Illegal fishing bycatch overshadows climate as a driver of albatross population decline

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ABSTRACT: Effective management of albatross populations requires understanding the impacts of environmental factors on albatross demographics. An integrated modelling approach incorporating multiple data sources can further the understanding of albatross demographics by incorporating error from all components of modeling, and help distinguish between variability related to one factor (e.g. environment) from that of another factor (e.g. density dependence). We applied such an integrated, spatially-explicit population model to quantify the impact of environmental conditions (sea surface temperature, SST), fisheries, and density dependence on a black-browed albatross *Thalassarche melanophris* population breeding on Kerguelen Island, southern Indian Ocean for the period 1950 to 2011. The model was structured by sex, age-class, and breeding stage, with a 5° × 5° spatial scale and monthly temporal scale. All parameters were estimated within a maximum likelihood framework. This includes estimation of seabird bycatch rates of each of 5 fishing super-fleets, grouped by gear type and reported bycatch rates: (1) Japanese pelagic longline, (2) other pelagic longline, (3) legal demersal longline, (4) trawl, and (5) illegal, unreported, and unregulated (IUU) demersal longline. A decline in the Kerguelen black-browed albatross population occurred between the mid-1990s through the mid-2000s. Our analysis attributes the majority of modelled bycatch to the IUU demersal longline super-fleet operating near Kerguelen Island for this period. Including SST during the incubation period indicated that warm SST favors high breeding success. These results indicate that effective management requires an integrated understanding of the impacts of the environment as well as illegal and legal fishing activities on vulnerable populations.

KEY WORDS: Demographics · Integrated population model · Illegal, unreported, and unregulated (IUU) fishing · Black-browed albatross · *Thalassarche melanophris* · Kerguelen Island

INTRODUCTION

The trajectory of an albatross population is the result of multiple factors, including historical feather and egg harvesting (Thomson et al. 2015), introduced predators (Cuthbert & Hilton 2004), environmental variation (Pinaud & Weimerskirch 2002, Inchausti et al. 2003, Chambers et al. 2011), interactions with fisheries (Tuck et al. 2001, Robertson et al. 2014), disease outbreaks (Rolland et al. 2009a), and demographic feedbacks (Fay et al. 2015). As albatross are long-lived, experience delayed maturity, and have a low reproductive rate, their populations can be slow to recover from a decline related to one or more of these factors. Managing albatross populations, many of which are endangered or threatened (Croxall et al.

2012), requires an understanding of these factors and their impact on albatross demographics.

A recent review of climate impacts on Southern Ocean seabirds, including albatross, found that sea surface temperature (SST) and broad-scale climate indices such as the Southern Oscillation Index (SOI) are commonly associated with albatross demographics, most frequently via breeding success (Barbraud et al. 2011). Environmental variation can have a strong impact on the early life stages of albatrosses, where natal conditions shape the likelihood of fledging, including breeding success (Nevoux et al. 2010a) and juvenile survival (Nevoux et al. 2010b, Fay et al. 2015). Upwelling intensity (Thomson et al. 2015) as well as disease (Weimerskirch 2004, Rolland et al. 2009a) can also affect breeding success, through changes in food availability and mortality, respectively. Regional variation in the relationship between demographics and environmental change has been observed (Delord et al. 2008). Moreover, the impacts of the environment or fisheries can be species-specific. In a study of 4 albatross species, Rolland et al. (2010) found that the relationship of the environment with adult survival and breeding success as well as longline fishing effort with adult survival differed among species. Even within species, the level of environmental variation experienced in different colonies has been associated with differences in adult survival and breeding success (Nevoux et al. 2010a). Therefore, the relationship between the environment, fisheries bycatch, and albatross demographics should be assessed at a population level.

Environmental conditions and fisheries affect black-browed albatross *Thalassarche melanophris* (BBA) breeding on Kerguelen Island in the southern Indian Ocean. Specifically, warm SST around Kerguelen Island during the breeding period is associated with increased breeding success, adult survival, and population growth rate (Rolland et al. 2009b). In the non-breeding period, warm SST south of Australia relates to lower breeding success the following year (Rolland et al. 2008, 2010), while positive SOI is associated with reduced survival of inexperienced birds but increased breeding success (Nevoux et al. 2007, Rolland et al. 2008, 2010). Additionally, the influence of environmental variation can be age-dependent (Pardo et al. 2013).

Longline fishing effort in the non-breeding grounds has a negative impact on adult survival (Rolland et al. 2010). Interestingly, the positive impacts of SST during the breeding period and negative impacts of longline effort in the non-breeding grounds can offset each other, which emphasizes the need for compre-

hensive approaches to demographic modelling. These complicated relationships make it difficult to attribute an observed change in the population to individual covariates, particularly when the response could be nonlinear (Barbraud et al. 2011). Furthermore, the impact of a given factor on the demographic parameters of the population can be masked or amplified by other factors, including density dependence, experience, and natal conditions (Maunder 2004, Nevoux et al. 2007, 2010b, Fay et al. 2015, 2017).

Integrated population models quantify the relative impact of multiple factors on population dynamics, enabling the concurrent estimation of multiple demographic rates (Schaub & Abadi 2011). These modes are often used in fisheries stock assessments (Maunder & Punt 2013, Methot & Wetzel 2013), and have recently been applied to albatross populations (Francis & Sagar 2012, Thomson et al. 2015, Tuck et al. 2015). In the case of albatross, this approach incorporates all relevant and available environmental, demographic, and fisheries data into a single estimation framework, simultaneously estimating the relative contribution of multiple potential drivers on population dynamics. These models are often structured by age, sex, and breeding stage and can be spatially explicit (Thomson et al. 2015, Tuck et al. 2015). Estimation of the impact of factors such as the environment or bycatch on the demographics of albatross populations differs from approaches using multiple estimation frameworks, which often quantify parameter-specific relationships external to the demographic estimation framework (e.g. Barbraud et al. 2011, Pardo et al. 2013, Fay et al. 2017).

To assess the individual and cumulative impacts of environmental variation as indicated by SST and fisheries bycatch on Kerguelen BBA population dynamics, we applied an integrated population model to this population. Our first aim was to quantify the impacts of climate, bycatch, and density dependence by estimating these terms in an integrated model framework. Our second aim was to determine which fishing super-fleet had the greatest historical impact on the population. The integrated population modeling framework applied here incorporates environmental impacts on breeding success, the spatial overlap and probability of bycatch in multiple fishing fleets, as well as density dependence on immature, juvenile, and chick survival. Parameters were estimated using a maximum likelihood framework. The level of independence between parameter estimates was quantified, and sensitivity analyses assessed the impact of data assumptions regarding illegal, unreported, and unregulated fishing fleet actions and

unobserved bycatch on the modelled outcome. Distinguishing demographic variation due to the environment versus fisheries bycatch enables identification of the likely historical drivers of the demographic observations. This will give managers insight into the potential impacts of the environment and fishing effort on this Near Threatened albatross population.

METHODS

Data sources

Data from multiple sources were available for this population. The data sources, similar to those used by others in earlier implementations of related models, are summarized in Table 1 and the corresponding Supplements referred to in the table. Data sources differing from these earlier implementations are described in the following subsections.

Demographic data

Demographic data were collected from 200 annually monitored BBA nests at the colony at Cañon des Sourcils Noirs, Kerguelen Island (48.24° S, 68.218° E) (Fig. 1) (Rolland et al. 2008, Barbraud et al. 2011), which comprises approximately 1000 breeding pairs. From 1967, adults and chicks were ringed with stainless steel rings, and since 1979 a capture–mark–recapture program has been undertaken annually between October and March. Most rings of breeding birds were checked in October, just after laying. Two

Table 1. Summary of data sources. Quantification: specific dataset (environmental variables) or the technique used to estimate the values of a given data type; related studies: studies using similar techniques; further details: all Supplement figs, tables and text can be found at www.int-res.com/articles/suppl/m579p185_supp.pdf

| Data	Quantification	Related studies	Further details
Albatross demographics	Mark capture–recapture analysis	Barbraud et al. (2013)	Supplement Text S1.1
Albatross distribution at-sea	Time spent per cell	Delord et al. (2013), Weimerskirch et al. (2015)	Fig. S1.1, Supplement Text S1.2, Table S1.1
Fishing effort	Reported or estimated	Thomson et al. (2015), Tuck et al. (2015)	Fishing effort data, Supplement Text S1.3, 1.4
Bycatch	Obtained from published literature and reports	Various	Supplement Text S1.5, Table S1.3
Environmental variables	NOAA ¼° monthly optimum interpolation dataset	Rolland et al. (2008, 2009b, 2010)	Environmental variables
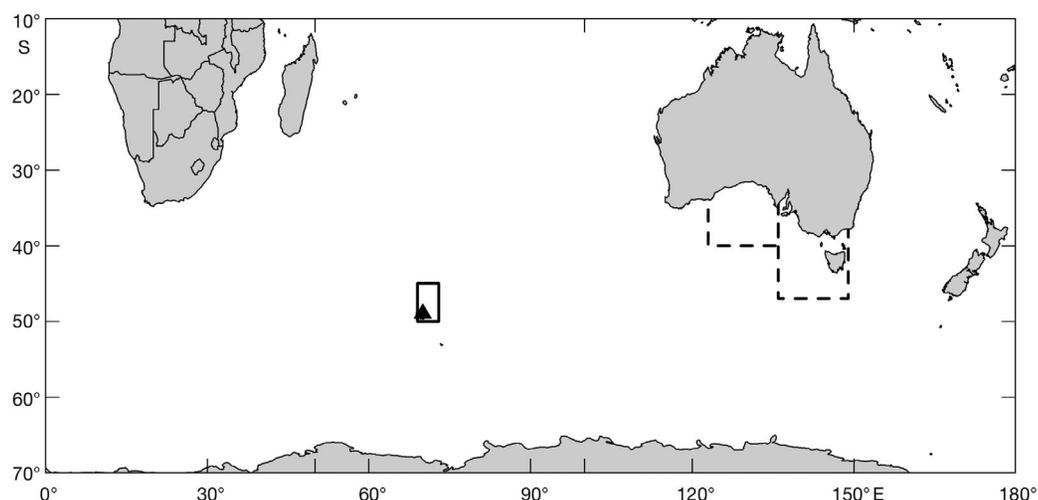
Fig. 1. Location of the focal black-browed albatross breeding colony on Kerguelen Island, at Cañon des Sourcils Noirs (triangle). The at-sea area during the incubation and rearing period (solid line) and non-breeding period (dashed lines) are shown

additional visits to monitored nests in late December and late March allowed determination of the breeding success of each pair. Each year, all un-ringed breeding individuals found in the study area and all chicks were ringed just before fledging. Individuals were sexed from blood samples and by using standard protocols elsewhere described (Angelier et al. 2007).

At-sea distribution data

In general, the Austral summer (breeding season) at-sea distribution of breeding birds is restricted to the eastern Kerguelen shelf, while in the Austral winter (non-breeding season), most birds remain off southern Australia with a few travelling to western New Zealand or southwest of South Africa (Delord et al. 2013, see Fig. S1.1a,b in Supplement 1). The at-sea distribution was modelled as time spent per cell (Louzao et al. 2011, Delord et al. 2016) at a 5 × 5° spatial and monthly temporal scale for 15 different categories of sex, time of year, breeding status, and age (see Text S1.2, Table S1.1 in Supplement 1). The breeding period lasts from October to April and the non-breeding period from May to September (Delord et al. 2013).

Fishing effort data

Given their relatively broad distribution, Kerguelen BBA may interact with a range of fishing fleets. This makes them susceptible to incidental mortality or bycatch in longline or trawl fishing gear (Brothers 1991, Sullivan et al. 2006, Croxall 2008). In addition to the fishing effort data used in Tuck et al. (2015) in a study on Crozet Island wandering albatrosses, we added data on demersal longline fishing effort in the Kerguelen French Exclusive Economic Zone (EEZ; see below) as well as updated estimates of pelagic longline effort from the Indian Ocean Tuna Commission (see Supplement Text S1.3). A summary of illegal, unreported, and unregulated (IUU) fishing effort is provided in Supplement Text S1.4, including the spatial distribution of effort (Fig. S1.4). Data on the French and Ukrainian trawl fleets in the Kerguelen French EEZ were obtained from the French Museum of Natural History. These data did not include spatial coordinates, so the location of effort relative to 5° × 5° spatial cells was estimated based on Weimerskirch et al. (2000). Information on all individual fleets included in the model is presented in Table S1.2.

Effort was grouped into 5 'super-fleets', based on gear type and reported bycatch rates as follows: (1) Japanese pelagic longline south of 30°S, (2) other pelagic longline, (3) trawl, (4) legal demersal longline, and (5) IUU demersal longline. Details on these super-fleets are provided in Supplement Text S1.4, Table S1.2, and Fig. S1.5. When the available effort data for a fleet ended before 2011, the effort for the last year of data was repeated for each year through 2011, with the exception of fleets known or suspected to be inactive.

Environmental covariates

Relationships between SST and breeding success have been identified in previous studies (Rolland et al. 2008, 2010), which informed our development of 4 SST-based environmental covariates corresponding to areas occupied by the birds in different seasons (Fig. 1). Specifically, the average SST in the foraging grounds near Kerguelen during the (1) incubation (October to December) and (2) rearing (January to April) periods, and the non-breeding period (May to September) of the year prior to breeding in areas of (3) broad habitat use south of Australia and (4) intense use of northwest Tasmania.

The average SST across these regions for the given monthly time periods was calculated using the NOAA ¼° monthly optimum interpolation dataset (Reynolds et al. 2008). In the model framework, these environmental covariates can alter breeding success by affecting chick mortality (see Text S2.5 in Supplement 2). While environmental variation has been associated with the survival of adults (Rolland et al. 2010, Pardo et al. 2013) and inexperienced birds (Nevoux et al. 2010b), we only assessed their impacts on chick mortality as the current model framework does not allow covariates on adult survival rate.

Population model

We applied an integrated population model to assess the impacts of SST and bycatch of several fishing fleets on the demographics of a BBA population at Kerguelen. SST was used to indicate regional environmental variation. Key aspects of this integrated framework were introduced in earlier studies (Tuck et al. 2001, Tuck 2004) and have been further developed in recent years (Thomson et al. 2015, Tuck et al. 2015) including the use of updated fishing effort for major Indian Ocean pelagic longline fleets (see

Supplement Text S1.3). The model applied here was structured by sex, age-class, breeding stage, and operated on a monthly temporal and 5° × 5° spatial scale. Age classes include chicks (from eggs to pre-fledging), juveniles (from departure from the colony to the end of the following year), immatures (from the start of the second full model year after fledging to <5 yr), and adults (age at first breeding to 70+ yr). Reported bycatch values were scaled to reflect the proportion of BBA in the area that were likely to be from the Kerguelen population using a population multiplier term (see Supplement Text S2.7, Table S1.3).

This model was used to estimate demographic parameters for the virgin focal population (i.e. unaffected by bycatch, environment, or other factors), virgin number of breeding pairs, susceptibility to bycatch (catchability) by different super-fleets, and environmental influences on chick mortality using a likelihood approach. This approach minimizes the differences between observed demographic time series and observed bycatch rates compared with their model estimated equivalents (see Supplement 2

for details of the model, and Fig. 2 for a schematic representation of the model). Bycatch rates and the techniques used to reduced or mitigate seabird bycatch, such as the use of bird-scaring or 'tori' lines, night setting, and line-weighting, can differ between fleets and across time within a super-fleet (e.g. Baird 2001, Dietrich & Fitzgerald 2010, Rollinson et al. 2016). While we have included all known bycatch reports for the focal species with sufficient temporal and spatial information to allow inclusion in the model at the time of publication (Table S1.3), reported bycatch is not currently available for all individual fleets within the model. Thus, generalizations in catchability were made within super-fleets. As the Japanese pelagic longline fleet operating south of 30° S introduced voluntary bycatch mitigation measures in the late 1980s and early 1990s (namely tori poles), we assumed that this resulted in a bycatch reduction of 20% after 1992 (Tuck et al. 2015). Model results were insensitive to this choice. However, allowing a separate bycatch catchability to be estimated for the Japanese pelagic fleet did not significantly improve the model (likelihood ratio test, df = 1,
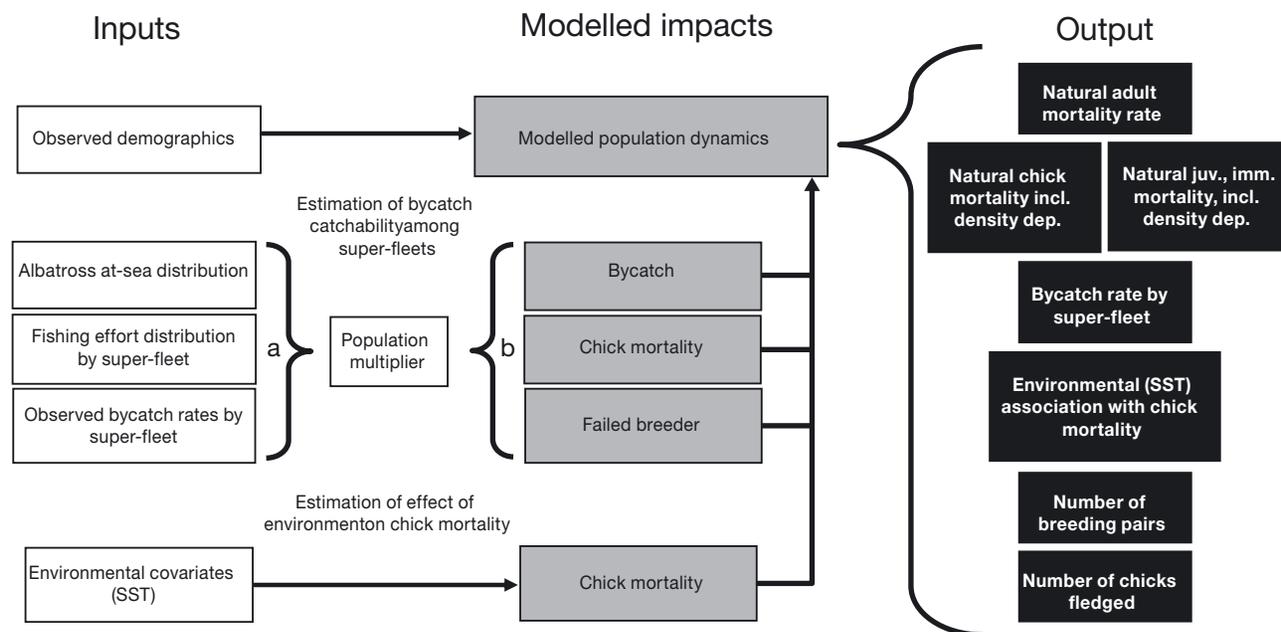

Fig. 2. Schematic representation of flow of information through the integrated population dynamics model inputs (white boxes), to modelled impacts (grey boxes), to outputs (black boxes), estimated using maximum likelihood. See 'Methods' for general information; details on inputs are in Supplement 1 and technical model aspects are described in Supplement 2. Estimation of a bycatch event (a) considers information from known albatross at-sea distributions, fishing effort by super-fleet, and observed bycatch rates by super-fleet. This is scaled to the proportion of birds from the focal colony by the population multiplier. When a bycatch event is estimated to occur, it can have multiple modelled impacts (b); in addition to an estimated bycatch event, if the individual was a breeding adult it is assumed provisioning from a single parent will be insufficient, therefore resulting in the death of the chick and the partner becoming a failed breeder. Environmental covariates can have a positive or negative impact on chick mortality. Further details on modelled impacts are described in Supplement 2. 'incl. density dep.' = including density dependence as specified in Supplement 2, 'juv., imm.' = juvenile and immature

p = 0.81; difference between log likelihoods = 0.06). Therefore, the same parameter value for bycatch catchability was used for the Japanese and all other pelagic longline fleets.

Selecting environmental covariates

To identify which of the 4 environmental SST covariates had the largest influence on chick mortality, we tested all combinations of up to 2 environmental variables at a time in fitted models. Model selection was conducted using the likelihood ratio test, assessed at a significance level of 0.05. We did not test all combinations with 3 or 4 environmental variables as co-linearity between some variables prevented tuning. The model without any environmental covariates is referred to as the 'null' model.

Assessing and distinguishing between parameter estimates

To assess the model's ability to precisely estimate parameter values, standard errors for parameter estimates were approximated using the inverse of the Hessian matrix evaluated at the maximum likelihood, which was estimated using the 'numDeriv' R package (Gilbert & Varadhan 2015). The Hessian matrix was also used to estimate covariance between parameters and hence the model's ability to isolate the influence of one parameter from another. The data were uninformative for the value of the adult natural mortality parameter. This was evident from the high correlation between that parameter and several others. The adult mortality parameter is the theoretical mortality rate in the absence of fisheries bycatch and when environmental parameters are at their historical mean levels. A value of 0.045 was chosen. This is lower than the mean adult BBA mortality that has been observed in field studies (0.075; Nevoux et al. 2010a) and slightly higher than an earlier estimate for natural mortality excluding the impacts of fishing effort (0.032; Rolland et al. 2009b).

To assess the sensitivity of the model-estimated parameters to our assumptions regarding the IUU demersal longline super-fleet including magnitude of effort, bycatch rate, and the assumed probability that a BBA caught originated from the study population, we evaluated a range of model scenarios, and altered our assumptions of this super-fleet accordingly (see Supplement 3). As reported bycatch rates likely underestimate the total magnitude of seabird bycatch since not all individuals that are killed will be observed or recorded, we also assessed the model assuming 2 and 8.66 times the observed bycatch rates for pelagic longline and trawl fleets, respectively (Brothers et al. 2010, Richard & Abraham 2013, Supplement 3). Large differences in model results by one of these modelled scenarios versus the identified model, without markedly poorer agreement with the observed data, would indicate that the model is sensitive to the tested assumption, which would reduce confidence in the model implications.

RESULTS

Environmental covariate selection

The set of model parameter values producing the best fit to the observed data indicated a negative relationship between the average SST around Kerguelen Island during incubation and chick mortality (hereafter 'Ix' model; Table 2). In other words, warmer SST during this period resulted in greater chick survival.

Model fit

The Ix model provided reasonable fits between modelled and observed time-series of the number of breeding pairs and chicks fledged, juvenile survival, and adult mortality (Fig. 3a–d), and improved the fits to the estimated chicks fledged and juvenile survival compared to the null model (Fig. 3b,c). Both models captured the observed decrease in the number of breeding pairs from the late 1990s to the mid-2000s, as well as the increase from the mid-2000s to the end of the time series (Fig. 3a). The low number of breeding pairs modelled in the 1983 breeding year relates to a particularly low rate of return to the colony for that year (Fig. S1.6), which in turn corresponds to low juvenile survival 5 yr prior (Fig. 3c). The model did not reproduce the low number of breeding pairs observed in 2007 (Fig. 3a). Although the large number of chicks that fledged in the 1990s is not captured by either model, agreement with the observed data improves from 2000 onward (Fig. 3b). Both the null and Ix models tended to estimate lower chick fledging values than observed. The greater variability in chick fledging in the Ix model is due to the influence of environmental variables on chick survival and thereby breeding success.

Table 2. Summary of models tuned using different combinations of environmental variables and their significance compared to the null model. df: degrees of freedom; negLL: negative log likelihood. The 'null' model includes no environmental variables. The smaller the negative log likelihood, the better supported the model. I: average sea surface temperature (SST) around Kerguelen (see Fig. 1) during incubation (October to December); R: average SST around Kerguelen during rearing (January to April); G and T: average SST values for the boxes south of Australia and northwest of Tasmania, respectively, during the non-breeding period (May to October) prior to the breeding season. **Bold** text indicates the only model for which inclusion of an environmental parameter was significant at p < 0.05; na: not applicable

Model name	Variable	Estimated slope	df	negLL	negLL model – negLL null	Likelihood ratio test p-value
null	none	na	0	285.76	na	na
Ix	**I**	**−0.552**	**1**	**281.54**	**4.22**	**0.04**
Rx	R	−0.167	1	285.37	0.39	0.53
Gx	G	0.392	1	284.67	1.09	0.30
Tx	T	0.504	1	282.98	2.78	0.10
IT	I	−0.459	2	280.41	5.36	0.07
	T	0.346				
IG	I	−0.509	2	281.24	4.52	0.10
	G	0.208				
IR	I	−0.511	2	281.54	4.22	0.12
	R	0.000				
TG	T	0.504	2	282.98	2.78	0.25
	G	0.000				
TR	T	0.496	2	282.66	3.10	0.21
	R	−0.149				
GR	G	0.414	2	284.16	1.61	0.45
	R	−0.188				

An increase in juvenile survival was observed during the 1980s and 1990s. The model does show an increase, but only in the late 1990s to 2000s. Overall, the modelled rates for juvenile survival were higher than observed until the late 1980s, then lower than observed for the remainder of the time-series (Fig. 3c). The sharp decline after 2001 relates to the temporal lag required to estimate survival of each cohort and does not reflect a predicted decline in juvenile survival. The low observed adult survival in the early 1980s was not reproduced by the model. This could relate to factors not included in the model, such as the impact of the environment on adult mortality. The decline in adult survival from the mid-1990s to the early 2000s and subsequent increase is slightly over-estimated but well represented by the model (Fig. 3d).

Parameter estimation

Including the SST parameter near Kerguelen during the incubation period resulted in greater esti-

mated juvenile and immature mortality, lower chick mortality, and a slightly lower trawl bycatch rate than the null model (Table 3). Albatross bycatch rates associated with the pelagic longline and legal demersal longline super-fleets did not differ between models, and changes in the other parameter values were relatively small. In both models, the estimated bycatch rate associated with IUU demersal longline fishing was much greater than the rates estimated for the legal demersal and pelagic longline super-fleets. Both models indicated that the BBA population at Kerguelen is rebounding from lower numbers in the 1990s and is approaching (or at) its theoretical equilibrium number of breeding pairs (~1110; Table 3). The lower than observed chick fledging and juvenile mortality rates since the late 1980s estimated by the model suggest that the value assumed for natural adult mortality may be slightly high (Fig. 3b−d). High correlation between adult mortality and several other parameters prevented model-based estimation of this parameter.

Bycatch

The majority of the estimated BBA bycatch was allocated to the IUU demersal longline super-fleet from the mid-1990s through the mid-2000s, with peaks in estimated effort and bycatch in 1997 and 2001 (Figs. 4 & S1.5 in Supplement 1). Although BBA from Kerguelen Island overlap with all super-fleets (see Fig. S2.1a in Supplement 2) and bycatch was estimated to occur in most super-fleets, the number of estimated birds killed in these is small relative to the IUU super-fleet. High overlap with IUU activities occurred during the breeding period, corresponding to high bycatch rates near the colony (Figs. S2.1b & S2.2). Overlap of BBA from Kerguelen Island with trawl effort was high during the non-breeding period, when habitat use is more diffuse than during the breeding period (Figs. S1.1 & 2.1b).
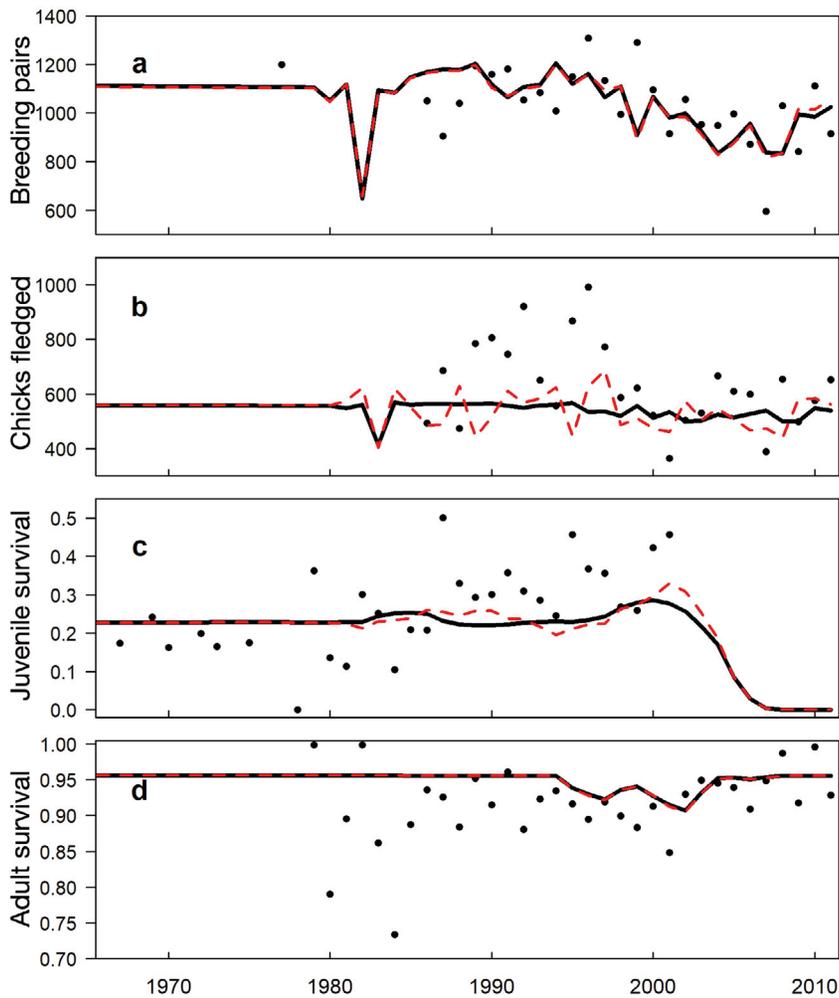
Fig. 3. Time series of observed (circles) and modelled (lines) (a) number of breeding pairs, (b) number of chicks fledged, (c) average survival to age 5, and (d) adult survival expressed as a percent. Black solid line: the null model; red dashed line: the best (Ix) model. The sharp decline in (c) juvenile survival after 2001 relates to the temporal lag required to estimate survival of each cohort, and does not reflect a predicted decline in survival. Modelled values from 1950 to 1965 are not shown

Assessment of parameter estimates

In assessing the covariance between estimated parameter values, there was a high degree of independence between most pairs of parameter estimates, with slight covariance between SST during the incubation period and juvenile and immature mortality (Fig. 5). Agreement between the model-estimated and observed bycatch rates varied between super-fleets (Fig. S2.2). Agreement was greatest for pelagic (non-Japanese) and demersal longline super-fleets, with a slight tendency to over- and underestimate the respective bycatch rates. Agreement with Japanese pelagic longline and trawl super-fleet bycatch was

weaker, with a tendency for the model to underestimate the averaged observed bycatch rates. Agreement with the single IUU demersal longline bycatch rate was poor with the model estimating a bycatch rate 4 orders of magnitude lower than the observed (Fig. S2.2) However, this estimated bycatch rate was greater than for any other longline super-fleet (Table 3).

The scenarios assessing the impact of the assumptions of the IUU demersal longline super-fleet data indicate that the model performs best (i.e. lowest negative log likelihood) when the IUU estimates are included and the estimated bycatch rate of the IUU super-fleet is proportionally consistent (see Supplement 3, Table S3.1). Incorporating unobserved bycatch altered the estimated super-fleet bycatch rates and the proportion of birds estimated as bycatch for IUU and trawl super-fleets. However, the estimated bycatch rate for the IUU fleet was still greater than the other longline super-fleets, and produced a model with weak agreement with the assumed bycatch rate (Table S3.1, Fig. S3.1). Therefore, the implications of the model are robust to the tested assumptions.

DISCUSSION

Quantifying the relative impacts of environmental and fisheries bycatch variables on black-browed albatrosses *Thalassarche melanophris* breeding at Kerguelen Island provides insight into the historical drivers of the observed population trends. This creates the opportunity to improve conservation and management of this population in the future. Our study confirmed the positive impact of warmer conditions during the breeding period on chick survival (Rolland et al. 2008, 2010). Given the implicated role of bycatch associated with the IUU demersal longline super-fleet as a major cause of the observed Kerguelen BBA decline from the mid-1990s through the early 2000s, continued monitoring and exclusion of IUU activities in BBA at-sea habitat is important for the long-term viability of this population. The low

Table 3. Final parameter estimates for the null and Ix models. Mji: juvenile and immature mortality and associated density-dependence; NBop: number of breeding pairs; qJpel: Japanese pelagic longline super-fleet bycatch south of 30° S catchability; qpel: other pelagic longline super-fleet bycatch catchability; qdem: demersal longline super-fleet bycatch catchability; qill: illegal, unreported, and unregulated super-fleet bycatch catchability; qtrawl: trawl super-fleet bycatch catchability; MCpar: chick mortality rate including density dependence; prod: productivity of the albatross population; inc: slope of the relationship between the average sea surface temperature (SST) near Kerguelen during the incubation period and chick mortality; Madult: adult mortality

Parameter	Estimate	
	null	Ix
Mji	6.25	8.80
NBop	1111	1107
qJpel[a]	3.58E−10	3.58E−10
qpel	3.58E−10	3.58E−10
qdem	5.92E−10	5.92E−10
qill	1.54E−08	1.57E−08
qtrawl	7.67E−08	7.55E−08
MCpar	0.626	0.551
prod	0.586	0.589
inc	–	−0.552
Madult[b]	0.045	0.045

[a]The bycatch rate was not estimated separately from other pelagic longline fleets
[b]The parameter value was fixed (see Supplement 2)
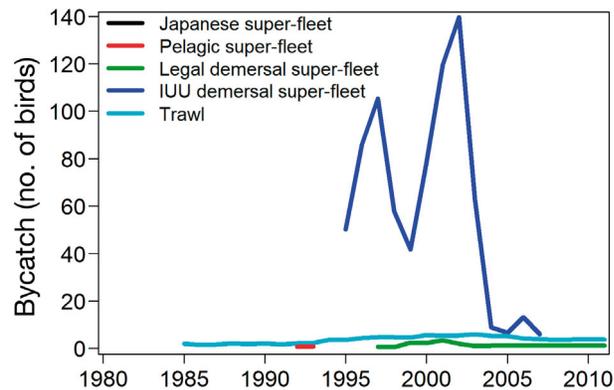
Fig. 4. Estimated annual number of birds caught as bycatch by each super-fleet. As estimated bycatch can be a fraction of a bird, values >0.5 are not shown and assumed to be 0. Zero estimated bycatch above 0.5 birds occurred before 1980

covariance among parameter estimates indicates independence between the estimated parameter values, supporting the relative allocation of bycatch across super-fleets. Furthermore, an analysis of alternate assumptions regarding the IUU super-fleet and unobserved bycatch indicate the model findings are robust to these assumptions. Characterizing the rela-

tive impact of a range of factors on albatross demographics shows how to improve management of this population by providing ecological context for observed population trends, and underscores the importance of addressing IUU fishing.

Incorporating incubation SST

Despite different analytical approaches, the positive relationship between warm conditions near the colony during the breeding period and chick survival agrees with recent work at this colony (Rolland et al. 2008, 2009b, 2010). The impact of including SST is seen in the reduced chick mortality in the Ix versus the null model (Table 3) and the improved estimates of the number of chicks fledged and juvenile survival (Fig. 3b,c). Specifically, the reduced chick mortality in the Ix versus the null model indicates that some of the chick mortality estimated by the null model was actually associated with environmental conditions reflected by SST during the incubation period. The mechanism for this association is uncertain, but it is likely that enhanced foraging conditions for breeding albatross enable efficient provisioning of chicks. This could occur through 2 non-exclusive mechanisms. First, warmer SST may reflect a change in water mass distribution, which could bring carrion of cephalopods and fish within access of foraging breeding albatross. Second, warmer SST may increase zooplankton by supporting phytoplankton growth. As Kerguelen surface productivity is likely iron-limited, SST may set an upper limit to the potential response of iron availability (Blain et al. 2007, d'Ovidio et al. 2015, Obernosterer et al. 2015). While BBA in this region are not known to forage heavily on zooplankton (Cherel et al. 2000, 2002), changes in phytoplankton communities may indirectly enhance albatross by supporting growth of other predators, such as squid.

The slight covariance between SST during the incubation period and juvenile and immature mortality (Fig. 5) likely relates to warmer SST indirectly supporting population growth through reduced chick mortality, which could increase juvenile and immature mortality through density dependence. The greater impact of juvenile and immature mortality including density dependence estimated by the Ix model versus the null model could reflect the important role that natal conditions can have on juvenile survival (Nevoux et al. 2007, Fay et al. 2015). The mechanism for the slight decrease in the trawl superfleet bycatch rate estimated by the Ix versus null model is unclear and may be a non-significant out-
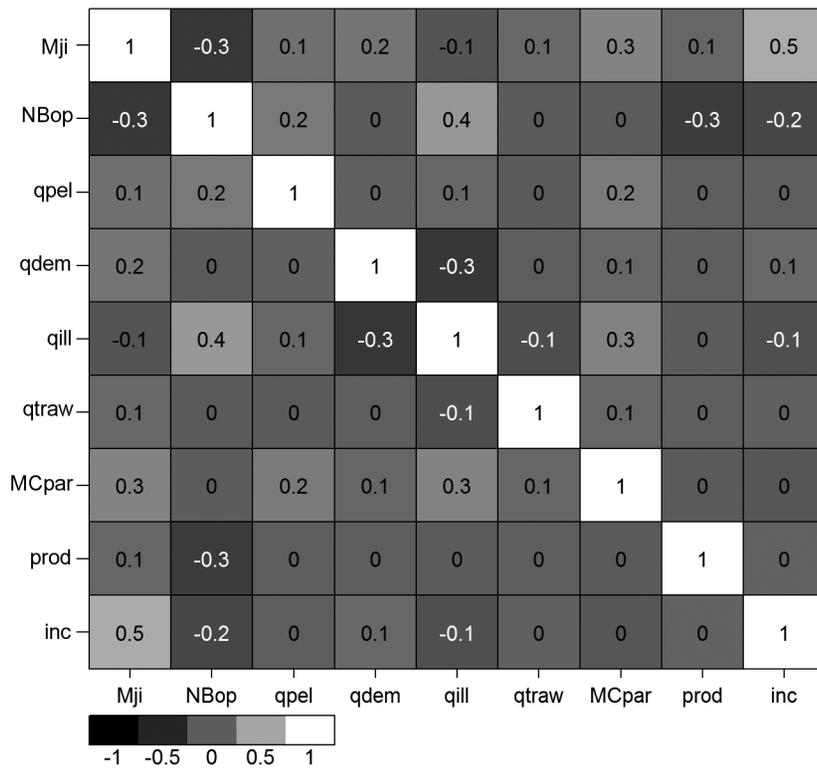
Fig. 5. Inverse Hessian matrix evaluated at the maximum likelihood for model-estimated parameters. Values indicate covariance between estimated parameter values. Values close to |1| indicate high covariance between parameters, thus low confidence in the model's ability to attribute a change in the population to either member of the pair of parameters. Parameter names are described in Table 3

bility parameters is expected, as the observed IUU bycatch rate was based on the observed bycatch rate of the legal fleet before the application of efficient mitigation measures (Agnew & Kirkwood 2005, Anonymous 2006). Others have also estimated high seabird (including albatross) bycatch associated with the IUU fleet in this region and timeframe (Tuck et al. 2003, SC-CAMLR 2007 [Part II, Table 18]). Given the limited spatial distribution of the IUU demersal longline super-fleet's main target species, Patagonian toothfish *Dissostichus eleginoides* (Duhamel & Williams 2011, SC-CAMLR 2015), the seasonal conditions in the fishing grounds, and the scale of our analysis, the spatial or temporal distribution of this fleet is not likely to notably differ from the legal fleet on which it is based.

Regarding the estimated bycatch parameters across super-fleets, there is general agreement with the bycatch rates of the legal super-fleets (Fig. S2.2 in Supplement 2), supporting the implications of the model. Imperfect agreement between modelled estimated and observed bycatch rates could relate to fleet-specific or temporal changes in bycatch rates not represented in our model, inaccurate population multiplier estimates, or both, as comprehensive bycatch and at-sea distribution data were not available. Furthermore, difficulty ascertaining the level of compliance with mitigation measures to reduce seabird bycatch likely contributes variability to bycatch rates within super-fleets, which is unaccounted for in the model (Anderson et al. 2011, Lewison et al. 2012, Phillips 2013, Gilman et al. 2014).

While the model assuming unobserved bycatch for pelagic longline and trawl fleets produced weak agreement with the data, it demonstrates the importance of considering unobserved bycatch when estimating bycatch by fleets using different gear types (Table S3.1, Fig. S3.1). Neglecting to consider the biases in bycatch observation across gear types can influence the proportion of bycatch estimated for each fleet, altering the inference provided by a model. Continued efforts to understand the causes and magnitude of unobserved mortality and a better understanding of the variability in bycatch rates within and across gear types, are needed (e.g. Baird

come of model tuning. Overall, the positive relationship between SST during the breeding period and chick survival is robust across modelling approaches. Although we also identified a negative impact of SST in the non-breeding grounds prior to breeding on chick fledging rates, this relationship did not contribute significantly to the model (Table 2).

Impacts of the IUU super-fleet bycatch

Despite uncertainties associated with the estimated IUU effort and bycatch rate, the allocation of the majority of bycatch to the IUU fleet is robust to changes in its assumed magnitude of effort, observed bycatch rate, and the probability that a caught BBA originated from the Kerguelen colony (see Supplement 3). The models that exclude the IUU super-fleet produced overall weaker agreement with the observed data than the models that include IUU (Table S3.1). Furthermore, some covariance between the estimated IUU and legal demersal longline super-fleet catcha-

2001, Dietrich & Fitzgerald 2010, Gilman et al. 2013). Given the high overlap with IUU effort during the breeding season, the low overlap with pelagic longline super-fleets, and the temporal coincident decrease in the number of breeding pairs with the appearance of IUU effort, IUU demersal effort is highly likely to have played an important role in the decline of breeding pairs between the mid-1990s and early 2000s (Fig. 3a, see also Figs. S1.5 & S2.1 in Supplements 1 and 2).

Improving model fit

Disagreement between the observed and modelled demographic values could be reduced by incorporating additional factors, if these could be estimated. Explicitly modeling cohort effects reflecting natal environmental conditions or parental age could improve the estimates of juvenile survival (Nevoux et al. 2007, Fay et al. 2015, 2016). Incorporating a parameter to represent increased survival of chicks due to supplementary feeding on trawl offal (Rolland et al. 2008, 2010) could improve the estimate of the number of chicks fledged. As opposed to setting an adult mortality rate and estimating the parameters correlated with this term (i.e. juvenile mortality and chick mortality), we could have set one of these parameters and estimated adult mortality. As variation in shy versus bold behavior has been associated with differential breeding success in warm conditions in this population and can impact the rate of population growth, including individual behavioral characteristics in the future development of this model could be informative (Patrick & Weimerskirch 2014, Tuck et al. 2015). Bycatch rate estimates could also be improved by including additional bycatch reports representing a broader range of fleets, variability in bycatch within fleets and super-fleets, the implementation of mitigation by different fleets, and explicitly incorporating unobserved bycatch (Baird 2001, Dietrich & Fitzgerald 2010, Gilman et al. 2013).

The association of warm SST during the incubation period with enhanced chick fledging rates deserves additional study, as a mechanistic explanation remains conjectural. It is unclear if warmer SST relates to greater prey density and more efficient foraging (e.g. prey concentrated in a shallow mixed layer), higher quality prey (greater nutritional value), or a combination thereof. Incorporating the impact of the environment on the survival of additional age classes, particularly adults, could also improve mortality estimates (Rolland et al. 2010, Pardo et al. 2013). Incor-

porating further details on population dynamics as well as food web and predator–prey relationships into the model could improve the fit of the model and provide a mechanistic link between the environment and chick fledging rates.

The future of Kerguelen BBA

Currently, the BBA population on Kerguelen Island appears to have rebounded from a relatively low number of breeding pairs, and is near to its theoretical and observed maximum. As currently modelled, the projected increase in SST (IPCC 2013) would promote chick fledging rates and an increasing population in the absence of other impacts. Density dependence may then become the dominant factor controlling population size. However, the relationship with SST could be further complicated by extreme SST events (Pardo et al. 2017) or be non-linear (Barbraud et al. 2011); the true functional relationship between SST and chick survival is unknown (Thomson et al. 2015).

Even assuming a linear, positive relationship between warming SST and chick survival, increased fishing pressure could override the benefit of increased SST. Since the Treaty on Cooperation in the Maritime Areas Adjacent to the French Southern and Antarctic Territories, Heard Island and McDonald Island came into force in 2005, the French and Australian governments have developed a framework for information exchange and surveillance of IUU fishing, with a high degree of success in excluding IUU fishing within the region (Duhamel & Williams 2011, SC-CAMLR 2015). These efforts, which are critical to sustaining this and other albatross populations in the region, are likely to continue into the future. Specifically, the commissioning of 2 French vessels, continued surveillance, and greater use of satellite imagery to improve estimates of IUU fishing vessel presence in French Southern Territory EEZs (SC-CAMLR 2015) contribute to the framework for combating IUU in this region.

An important unknown in this system is the future distribution of fishing effort by the fleets in this region. While studies have predicted shifts in tuna distributions (Lehodey et al. 2010, Dueri et al. 2014, Lehodey et al. 2015), including poleward shifts for temperate species (Hobday 2010, Dell et al. 2015), the distribution of fishing effort is ultimately determined by the fishers. Their response will likely depend on multiple factors, including access to traditional fishing areas (Girardin et al. 2017), the movement of target species (Michael et al. 2015), fishing

strategy (Michael et al. 2017), and perceived risk (Dowling et al. 2015). Although bycatch of albatross was estimated to be relatively low in the legal super-fleets, shifts in the distribution and timing of effort, as well as in the distribution of the birds, could result in different bycatch patterns in the future. Recent studies show that economic incentives could be used to reduce bycatch in some fleets (Pascoe et al. 2013, Mangel et al. 2015) and offer new insights into the potential applications of fleet dynamic models and the estimation of future bycatch risk.

Given the implicated role of IUU demersal longline effort in the decline of the Kerguelen BBA population, and estimates of between 2700 and 6300 seabirds caught annually by IUU activities in tuna and swordfish fleets south of 30° S (MRAG 2005 in Anderson et al. 2011), characterizing the distribution and behavior of these fleets demands greater attention. Although the unreported nature of the IUU effort makes it difficult to quantify, this and other studies (e.g. Tuck et al. 2003, 2004, Agnew & Kirkwood 2005, MRAG 2005) provide a range of approaches for estimating the distribution and magnitude of effort and the potential impacts of IUU effort through bycatch. These approaches can be improved as additional information arises, and applied to different regions. Although international pressure to eliminate IUU fishing is mounting (FAO 2016), the continued development and strengthening of policy tools and information exchange between nations, management organizations, the fishing industry, and non-governmental organizations is essential to reducing IUU fishing (Österblom et al. 2015).

Attributing bycatch to different super-fleets and the relative impacts of environmental conditions on population dynamics provides novel insights into the factors driving albatross population dynamics. Integrated approaches allow the quantification of the impact of each factor, and the resulting estimates are readily interpreted and assessed for covariance (Francis & Sagar 2012, Thomson et al. 2015, Tuck et al. 2015). Key data assumptions within the model can be assessed and the results used to indicate the sensitivity of the conclusions reached to the uncertainty in the data. Furthermore, the results can be used to inform managers about key interactions, and direct the design of critical experiments. For example, studies investigating the potential mechanisms producing the relationship between chick survival and SST, or simulations of fleet behavior to better understand the IUU fleet, could ultimately improve the management of these vulnerable species into the future.

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