

## Some like it hot: effect of environment on population dynamics of a small tropical seabird in the Caribbean region

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**Abstract.** An understanding of how environmental changes affect life history traits and population dynamics is essential for predicting the effects of climate change, managing ecosystems, and determining how species and habitats can best be preserved. This applies particularly to seabirds, which, as top marine predators, are often considered as indicators of marine ecosystem changes. Most studies have so far been conducted in polar or temperate regions. However, important changes in the functioning of tropical marine ecosystems have been reported, but the responses of top predators remain poorly known. This study focused on a tropical seabird, Audubon's shearwater *Puffinus lherminieri*, analyzing the relationships between climate change and the survival of adults, nesting success, and population dynamics. The population studied breeds in Martinique, in the south of the Caribbean region, which is strongly influenced by the Amazon and Orinoco rivers. A data set for the period 1995 to 2014 was used to estimate the survival by age classes and breeding success and to determine which climate variables most affected demographic parameters. The population dynamics were modeled to predict the future population growth rates in response to climate change. The annual adult survival rate increased over the last 20 years, currently standing at 94% for adult birds more than 6 years old. Adult survival increased with sea surface temperature (SST) during the nonbreeding season as well as with Amazon River discharge, although the latter with a lag of 1 year. The effect of SST was explained by the positive relationship between SST and chlorophyll *a* during years of high discharge from the Amazon and Orinoco. The population decreased between 1995 and 2007 at a rate of 3% per year and then increased between 2008 and 2014 at a rate of 7% per year. The increase in adult survival observed should continue as temperatures increase in the future, and the population models predicted a stable or increasing population over the next 50 years ( $\lambda = 1.018$ ). These results contrast with the negative effect of increasing SST on seabird populations found in temperate and polar regions, emphasizing the need to study the impact of climate change on tropical seabirds.

**Key words:** Audubon's shearwater; Caribbean region; climate change; population dynamics; *Puffinus lherminieri*; sea surface temperature; seabird; survival.

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## INTRODUCTION

An understanding of how changes in the environment affect life history traits and population dynamics is essential to predict the effects of climate change, manage ecosystems, and determine how species and habitats can best be preserved (Clark et al. 2001, Mccarty 2001, Mawdsley et al. 2009). Climate change has been shown to affect the physiology, behavior, and demographic traits of marine organisms, from primary producers to top predators (Walther et al. 2002, Root et al. 2003, Doney et al. 2012), and to result in shifts in population size, distribution, and seasonal abundance (Stenseth et al. 2002, Doney et al. 2012). Seabirds are also considered as mesoscale marine predators that are mainly regulated by bottom-up processes through the abundance of their marine prey (Piatt et al. 2007a), which affects their fecundity and other population-specific vital rates (e.g., Curry et al. 2003, Frederiksen et al. 2006). They are therefore considered as indicators of global marine environmental conditions (Piatt et al. 2007b, Parsons et al. 2008), and changes in their demographic traits or population trajectories are often interpreted as the responses to changes in oceanographic conditions (Jenouvrier et al. 2003, Sandvik et al. 2005, Nevoux et al. 2010, Oro et al. 2010).

Most studies on the response of seabirds to climate change have been conducted in temperate or polar environments (Draycott 2012, Sydeman et al. 2012), probably because warming of the atmosphere is more pronounced in higher latitudes. However, major changes are affecting tropical marine ecosystems including coral reef bleaching, ocean acidification, and shifts in mid-latitude upwelling systems (Hughes et al. 2003, Wilkinson 2008, Doney et al. 2012). Tropical seabirds live in marine oligotrophic environments, where food availability is less predictable (Ballance and Pitman 1999, Weimerskirch et al. 2007), and so climate change may have a strong effect even though the magnitude of the changes is not as great as in polar regions.

The impact of large-scale oceanic-climatic events such as El Niño Southern Oscillation (ENSO, Philander 1989) and the North Atlantic Oscillation (NAO) is generally negative with a strong effect on seabird breeding failure and mortality (Duffy 1990, Sandvik et al. 2008).

Furthermore, other climatic processes affect marine systems at smaller spatial scale, such as changes in sea surface temperature (SST) that affect the availability of food with consequences for mortality or fecundity (Barbraud et al. 2008, Grosbois et al. 2008, Cubaynes et al. 2011). Given that seabirds are generally long-lived (Stearns 1992), fecundity parameters are the traits that are usually first affected by changing environmental conditions (Schreiber 2002), although in some cases adult survival rates are also affected (Jenouvrier et al. 2003, 2009, Sandvik et al. 2005, Barbraud et al. 2008). Few studies have investigated how adult survival of tropical seabirds is affected by climate change (Beadell et al. 2003, Feare and Doherty 2004). This study assessed how a tropical pelagic seabird, Audubon's shearwater (*Puffinus lherminieri*), from the Caribbean region is responding to its changing environment. It analyzed the large- and small-scale effects of marine environmental changes on population parameters and predicted how the population may change in response to projected marine environmental change. In this region, primary production, and therefore food availability for seabirds, is strongly influenced by the interaction between the southern upwelling system along the coast of South America in Caribbean Sea and the high nutrient supply from the Amazon and Orinoco rivers in the Lesser Antilles region (Taylor et al. 2012, Goes et al. 2014). ENSO and NAO also have a considerable impact on the Caribbean ecosystem and Northern South America, affecting trade winds, SST anomalies, and rainfall, with various different time lags (Giannini et al. 2000, 2001, Anthony Chen and Taylor 2002). During the last decades, the Caribbean shearwater population experienced an increase in SST as well as an increase in the Amazon discharge reported in the Lesser Antilles (Gloor et al. 2013). The population was also exposed to predation by introduced black rats (*Rattus rattus*) that preyed on eggs or small chicks (Pascal et al. 2003).

The Audubon's shearwater used as a model for the study is a long-lived species, although the smallest of its genus. In the Caribbean, the Audubon's shearwater population is considered as near threatened (Schreiber and Lee 2000) because of its small population that has recently decreased. A 20-year data set was used to estimate (for the first time for this species) key

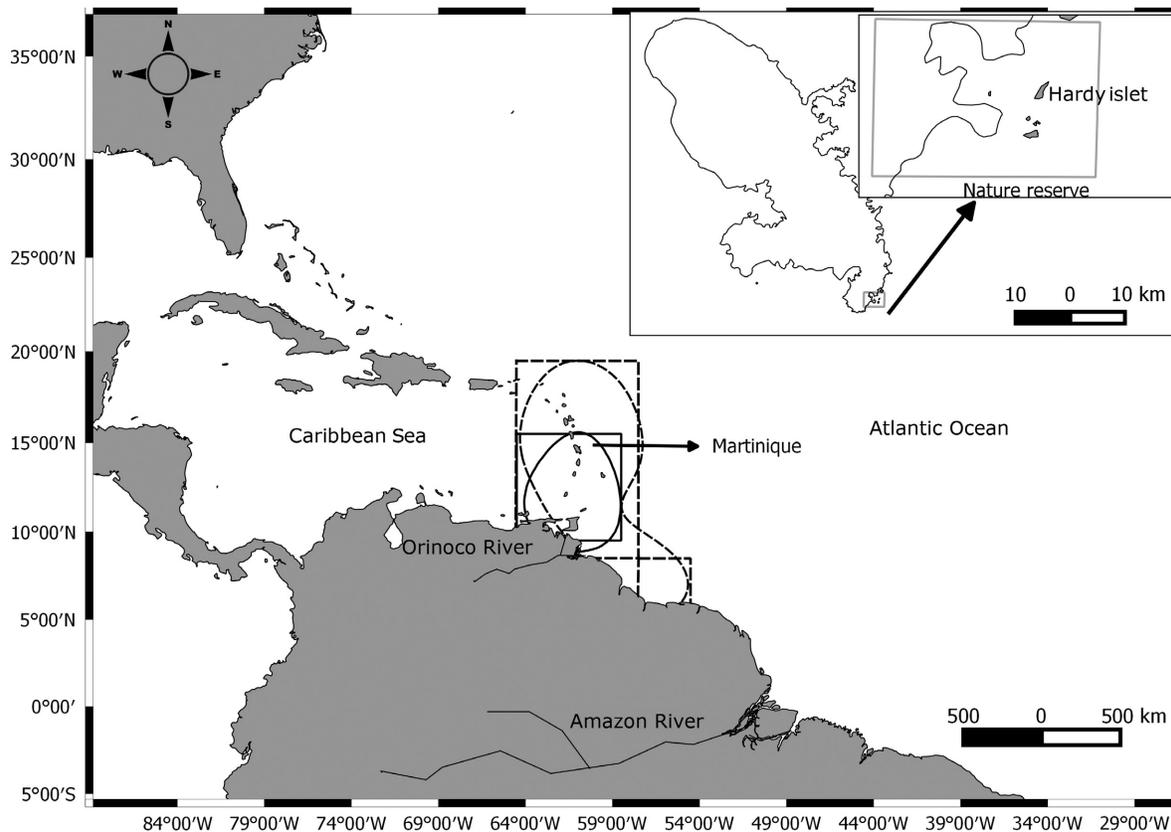


Fig. 1. Map showing the study area. Location of Hardy islet within Martinique and the Caribbean. The location of the main foraging areas with 50% kernel contours based on 564 locations from light-level geolocators fitted to eight individuals (2012–2014). Solid curves enclose the breeding season areas (January to June), and dashed curves enclose the nonbreeding season areas (July to December). The solid rectangle and the dashed rectangles represent the areas used to extract the sea surface temperature variations during and out of the breeding season, respectively.

demographic parameters, such as age-specific survival probabilities and fecundity rates. The study quantified the relative effects of large-scale (ENSO, NAO) and local-scale (SST, Amazon discharge) climate events on the adult survival rate, which is the most sensitive determinant of the population growth rate in seabirds (Sæther and Bakke 2000). Finally, to assess the current and future fates of this population and provide guidance on management actions, the population trajectory was analyzed and the viability of the population was modeled using matrix population models (Caswell 2001) to assess the population growth rate under various climatic scenarios over the next 50 years, taking account of changes in the environment.

## MATERIALS AND METHODS

### Study site and species

Audubon's shearwater is endemic to the North Atlantic (Austin et al. 2004). The Caribbean subspecies *lherminieri* breeds on small cays and cliff sites from the Bahamas to the Lesser Antilles and along the Caribbean and Atlantic Coasts of South America (Lee 2000, Efe and Musso 2001, Silva and Olmos 2010). The study colony was located in Martinique, Lesser Antilles, on Hardy islet (2.63 ha, 14.42° N; 60.83° W), a slightly elevated coral shelf (see Fig. 1). The islet has been managed as a nature reserve since 1995 (Réserve Naturelle des îlets de Sainte-Anne) by the Parc Naturel Régional de Martinique. Rats were found

to be numerous in the 1990s (e.g., 121 rats caught in a single trapping session in 1999), predated small chicks. An attempt was thus made to eradicate rats in 1999 (Pascal et al. 2003). Yearly monitoring afterward showed that rats recolonized the islet, and intensive trapping was carried out to eliminate the rats between 2001 and 2006 (mean: 36 rats captured per year  $\pm 71$  [SD]). Only two rats were caught since 2007.

Audubon's shearwaters are fairly widespread in the Bahamas (Lee 2000, Trimm and Hayes 2005, Mackin 2009) and nest on sandy and rocky islets. They used to breed in Bermuda (Olson 2010). Like other petrels, they usually dig burrows or use small natural cavities for breeding, but on Hardy islet, shearwaters nest exclusively in a network of caves covering an area of 675 m<sup>2</sup> (Pinchon 1964), with nests on bare soil on the floor of the caves. The size of the colony was estimated at several hundred pairs in the 1950s, but is now estimated at around 100 pairs (C. Precheur and V. Bretagnolle, *unpublished data*). The nearest known breeding colony is on Diamant islet, Martinique (Pinchon 1964) with fewer than 10 pairs (V. Bretagnolle, *personal observation*). The next known breeding colony, outside Martinique, is on Saint-Vincent (100 km south) and Guadeloupe (150 km north) (Lowrie et al. 2012), both with unknown numbers. Emigration/immigration between our studied colony and other colonies, although unlikely given the philopatric behavior of petrels and shearwaters (review in Warham 1990), cannot, however, be ruled out. Shearwaters return to Martinique in November and December and lay a single egg in January (Bretagnolle and Precheur 2012), about 2 months earlier than in the Bahamas (Lee and Clark 1994, Mackin 2009). The eggs hatch between March and April (incubation time of 54 days) and chicks fledge from May to June (review of unpublished reports in Bretagnolle and Precheur 2012).

Audubon's shearwaters off the Eastern United States are closely associated with drifting banks of sargassum (floating macroalgae) where they feed mainly on small fish and, to a lesser extent, squid (Moser and Lee 2012). The foraging distribution for the Martinique colonies was not known (but see Jodice et al. [2010] for the Bahamas). We used geolocators (MK18h) between 2012 and 2014 (Biotrack, Wareham, UK) and showed that breeding and nonbreeding areas overlapped to some

extent (see Fig. 1; Appendix S1: Fig. S1). During the breeding season (considered here to be from January to June inclusive), birds foraged mainly to the south of Martinique, off the Orinoco River between latitudes 10° N and 15° N. In the non-breeding season (from July to December), birds ranged off the arc of the Lesser Antilles and close to the coast of South America, between the Orinoco and Amazon rivers between latitudes 6° N and 19° N (Fig. 1; Appendix S1: Fig. S1).

#### *Capture–mark–recapture data sets*

Ringling operations on Hardy started in the late 1950s, but regular banding and recapture started in 1995, mainly by dedicated birdwatchers. From 1995 to 1998 and 2000 to 2014, banding was carried out by blocking the exits from the caves with a mist net from 03:00 to 06:00 to catch adults as they left their nests. In 1999, rats predated apparently all chicks and all adults deserted the colony in May to June, when capture sessions are usually organized, so neither fledglings nor adults were ringed that year. Chicks and a few adults were ringed inside the caves from 1995 to 2007, but this was discontinued after 2007 (see Appendix S2: Table S1). Although the birds were ringed either as chicks or as adults (either at nest or at mist nets), all recaptures were during mist-netting operations.

Mist nets were mainly deployed in May (one to five nights per year) up to 2011, but banding operations were intensified from three to five nights per month in 2012 (January, April, June), 2013, and 2014 (monthly from January to June). During mist-netting operations, the breeding status and the sex of the birds caught were unknown. All birds caught (chicks and adults) were ringed with a stainless steel ring round the tarsus.

Two data sets were used for analysis. A first data set was used to estimate the survival of individuals captured as adults (unknown age) and to test the effects of time and environmental conditions on adult survival. The second data set used shearwaters ringed as fledglings to estimate the age-specific survival probabilities and model population trajectories in various climatic scenarios.

#### *Modeling demographic parameters and the influence of environmental covariates*

Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) were used to estimate the adult annual

survival ( $\phi$ ) and recapture ( $P$ ) probabilities from the data set of birds of unknown age. The initial model was model ( $\phi_t, P_t$ ) where adult survival and recapture probabilities were time dependent. The goodness of fit (GOF) of the CJS model was assessed using U-CARE 2.3 (Choquet et al. 2000). The GOF test indicated a lack of fit (global GOF test,  $\chi^2_{105} = 137.5, P = 0.02$ ) mainly due to a trap-dependent effect in the form of trap happiness (test 2CT,  $\chi^2_{15} = 30.54, P < 0.01$ ), indicating that birds captured at time  $t$  were more likely to be captured at time  $t + 1$  than birds not captured at time  $t$ . To take account of this bias, a model ( $\phi_t, P_{t+m}$ ) based on trappability states (Pradel and Sanz-Aguilar 2012) was used that provided a better fit ( $\chi^2_{90} = 106.95, P = 0.11$ ; see Appendix S3: Table S1).

As the capture effort (estimated as the number of days of capture using mist nets and by entering the caves) varied from year to year (Appendix S2: Table S1, first column) and increased over the years (linear regression:  $P = 0.046$ ), we tested whether the temporal variation in recapture probability could be explained by a linear trend, by quadratic (to model an eventual stabilization of recapture effort) trend, or by the capture effort. Year-specific, linear, and quadratic functions were used to model the variation in survival probability over years.

We investigated the relationships between four environmental covariates potentially affecting the survival rates. Two climate indices, ENSO that was quantified by the Southern Oscillation Index (SOI) and the North Atlantic Oscillation (NAO) Index, were obtained from the National Oceanic and Atmospheric Administration (NOAA) Web site (<http://www.esrl.noaa.gov/>). ENSO can affect negatively or positively SST and rainfall in the Caribbean region and Northern South America, with or without time lag (Giannini et al. 2000, Anthony Chen and Taylor 2002). NAO is negatively correlated with Caribbean rainfall, indirectly via SST associated with trade wind anomalies (Giannini et al. 2001). Both were used to describe the large-scale climatic effects on environmental conditions in the Caribbean region. Local environmental covariates were the SST (<http://iridl.ldeo.columbia.edu/>, Reynolds et al. 2002) and the discharge of the Amazon River obtained online from the Environmental Research Observatory (ORE) HYBAM. Particular attention was paid to temporal effects, including

time-lagged effects, which could be expected if environmental changes affected the survival rates of shearwaters through bottom-up effects. Time lags of 0, 1, and 2 years were used to model the effects of environmental covariates on annual survival in order to take account of the time taken for physical changes to affect the trophic web, as well as to model the effect of environmental conditions during the previous breeding season (Oro 2014) (Appendix S4: Fig. S1). Attention was also paid to the spatial scale over which the environmental covariates were analyzed. The year was split into breeding and nonbreeding seasons (6 months each) because foraging areas were different in the two seasons (Fig. 1). The SST was selected for the spatial sectors appropriate for the periods being modeled. A similar approach was used for the discharge from the Amazon out of breeding season (see Appendix S4: Fig. S1). It was not possible to test whether the presence of rats had any effect on survival or recapture, because although the number of rats caught was obtained, no data were available on the rat capture effort.

To avoid model redundancy and colinearity between variables, a subset of uncorrelated covariates (Grosbois et al. 2008) were selected, using a Pearson's correlation coefficients matrix with all environmental covariates. This method was preferred to a PCA because the PCA axes obtained were difficult to interpret. As five pairwise correlations exceeded 0.5 (of 45 resulting from the nine environmental covariates, Appendix S5: Table S1), four variables—NAO, SOI with a 1-year lag, SOI with a 2-year lag, and SST during the breeding season—were excluded. Where a pair of environmental variables was correlated, local environmental variables were retained in preference to the large-scale climate indices, as little is known about the effects of large-scale indices on the breeding and foraging habitats of shearwaters and local environmental indices tend to be more explanatory. SST during the breeding season and SST during the nonbreeding season were strongly correlated, and SST during the breeding season was excluded as some studies have shown that seabird survival tends to be more affected by climate during the nonbreeding season (Barbraud and Weimerskirch 2003, Ballerini et al. 2009). The five remaining covariates, NAO with a 1-year lag, SOI, SST in the

nonbreeding season, and Amazon discharge in the nonbreeding season and with a 1-year lag, were then centered and normalized. The covariate SST used in our study and the one used in the cited studies (in the discussion) were not extracted in the same area (even these areas overlap) and during the same time period.

As there was a positive temporal quadratic trend in adult survival, these local covariates were also detrended (i.e., the trend was removed statistically by using the residual values of the covariates against time). This allowed us to analyze the effects of interannual variation in variables on interannual variation in adult survival by avoiding spurious detection of effects due to the co-occurrence of trends in survival and the climate covariate (Grosbois et al. 2008).

Model selection was performed using the Akaike information criterion corrected for differences in the effective sample size (AICc, Burnham and Anderson 2002). A model was selected when the difference in AICc was more than 2. The models were selected and the parameters estimated using Mark 7.1 (White and Burnham 1999). Analysis of deviance (ANODEV) was applied to determine the significance of covariate effects on adult survival, comparing the deviance between models including the environmental covariate with the deviance of the constant model and the time-dependent model (Grosbois et al. 2008). The proportion of variance explained by a given covariate,  $R^2$ , was

$$\frac{\text{dev}(\text{model}(\cdot)) - \text{dev}(\text{model}(\text{cov}))}{\text{dev}(\text{model}(\cdot)) - \text{dev}(\text{model}(t))},$$

where dev is the deviance of the model, ( $\cdot$ ) constant, (cov) covariable, and ( $t$ ) time dependent (Skalski et al. 1993). ANODEV is more robust than AICc in testing the effect of covariates on vital rates (Grosbois et al. 2008).

To assess the effect of age on recapture and survival probabilities, models were built where survival and recapture probabilities were age dependent using the subset of birds ringed as chicks. Models with different age classes were compared starting from the general model with 10 age classes [ $\phi(a1\_a10)$ ,  $P(a1 = 0, a2\_a10)$ ]. We considered 10 age classes, with individuals more than 10 years old grouped, because, after 10 years old, the cumulative return rate of ringed chicks was >90% (Fig. 2).  $P(a1)$  was set to 0 because

juveniles stayed at sea during their first year and no individual was recaptured at this age. The survival rate at age 1 (from birth to 1 year old) was arbitrarily set to 1. The GOF test of this age-dependent model was assessed using a bootstrap method with 100 simulations, which showed a good fit to the data ( $P = 0.60$ ). Juvenile survival was estimated by taking the square root of the survival estimated over the first 2 years of life. Different models were then tested by decreasing sequentially the number of age classes on detection and survival probabilities, and the best model was selected using AICc.

### Modeling population dynamics

Female-only, age-class, postbirth pulse matrix population models (Caswell 2001) were built to

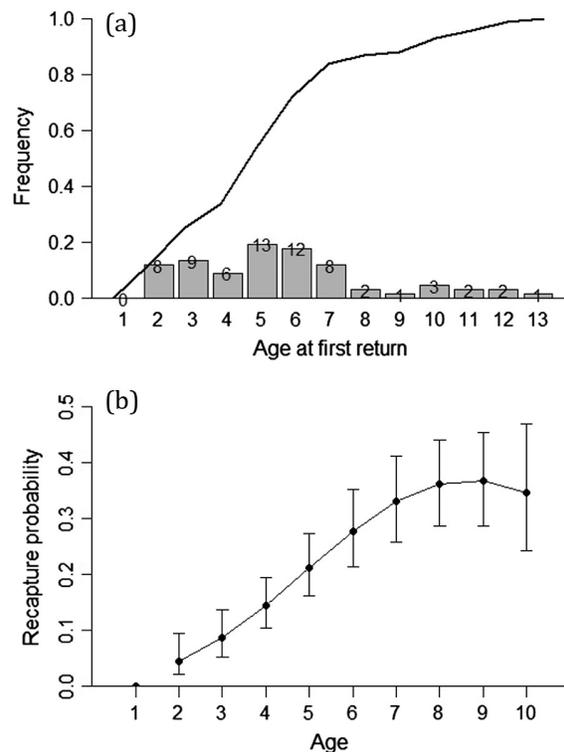


Fig. 2. Observed age at first return (a) and age-dependent recapture probabilities (b) of the Audubon's shearwater from Hardy islet (Martinique Island): (a) cumulative frequency (curve line) and abundance expressed as the number of individuals returned (histograms); (b) the selected model includes a quadratic age effect on recapture probabilities (model 2, Appendix S8: Table S1). Error bars represent 95% CI.

model population dynamics. The life cycle considered went up to 11 age classes (Appendix S6: Fig. S1), from 1 to 11 years old or more, taking account of the age-dependent survival model described above. The age at which individuals start breeding was set to 5 years (as in the Bahamas, Mackin 2009), and from 5 to 11 years old or more, the proportion of breeders and age-specific fecundities were used. As no data were available on age-specific breeding proportions for the Audubon's shearwater, the proportion of breeders for *Puffinus tenuirostris* was used (Bradley et al. 1999), as this other *Puffinus* species has similar adult survival rates, clutch size, and breeding frequency. Nest monitoring data for the colony managed by the Parc Naturel Régional de la Martinique from 1998 to 2005 were used to estimate the average fecundity (and its variance), defined as the average number of female fledglings produced per breeding female (i.e., that laid one egg). Nests were monitored every 15 days from January to July 1998 to 2005 (except 2003 where data were too scarce), with the average number of nests monitored being  $19 \pm 4$  (range: 12–23). In 1999, all incubating adults failed ( $N = 19$  nests monitored that year), presumably because of the extremely high population of black rats (*Rattus rattus*) that preyed on eggs or small chicks. Therefore, the breeding success was zero for this year. The breeding success of the colony was estimated as the proportion of eggs laid that produced a chick. Age-specific fertility was then estimated as the product of the proportion of breeders and the mean breeding success of the colony.

A deterministic model was first used, which assumed constant environmental conditions, by incorporating average demographic parameters. This model was used to calculate the deterministic growth rate, elasticity, and sensitivity of the population growth rate in response to changes in the demographic parameters. Then, to account for more realistic conditions (i.e., stochastic variations in environmental parameters), the models were extended to calculate the mean stochastic growth rates. The first scenario only included the process variance of the demographic parameters. The process variance of breeding success and survival parameters was estimated from the mark-recapture models following White (2000) and Morris and Doak (2002). Breeding success was assumed to follow a lognormal distribution,

and survival parameters to follow a beta distribution. Because juvenile survival was estimated over two age categories, the yearly juvenile survival was estimated by taking its square root and its process variance was estimated using the delta method (Seber 1982):  $[(1/2)\phi^{(-1/2)}]^2\sigma^2$ , where  $\sigma^2$  is the process variance of juvenile survival.

A second scenario took account of predicted changes in environmental covariates affecting the survival rates, as obtained from predictions in the Caribbean region made using global general circulation models (Angeles et al. 2007). Outputs from the general circulation models for the Caribbean region under three Intergovernmental Panel on Climate Change scenarios, that is, the business-as-usual scenario (BAUS), A2 and B2 scenarios, gave a predicted relative increase in SST of  $0.4^\circ\text{C}$  (SD: 0.17) between 2014 and 2064. In this case, changes in adult survival were modeled as a function of SST using the functional response of survival to SST obtained when modeling the demographic parameters. The original slope of the functional response was adjusted, owing to the differences in estimates of adult survival between the two data sets. The initial abundance of females was fixed arbitrarily at 250 individuals ( $\sim 4.5 \times$  the number of breeding pairs; Brooke 2004, Dillingham and Fletcher 2011). The models did not consider the dependence of the demographic parameters on the population size. Monte Carlo simulations were used to calculate the population trajectories (1000 runs) over 50 years, and extinction probabilities were estimated using the ULM program (Legendre and Clobert 1995).

Finally, in addition to the matrix models, Pradel's models (Pradel 1996, Nichols et al. 2000) were used to estimate the retrospective population growth rate of marked birds ( $\lambda_{\text{Pradel}}$ ) during the period 1995–2014. Tests were carried out to determine whether there was a significant difference in population growth rate between two different periods (before and after the rats had been quasi-exterminated), that is, from 1995 to 2007 and 2008 to 2014.

## RESULTS

### *Effect of climate and environment on adult survival rates*

Of the 1138 adults ringed between 1995 and 2014, 51.5% were subsequently recaptured at

Table 1. Modeling the effects of local and global climate covariates on Audubon’s shearwater adult survival ( $\emptyset$ ) on Hardy islet, Martinique.

Models	Np	Deviance	$\Delta$ AICc	AICc weight	$P_{(ANODEV)}$	$R^2$	Slope
1. $\emptyset(t)$	22	1505.69	0.00	1			
2. $\emptyset(\text{SST\_nbr} + \text{Amazon disch\_lag1y})$	7	1548.53	12.36	0	<b>0.003</b>	0.542	0.508, 0.275
3. $\emptyset(\text{SST\_nbr})$	6	1555.76	17.57	0	<b>0.002</b>	0.465	0.526
4. $\emptyset(T^2)$	7	1569.32	33.15	0	<b>0.032</b>	0.320	0.131, -0.004
5. $\emptyset(\text{Amazon disch\_lag1y})$	6	1579.60	41.42	0	<b>0.056</b>	0.210	0.54
6. $\emptyset(\text{NAO\_lag1y})$	6	1583.48	45.29	0	0.090		
7. $\emptyset(\text{Amazon disch\_nbr})$	6	1594.05	55.86	0	0.345		
8. $\emptyset(.)$	5	1599.28	59.08	0			
9. $\emptyset(\text{SOI lag0y})$	6	1599.07	60.88	0	0.851		

Notes: The five local and global climate covariates used are as follows: SST\_nbr = sea surface temperature during nonbreeding season; Amazon disch\_lag1y = Amazon discharge with a lag of 1 year; NAO\_lag1y = North Atlantic Oscillation Index with a lag of 1 year; SOI\_lag0y = Southern Oscillation Index with no lag. Other abbreviations in the models are as follows: (t), time-dependent model; (T<sup>2</sup>), quadratic time-dependent model; (.), constant model. Np is the number of parameters;  $\Delta$ AICc is the difference in AICc between the current model and the best model;  $P_{(ANODEV)}$  is the P value of the analysis of deviance test;  $R^2$  is the proportion of variance explained by the covariate, and slopes are on the logit scale. For all models, the recapture probability was modeled as a function of the capture effort.

least once. The recapture probability varied with time (model 1, Appendix S9: Table S1), being on average  $0.398 \pm 0.013$ . The capture effort had a significant positive effect (slope =  $0.06 \pm 0.01$ ) on the recapture probability and explained more variation in recapture probability than a linear trend effect (57% vs. 30%). In addition, because a model with capture effort as a covariate had less parameters than a time-dependent model, capture effort was included in the subsequent models. The apparent adult survival rate was time dependent (model 6, Appendix S9: Table S1) with a significant positive temporal quadratic trend (linear slope  $\beta_1 = 0.131 \pm 0.051$ , quadratic slope  $\beta_2 = -0.004 \pm 0.003$ ) and a survival rate varying from 0.807 to 0.836 (95% CI) (mean:  $0.822 \pm 0.007$ ). The SST in the nonbreeding season had a significant positive effect (slope =  $0.526 \pm 0.078$ ) on the survival rate (ANODEV,  $P = 0.002$ ), and Amazon discharge with a lag of 1 year also had a positive effect, which was marginally significant (slope =  $0.544 \pm 0.122$ ; ANODEV,  $P = 0.056$ ). Together, these two variables explained 54% of the temporal variance in survival (model 2, Table 1, Fig. 3), of which SST alone explained 47%. The slopes for the covariates were not significantly different (z-test =  $1.75 < 1.96$  at 5% level). Only the SST covariate remained significant and with the same sign when using the detrended covariates (Appendix S10: Table S1). The presence of rats was extremely variable between years

(from 0 to 178 captures), but visual inspection of Fig. 3a does not suggest any strong direct or lagged effect of rat abundance on shearwater survival.

**Fecundity and age-specific survival**

The mean breeding success from 1998 to 2006 was  $76.2\% \pm 16.9$  ( $N = 8$  years, excluding 1999) (Appendix S7: Table S1). Average breeding success varied from 55.0% (2003) to 100% (2005). Of the 358 chicks ringed between 1995 and 2007, 18.7% were subsequently recaptured at least once before 2014. Recapture probabilities had a quadratic dependence on age (Appendix S8: Table S1; Fig. 2). The average recapture probability of shearwaters aged 2 years or more was  $0.209 \pm 0.021$  (95% CI: 0.171–0.253). Using the model with the lowest AICc, the yearly apparent survival from age 1 to 2 was  $0.685 \pm 0.124$ , the apparent survival from age 3 to 5 was  $0.723 \pm 0.227$ , and the apparent survival from age 6 onward was  $0.943 \pm 0.063$ .

**Modeling population dynamics**

Population growth rates estimated during the two periods (before and after the rats had been eradicated in 2007) differed significantly, as estimated using Pradel’s model, being  $\lambda = 0.967$  (0.951–0.983) and  $\lambda = 1.073$  (1.015–1.102), respectively, indicating an annual decrease of 3.3% until 2007 and an annual increase of 7.3% from

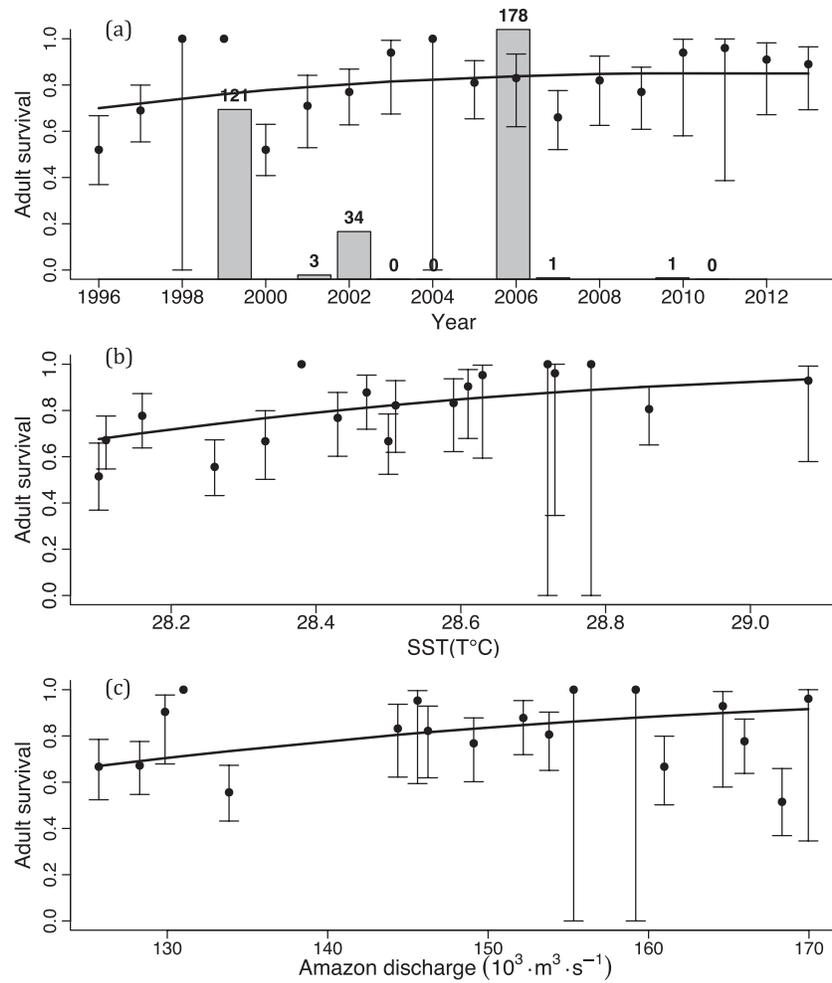


Fig. 3. Adult survival of the Audubon’s shearwater on Hardy islet (Martinique) and regression lines of the quadratic function as a function of (a) time (model 1, Table 1), (b) SST during the nonbreeding season (model 3, Table 1), and (c) Amazon discharge with a lag of 1 year (model 5, Table 1). Error bars represent 95% CI. The number of rats that were caught during eradication campaigns is shown as gray histogram bars on (a).

2008 onward. The deterministic matrix population model gave an asymptotic growth rate of 1.018 over the complete study period (Table 2). Elasticity and sensitivity analyses indicated that adult survival had a greater effect on the population growth rate than on the fecundity rate, the proportion of breeders and juvenile survival rate (Appendix S11: Table S1). Including stochastic variations in environmental parameters using the process variance of demographic parameters gave a mean growth rate of  $0.982 \pm 0.001$ . When stochastic variations in environmental parameters were included in the model for the functional response of survival to the changes in SST,

simulating an increase of  $0.40^{\circ}\text{C}$  over the next 50 years, the growth rate was  $1.018 \pm 0.001$  (Table 2) with a corresponding adult survival rate of 0.987.

### DISCUSSION

Long-term demographic data on a tropical pelagic seabird were used to estimate its key demographic parameters and quantify the effects of environmental change on adult survival. Over the period 1996–2014, the SST affected the adult survival, but unexpectedly, and conversely to almost all studies undertaken so far, increasing

Table 2. Population growth rates of the Audubon's shearwater colony on Hardy islet (Martinique) obtained using Pradel's capture-mark-recapture models, deterministic matrix population models, and stochastic matrix population models.

Models	Retrospective		Prospective		
	Growth rate	SE	Growth rate in next 50 years	Mean growth rate	SE
Pradel's model (1995–2007)	0.967	0.0079	–	–	–
Pradel's model (2008–2014)	1.073	0.0153	–	–	–
Deterministic	–	–	1.018	–	–
Stochastic environmental variations	–	–	–	0.982	0.0006
Stochastic environmental variations with predicted SST	–	–	–	1.018	0.0005

Note: SE, standard error of the mean growth rate.

temperature was shown to have a positive effect during the nonbreeding season of the shearwater. This effect, combined with a predicted increase in SST and the Amazon River discharge, probably explained the long-term positive trend in both adult survival and, to a lesser extent, population size (although the increase in population probably also resulted from the eradication of rats in 1999). These results suggest that, unexpectedly, the rising SST, predicted by climate models in the Caribbean region, may have a beneficial effect on the dynamics of this population.

#### Audubon's shearwater demographic parameters

Modeling population dynamics of Audubon's shearwaters indicated that population growth rate was mainly affected by adult survival, as expected in long-lived birds (Sæther and Bakke 2000). From 1995 to 2007, the slight decrease in the population (3.3%) occurred when the adult survival rate was low and the presence of rats affected the breeding success; then from 2008, an increase of 7.3% occurred due to higher adult survival and breeding success.

Other striking results of this study were the steady increase in adult survival rate with a ~15% increase in just 20 years, a parameter that usually does not vary to any great extent in long-lived organisms (Sæther and Bakke 2000, Weimerskirch 2002, Gaillard and Yoccoz 2003), and the fact that adult survival was as high as 0.94 in birds more than 6 years old, which is comparable to the annual survival of larger species of albatrosses (e.g., black-browed albatross *Thalassarche melanophris*: 0.91–0.95 for three distinct populations, Weimerskirch 2002). Three demographic parameters or issues were not included in the study,

which may have biased the results. Firstly, the status of the birds (breeding vs. nonbreeding) was not known, and so could not be accounted for in survival estimates, even though, for seabirds, breeders often have higher survival rates than nonbreeders (Barbraud and Weimerskirch 2005). Secondly, it was not possible to quantify the dispersal rate, and so the results describe the apparent survival rates. In smaller shearwater species, natal dispersal (and therefore permanent emigration) can be high (e.g., half of birds emigrate in *P. tenuirostris* [Serventy and Curry 1984]), but our high estimate of adult survival suggests that emigration was very low. Immigration, which was not taken into account in our population models, may play an important role in population dynamics of petrels (Jenouvrier et al. 2003, Sanz-Aguilar et al. 2016). The difference in population growth rate estimates between Pradel's models (+7.3% per year from 2008) and stochastic models (from –2% to +2%) thus potentially indicates the presence of immigrants. Nevertheless, the maximum intrinsic annual population growth rate for this shearwater population can be estimated at 7.5% with an adult survival of 0.94 and a mean age at first breeding of 6 years (Dillingham and Fletcher 2011), very similar to the observed population growth rate since 2008.

Thirdly, the immature survival estimate showed a large sampling variation. This is probably due to the relatively low numbers of immature individuals recaptured, explaining in part the difference between the deterministic and mean stochastic growth rates.

Previous survival estimates for Audubon's shearwater in the Bahamas (Lee and Haney 1996, Mackin 2004, 2009) varied from  $0.80 \pm 0.02$  SE

Table 3. Demographic parameters of the genus *Puffinus* (shearwaters) taken from a literature review.

Species	Average body weight	Region	Adult survival	Rat presence	Other threats	Source
<i>P. lherminieri</i>	207	Lesser Antilles (Caribbean)	0.82–0.94	First 11 years	None known	This study
<i>P. lherminieri</i>	190	Greater Antilles (Caribbean)	0.80–0.92	Yes	Predation by owl <i>Tyto alba</i>	Mackin (2009)
<i>P. puffinus</i>	473	United Kingdom	0.91	No	Unknown	Brooke (1990)
<i>P. mauretanicus</i>	522	Mediterranean	0.78	Yes, but the density of rats was low, so predation overlooked	Long-line bycatch	Oro et al. (2004)
<i>P. yelkouan</i>	383	Mediterranean	0.82–0.85	Yes	Predation by cats, illegal shooting, light pollution, fisheries bycatch	Oppel et al. (2011)
<i>P. huttoni</i>	364	New Zealand	0.93	No	Predation by stoat <i>Mustela erminea</i>	Cuthbert and Davis (2002)
<i>P. griseus</i>	803	New Zealand	0.95	Yes	Predation by stoat <i>Mustela erminea</i> , cats	Clucas et al. (2008)
<i>P. tenuirostris</i>	619	Australia	0.90–0.92	Unknown	Unknown	Wooller et al. (1989, 1992)
<i>P. carneipes</i>	609	New Zealand	0.93–0.94	No	Fisheries bycatch, plastics ingestion	Barbraud et al. (2014)
<i>Calonectris diomedea</i>	840	Mediterranean	0.89 0.83–0.95	Yes	None known	Jenouvrier et al. (2008, 2009)
		Azores	0.87–0.88 0.93	No	Poaching	Fontaine et al. (2011)

(using CMR methods) to 0.92 (range: 0.89–0.94), values that are slightly lower than the estimates in this study. No other value is available for similar-sized shearwaters, such as the little shearwater (*Puffinus assimilis*), tropical shearwater (*P. bairdii*), and Galapagos shearwater (*P. subalaris*). However, adult survival rates have been produced for at least seven other (larger) species of shearwater (Table 3). Comparisons show a wide variability, with maximum rates (0.95) reached by *P. griseus* and some *Calonectris diomedea* populations, two species that are, however, much larger than *P. lherminieri* (Table 3). Although body size variations within a species have been shown to affect the survival rates in several shearwater species (e.g., Jenouvrier et al. 2008, Fontaine et al. 2011) and other petrels (Barbraud et al. 1999), body size is not the only factor. Predation on adults, poaching, and the presence of invasive mammalian predators are also known to affect life history traits in petrels and shearwaters (review in Moors & Atkinson 1984, Jones et al. 2008). Part of the interspecific variability shown in Table 3 may be accounted for by the presence

of rats in study colonies, although the rats do not prey on adult shearwaters. Eradicating rats was shown to increase the breeding success of Cory's shearwater from 45% to 86% in Corsica (Pascal et al. 2008). In Martinique, rat eradication since 1999 has allowed a sharp increase in breeding success, from 0 to 85–90% between 1999 and 2001 (Pascal et al. 2003). The average breeding success found in our study, 64.5%, is slightly higher than the breeding success found in the Bahamas for the same species, between 48% and 61% where there were rats (Mackin 2009). The higher breeding success is likely to be a consequence of rat eradication and control, although other factors (such as food availability) may play some role. We suggest that recent rat management (almost to the point of complete eradication), in addition to the improved breeding success, may have the improved apparent adult survival. Although the presence of rats is not thought to have a direct effect on adult survival in *Puffinus* species, as the adults are far too large to be prey for rats, there are at least three indirect processes by which the presence of rats may decrease the apparent or

actual adult survival. Firstly, rats may provoke a landscape of fear (for the adults), which may result in additional energy costs for adults and thus reduce their survival probability. Secondly, there are the delayed costs of failed breeding, with adults investing in unsuccessful breeding attempts regardless of oceanographic conditions and paying the cost of reproduction (Barbraud and Weimerskirch 2005, Sanz-Aguilar et al. 2008). Thirdly, successive breeding failures due to predation on eggs and/or chicks may increase temporary or permanent emigration from breeding colonies leading to the apparent survival being underestimated. This indirect effect on the adult survival of shearwaters is supported by observations; for example, the apparent survival of *P. yelkouan* was 0.82 (Oppel et al. 2011) in a colony with rats, against 0.90 (Warham 1990) in the closely related, similar-sized *P. puffinus* in a rat-free colony. Although speculative at this stage, eradicating rats may have slightly increased the apparent adult survival (possibly through a reduction in permanent emigration), but this on its own cannot account for the 15% increase in adult survival rate, as most of the increase occurred when the rats were present (i.e., before 2007).

#### *Effects of environmental parameters on adult survival*

Alternatively, the increasingly high adult survival rate may be related to an improvement in oceanographic conditions, especially if these improvements are during the nonbreeding season when most seabird mortality occurs (Barbraud and Weimerskirch 2003). Although correlative, increasing SST was, surprisingly, found to have a positive effect on adult survival in the nonbreeding season, whereas for most seabird species studied so far, an increase in SST has generally reduced the adult survival (see, e.g., Jenouvrier et al. 2003, Grosbois and Thompson 2005, Sandvik et al. 2005), even in tropical regions (Carlos 2008, Oro et al. 2010). This unexpected relationship may be explained by the specific oceanographic and climatic conditions in the Caribbean region. The remote influence of ENSO (+1 year) on atmospheric and oceanographic conditions (positive effect on rainfall and SST) in the Caribbean region (Saravanan and Chang 2000, Anthony Chen and Taylor 2002) has been well established. ENSO signal contributes significantly

to the dipole correlation structure between tropical Atlantic SST and rainfall in the Nordeste Brazil region (Saravanan and Chang 2000). The region is also strongly influenced by the Amazon plume that can extend up to 1000 km north of the Amazon delta in the Atlantic Ocean, increasing the marine productivity (Hu et al. 2004, Moller et al. 2010). In situ and satellite data indicate that Amazon discharge has increased over the last 25 years, as has SST in the Caribbean region (Giannini et al. 2000, Saravanan and Chang 2000). The suggested cause of the increase in discharge is the increased SST during this period, which causes an increase in water vapor import from the tropical Atlantic Ocean (Gloor et al. 2013). It is therefore possible that the positive correlation between SST and adult survival may be an artifact caused by the rising SST increasing the discharge from the Amazon and Orinoco rivers that propagates to the Lesser Antilles region through the north Brazil current and Guiana currents (Hu et al. 2004, Chérubin and Richardson 2007), which increases the marine productivity and improves the food availability. Jutla et al. (2011) found a positive association between SST and chlorophyll *a* concentrations during high levels of discharge from the four largest rivers in the world (and a negative relationship during months with low levels of discharge), highlighting the major role of these warmer river plumes in driving phytoplankton growth. The nutrients from these river plumes together with favorable hydrodynamic conditions contribute to the regional marine productivity (Goes et al. 2014) with the reduced sea surface salinity and the increased chlorophyll *a* concentrations (Hu et al. 2004). The positive effect of increased SST associated with the slightly positive effect of increased Amazon discharge is therefore consistent and confirms the hypothesis put forward by Duffy (1990) that the Amazon and Orinoco rivers might have an effect on regional seabird productivity.

#### *Conservation outlook*

The colony studied here was much larger in the 1950s and 1960s (about 500 pairs: Pinchon 1964), but dropped to a low of about 100 pairs in the 2000s, probably as a combined effect of human disturbance and rats. It is not known how many Audubon's shearwaters are currently breeding in the Lesser Antilles, although they were found to

be breeding in at least 10 of the 16 countries or territories (Lowrie et al. 2012). So far as we are aware, this is the only known population of this species breeding only in caves, although this is found in other petrels that usually breed in burrows (e.g., *Hydrobates pelagicus* breeding in caves in Benidorm, Spain (Oro et al. 2005), *Puffinus mauretanicus* breeding in caves on the Balearic Islands, Oro et al. 2004). Currently, almost all breeding pairs are nesting at the limits of the cave and have completely vanished from the large chambers where they were most abundant when the cave was discovered (Pinchon 1964). Since 2007, access to the colony has been banned (even for banding operations), and this ban has been continued under the new action plan of the nature reserve (2014). With rat eradication in 1999 (and permanent rat control since then) and a ban on access to the colony, the population should be recovering, and there are currently clear indications that this is the case: The population growth rate of the colony, as obtained from adult recaptures (using Pradel's method), suggests that over the last 7 years, the annual population growth rate is about 7%. This is probably linked to very high fecundity rates since 2007 (nearly 75%), to the exceptionally high apparent adult survival rate (94%), and possibly to early age at primiparity. Reserve managers now expect that the increase in population size will lead to shearwaters breeding again in the open parts of the cave.

In the medium term, if the nesting conditions are maintained, the population should remain stable according to our modeled scenarios, especially given the predicted increase in SST. The scenarios were, however, imprecise due to high variance in immature bird survival and density dependence overcome. It would be useful to band more fledglings and improve the estimates of survival rates, because juveniles and immature birds account for more than 50% of the population of colonial seabirds and their demography is of primary importance in the dynamics of seabird populations (Votier et al. 2008). Although access to the cave is banned to avoid disturbing the birds, it would be possible to band fledglings if this were restricted to the very end of the breeding season, in June (although there would be a bias because early fledglings would have already left the colony), and during daylight to avoid any adult presence (adults only return at

night to feed the chicks, and nonbreeders already have left the colony in June).

In long-lived birds, adult survival is the parameter to which the population growth rate is the most sensitive (Lebreton and Clobert 1991, Hunter et al. 2000), and thus should be targeted in management considerations. The positive effect of increasing SST in the Caribbean region on the Audubon's shearwater survival and population differs from the effect generally observed in temperate and polar regions. However, global climate models suggest that rising ocean SSTs may increase the frequency and intensity of hurricanes in the northwest Atlantic Ocean (Michaels 2006), which would have a severe effect on pelagic seabirds such as the black-capped petrel, *Pterodroma hasitata* (Hass 2012). Further studies should be undertaken in tropical regions to gain a better understanding of the impact of climate variability on tropical seabirds. Audubon's shearwaters are also threatened by human activities. Although the species should normally be safe from commercial long-line fishing owing to its small size, no detailed investigation of seabird bycatch in the Caribbean region has been undertaken (Bjorkland et al. 2007). Furthermore, there is ample evidence of massive mortality caused by the Deepwater Horizon Oil Spill in the Gulf of Mexico, which severely affected the population in the Bahamas (Mackin et al. 2013), and there are similar risks in the Lesser Antilles, with large oil fields around Trinidad and Tobago, an important foraging area for seabirds in general and Martinique's Audubon's shearwater in particular.

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