were targeted using a baited hook set from a gillnet vessel. GPS locations of albatross foraging trips overlapped with gillnet deployment by boats leaving from Salaverry more than with longline deployments from either Salaverry or Callao (Fig. 1).

3.2. Mark-resight analysis

In the highest ranking model in our CJS analyses, recapture probability varied with year and survival was constant except following the 2002 ENSO warm event (Table 1). Another model received moderate support ($\Delta\text{QAICc} = 3.6$), allowing survival and recapture to vary with year, and a third model received marginal support ($\Delta\text{QAICc} = 5.5$), allowing recapture and survival to vary with time and making survival dependent on sex. Estimates of annual adult survival since 1999 derived from averages of the top two models were distinctly lower than that for this same population in the 1960s (Harris, 1973), especially during the mild 2002 ENSO warm event (Fig. 2). Harris' data (1973, Table 17) permit a direct calculation of the weighted average annual adult survival in the 1960s (1961–1970), yielding an estimate of 0.953. The 95% binomial confidence limit of this estimate can be approximated by calculating the population sizes of banding-year classes at the beginning of each annual period, assuming constant annual survival of 0.953. These confidence intervals range from 0.941 to 0.964 in the year with the largest

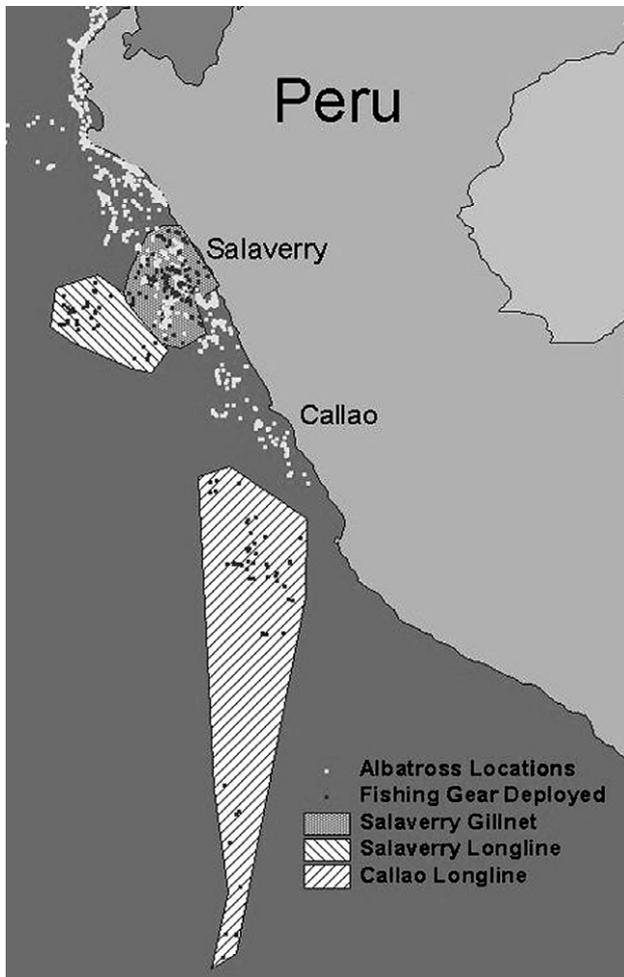


Fig. 1 – GPS locations of foraging albatrosses (light circles) and GPS locations of fishing gear deployment recorded by on-board observers (dark circles). Type of fishing gear and port of origin are denoted by background (gillnet boats from Salaverry, dotted background; longline boats from Salaverry, left to right diagonal; longline boats from Callao, right to left diagonal).

population to 0.940–0.966 for the year with the smallest; none include the estimate of 0.925 for most years during the period 1999–2005. Likewise, the 95% CIs for the 1999–2005 estimates do not include Harris' estimate (Fig. 2). Harris' methods did not correct for recapture probability (M.P. Harris, pers. comm.), suggesting that his values might underestimate actual adult survival. Our survival estimates were 2–3% lower than Harris' in non-El Niño years and 10% lower in 2003.

Our third model, which received marginal support, indicated higher mortality for males, and this was suggested by band returns from fishermen also. Sex ratio within the foraging area is unknown, but tracking data are similar for both sexes (Anderson et al., 1998, J.A. Awkerman, unpub. data). Of 33 known-sex birds whose bands were recovered throughout 2005, 82% (27) were male (binomial probability assuming even population sex ratio <0.001), and preliminary analyses suggest that the adult sex ratio in the colony is female-biased (Huyvaert, 2004, J.A. Awkerman unpub. data).

3.3. Matrix sensitivity analysis

Using stage-based life tables (Table 2), we calculated matrices for both non-ENSO and mild ENSO warm event years (Fig. 3) in order to evaluate elasticity of different parameters, recognizing that the λ values produced are probably over-estimates because only mild ENSO events were incorporated. A periodic matrix product with a six year ENSO cycle gave a λ value approximating 1 (1.01; a period of 5 years gave a λ of 0.99). Sensitivity analysis using a 6-year ENSO period indicated that elasticity of the dominant eigenvalue of this periodic matrix product was most sensitive to changes in adult survival (non-ENSO = 0.55, ENSO = 0.58) with juvenile (non-ENSO = 0.12, ENSO = 0.15) and young adult (0.10) survival the second and third most sensitive parameters (Fig. 4). Analysis using a 5-year period gave almost identical results (unpub. results).

4. Discussion

Mortality in Peruvian artisanal longline and gillnet fisheries operations might have contributed to the decline in the

Table 1 – Ten candidate models for survival (Φ) and recapture probabilities (p) as influenced by year (t), sex (g), or specific years during (E_{02}) and following (E_{03}) a mild El Niño-southern oscillation event (E_{03})

Model	QAICc	Δ QAICc	QAICc weights	Model likelihood	Num. par	QDeviance
$\Phi(E_{03})p(t)$	1370.155	0	0.80399	1	8	174.851
$\Phi(t)p(t)$	1373.800	3.645	0.1299	0.1616	11	172.4301
$\Phi(g + t)p(t)$	1375.656	5.501	0.05135	0.0639	12	172.2595
$\Phi(g)p(t)$	1378.782	8.627	0.01076	0.0134	8	183.4788
$\Phi(\cdot)p(E_{02})$	1381.610	11.455	0.00262	0.0033	3	196.3731
$\Phi(\cdot)p(E_{0203})$	1382.908	12.753	0.00137	0.0017	4	195.6616
$\Phi(\cdot)p(E_{03})$	1393.457	23.301	0.00001	0	3	208.2192
$\Phi(\cdot)p(\cdot)$	1394.689	24.534	0	0	2	211.4587
$\Phi(t)p(\cdot)$	1396.162	26.007	0	0	7	202.8758
$\Phi(g)p(\cdot)$	1396.654	26.499	0	0	3	211.4168

Model-averaged values of p ranged from 0.811 to 0.958.

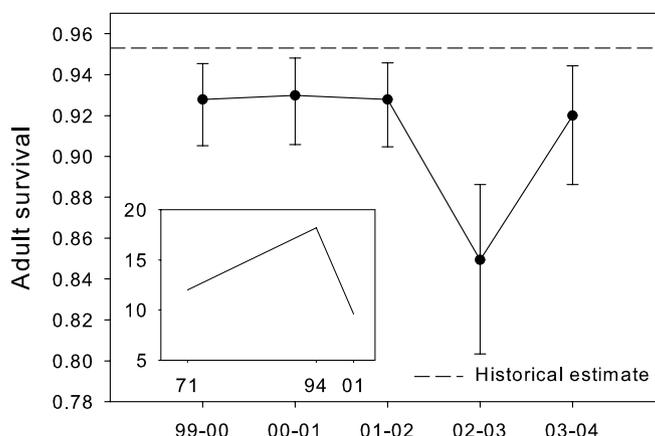


Fig. 2 – Parameter estimates and 95% confidence limits of annual adult survival for adult waved albatrosses based on model averaging of top two CJS models of band-resight histories. Approximations of the lower binomial 95% confidence limit of the historical estimate range from 0.940 to 0.941 and do not include any of our estimates. Inset: Time course of the three population counts for this species, expressed as thousands of breeding pairs for estimates in 1971, 1994 and 2001. The same methods were used in the last two counts, and did not permit estimation of confidence intervals.

Table 2 – Stage-based life tables for (a) non-ENSO and (b) mild ENSO years with survival and reproductive success reduced in mild El Niño years according to observations in 2002–2003

	Stage	Age	Years	Survival	Fecundity
<i>Non-ENSO year</i>					
Chick	1	0	1	0.23	0
Juvenile	2	1–5	4	0.92	0
Inexperienced breeder	3	6–8	3	0.92	0
Experienced breeder	4	9–50	42	0.92	0.88
<i>Mild El Niño</i>					
Chick	1	0	1	0.079	0
Juvenile	2	1–5	4	0.86	0
Inexperienced breeder	3	6–8	3	0.86	0
Experienced breeder	4	9–50	42	0.86	0.88

Juveniles and inexperienced breeders are assumed to survive as well as experienced breeders, for which we have quantitative estimates, but these values are probably higher than actual survival of less experienced birds.

waved albatross population observed in the late 1990s and early 2000s. A considerable number of adults are being taken incidentally and intentionally in that fishery, and we propose that this take is reflected in the lower annual adult survival observed now in comparison to that of the 1960s. Overlap of waved albatross distribution with tuna fisheries (Anderson et al., 1998) presents another potential source of adult mortality that is undocumented in this paper. Sensitivity analysis confirms the expectation that population growth rate in this potentially long-lived apex predator shows high sensitivity to adult survival rate, reinforcing the interpretation that fishery mortality is driving the rapid recent population decline.

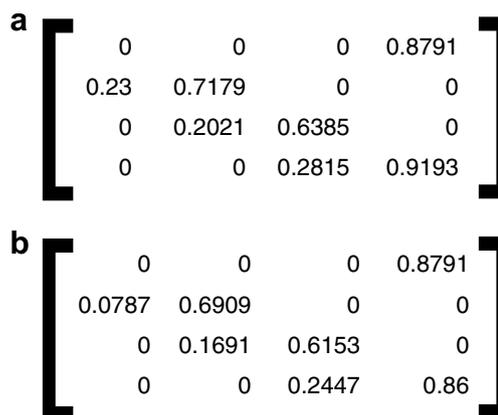


Fig. 3 – Matrices for (a) non-ENSO and (b) mild ENSO years.

We identified an acute effect of ENSO conditions on annual adult survival, which may reflect natural mortality and/or increased attention from fishermen, both due to reduced availability of forage prey. Adult fecundity could also effectively be reduced by bycatch if male-biased mortality occurs early in the albatross' life and curtails breeding lifespan. Both survival and fecundity effects can be expected to drive a population decline, as has been observed (Anderson et al., 2002). However, our ability to accurately project population dynamics into the near future is limited, in part due to lack of knowledge of the effect of more severe ENSO warm events on adult survival. Environmental fluctuations, the operational sex ratio, and frequency of intentional catch are three important factors that must be investigated further before population projections can be interpreted with confidence.

The periodic fluctuation that we present is a fairly simple representation of environmental stochasticity. Although ENSO is a much more dynamic phenomenon, data from recent years suggest that our representation is fairly accurate in terms of how this environmental variability affects the

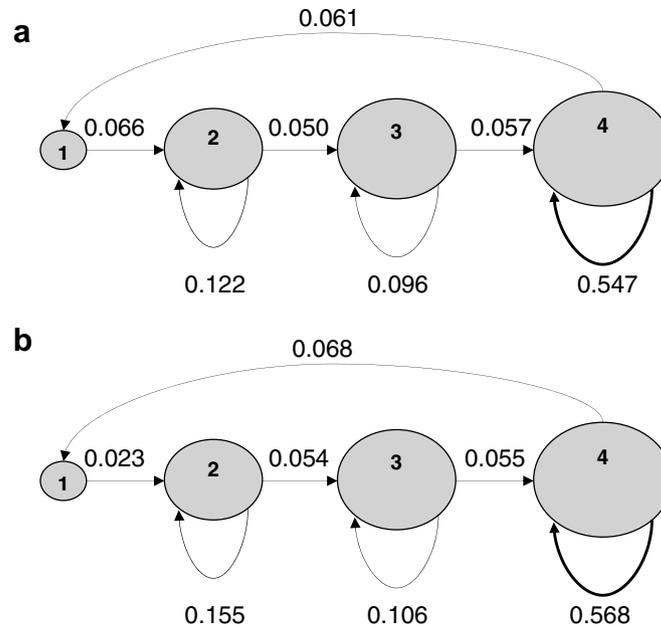


Fig. 4 – Elasticities of dominant eigenvalue of periodic matrix product for (a) non-ENSO and (b) mild ENSO years. Circles represent each stage in life table. Elasticities of intrinsic growth rate to transition between life stages are along the central horizontal arrows, to survival within each stage on the lower arrows, and to fecundity on the upper arrow.

breeding biology of waved albatrosses in the colony. The effects of the amplitude of the ENSO event have not been fully explored, but prior severe El Niño events have caused complete reproductive failure in the colony (Rechten, 1986, Anderson et al. unpub. data). A more complex model based on a longer dataset of environmental stochasticity would more accurately estimate population growth, but our preliminary model provided the useful result that the intrinsic growth rate of the population is most sensitive to changes in adult survival, as expected of a long-lived, slowly reproducing species. High elasticity of survival rate verifies that the population of such an animal will be severely affected by an additional source of mortality. The large decrease in adult survival around ENSO warm events is somewhat surprising (but not unprecedented; Doherty et al., 2004), given that survival rate, to which λ is thought to be most sensitive, is expected to have relatively little variation in response to environmental events. Additional, undocumented causes of lower adult survival in 2002–2003 remain a possibility that additional resight data could help elucidate.

Decades of banding data would also be required, but are not available, to determine the age distribution of a biased sex ratio in an albatross population. Band recoveries suggest that males are caught much more frequently than females, which could have further detrimental effects on this species with bi-parental care. Understanding the relationship between male-biased capture and female-biased adult population sex ratios requires further investigation into the ontogeny of sex ratio and could explain the unexpectedly high rate of extra-pair paternity in this species (Huyvaert et al., 2000).

Most band recoveries were reported from a localized area on the central Peruvian coast, although seabird bycatch is known to occur throughout the coastal region where fisher-

men were interviewed. We do not know whether the majority of the capture occurs mainly in this region, or whether the capture situation there is representative of the entire Peruvian coast. Quantifying the intensity and location of intentional catch as well as incidental catch is an important subsequent step in responding to conservation concerns.

The single breeding population of waved albatrosses is classified as vulnerable by IUCN (Croxall and Gales, 1998). Data presented here suggest that survival as well as reproductive success is affected by environmental stochasticity associated with ENSO events. Extrinsic sources of mortality might have reduced survival and population size in the past several years, and sex-biased capture could further compromise the fecundity of this obligately bi-parental species. These negative effects on the effective population size raise particular concern in the case of the waved albatross for several reasons. The species is represented by a point breeding population (Anderson et al., 2002), so we have documented the population decline of the entire species. The foraging range of the species is restricted to the small area (relative to those of other albatrosses) off the Peruvian coast during much of the year (Anderson et al., 2003) and the even smaller area of the Galápagos Islands during the remainder (Awkerman et al., 2005), so the fishery impact documented here potentially affects the entire population for much of the annual cycle. Finally, longline and driftnet fishing is presently illegal within their foraging area within Galápagos, but fishing interests continue to press for a longline fishery within the Galápagos Marine Reserve, which may exacerbate the population decline if permitted.

Our data from waved albatrosses foraging in tropical waters augments earlier studies of other species in higher latitudes, showing that unsustainable mortality of albatrosses in fisheries is a planetary phenomenon. As large, long-lived, apex predators with slow annual reproduction, albatrosses have few

sources of intrinsic mortality. Sudden increases in extrinsic mortality, such as harvesting for human consumption, have led to the extinction of other long-lived bird species in a matter of decades (Holdaway and Jacomb, 2000). Early realization of this effect on the single-island endemic waved albatross can prevent this outcome with appropriate mitigating action.

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