Ecology, 95(4), 2014, pp. 1075–1086

Demographic responses to mercury exposure in two closely related Antarctic top predators

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Abstract. Although toxic chemicals constitute a major threat for wildlife, their effects have been mainly assessed at the individual level and under laboratory conditions. Predicting population-level responses to pollutants in natural conditions is a major and ultimate task in ecological and ecotoxicological research. The present study aims to estimate the effect of mercury (Hg) levels on future apparent survival rates and breeding performances. We used a long-term data set (~10 years) and recently developed methodological tools on two closely related Antarctic top predators, the South Polar Skua *Catharacta maccormicki* from Adélie Land and the Brown Skua *C. lonnbergi* from the Kerguelen Archipelago. Adult survival rates and breeding probabilities were not affected by Hg levels, but breeding success in the following year decreased with increasing Hg levels. Although South Polar Skuas exhibited much lower Hg levels than Brown Skuas, they suffered from higher Hg-induced breeding failure. This species difference could be attributed to an interaction between Hg and other environmental perturbations, including climate change and a complex cocktail of pollutants. By including Hg-dependent demographic parameters in population models, we showed a weak population decline in response to increasing Hg levels. This demographic decline was more pronounced in South Polar Skuas than in Brown Skuas. Hence, Hg exposure differently affects closely related species. The wide range of environmental perturbations in Antarctic regions could exacerbate the demographic responses to Hg levels. In that respect, we urge future population modeling to take into account the coupled effects of climate change and anthropogenic pollution to estimate population projections.

Key words: Brown Skua; capture–recapture; Catharacta lonnbergi; Catharacta maccormicki; *heavy metals; pollution; population dynamics; population projections; reproductive performance; South Polar Skua; Southern Ocean; survival.*

Introduction

A major challenge in ecological research is to assess and predict the ecological impact of environmental changes on demographic traits and on population dynamics. In that respect, many studies have evidenced steep population declines and high extinction risks in response to ongoing climate change (Frederiksen et al. 2004, Thomas et al. 2004, Jenouvrier et al. 2009, Barbraud et al. 2011). In the case of toxic chemicals, organic and metallic pollutants constitute another major threat for wildlife. However, their toxic effects have been assessed mainly at the individual and the cellular levels, under laboratory conditions. Translating these individual-level effects to population-level processes is an ultimate goal in ecotoxicology and conservation biology (e.g., Forbes and Calow 2002, Tanaka 2003). However, this population-level approach has been poorly applied in free-living species and some toxic effects have been estimated from controlled laboratory conditions and using closely related species (Nakamaru et al. 2003, Miller and Ankley 2004, Willson et al. 2012).

Mercury (Hg), a heavy metal of both natural and anthropogenic releases, is a globally distributed contaminant of particular concern for aquatic biota (Wolfe et al. 1998, Scheuhammer et al. 2009). Toxic effects of Hg have been extensively studied in vertebrates and may include developmental, neurological, immune, behavioral, and physiological impairments (Wolfe et al. 1998, Heath and Frederick 2005, Tan et al. 2009, Frederick and Jayasena 2010). Hence, one may predict strong fitness consequences in terms of mortality and lifetime reproductive success. Furthermore, the expected increase of anthropogenic Hg emissions in the next decades (Streets et al. 2009) raises serious environmental concerns, including population declines and extinction risks.

In that context, previous studies have investigated the effect of Hg levels on survival rate. There is no evidence of Hg-induced effects on return rate in adult Great Skuas *Catharacta skua* (Thompson et al. 1991), or on apparent adult survival rates of Common Loons *Gavia immer* (Mitro et al. 2008), King Eiders *Somateria*

Manuscript received 27 June 2013; accepted 12 September 2013. Corresponding Editor: D. R. Strong.

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spectabilis, and White-winged Scoter *Melanitta fusca* (Wayland et al. 2008), using capture–mark–recapture (CMR) studies. Only a 1% difference in adult survival rates was detected in Tree Swallows *Tachycineta bicolor* between Hg-contaminated and reference sites (Hallinger et al. 2011). Regarding reproductive performance, the most Hg-contaminated individuals were less likely to breed successfully during the current reproductive attempt (Brasso and Cristol 2008, Burgess and Meyer 2008, Frederick and Jayasena 2010, Jackson et al. 2011). Moreover, individuals that skipped the immediate breeding attempt had the highest Hg levels during the pre-breeding period (Tartu et al. 2013). Long-term data sets and recent and robust methodological approaches may be useful to estimate the effects of Hg on multiple life history traits, including survival rate, breeding probability, and breeding success in the following year.

The present study focuses on two Antarctic top predators: the South Polar Skua, *Catharacta maccormicki* and the Brown Skua *C. lonnbergi* breeding in Antarctica and on subantarctic islands, respectively. These two *Catharacta* skua species are closely related, with frequent cases of hybridization (Ritz et al. 2008). Hence, we expected that Hg effects on demographic parameters and on population dynamics would not significantly differ between the two skua species. Top predators are expected to be the most contaminated among the organisms of food webs, because of Hg biomagnification with increasing trophic level (Bargagli et al. 1998). In the Southern Ocean, Hg may reach some of the highest concentrations so far observed in surface waters of open oceans (Cossa et al. 2011). However, Hg levels have been poorly described in southern hemisphere seabird populations (Bocher et al. 2003, Blévin et al. 2013), and historical increases have been slower than in northern hemisphere seabirds (Thompson et al. 1993). The first aim of this study was to detect whether demographic traits (survival, breeding decision, probability of successfully raising at least one chick, and probability of successfully raising two chicks in the following year) are affected by Hg levels in both species, using long-term (~10-year) data sets, individual Hg blood concentrations, and multistate mark–recapture (MSMR) models (Lebreton and Pradel 2002). The second aim of this study was to assess population-level responses to an increase in Hg levels. This was done by establishing a life cycle for the two skua species by constructing corresponding matrix population models (Caswell 2001) and by including Hg-dependent and Hg-independent demographic traits in the models.

Methods

Study species and sites

The study was carried out at two sites in the French Southern Territories. The South Polar Skua (see Plate 1) was studied on the Pointe Géologie Archipelago, Adélie Land, Antarctica (66°40′ S, 140°01′ E), where ~50 breeding pairs have been monitored annually since 1964/1965 (named the 1964 breeding season). This annual breeder forages on fish and Adélie Penguin (*Pygoscelis adeliae*) eggs and chicks during the breeding season from October to early April (Le Morvan et al. 1967). The Brown Skua was studied in Mayes Island (48°28′ S, 69°57′ E), a subantarctic island of 2.3 km^2 within the Morbihan Gulf of the Kerguelen Archipelago, where ~50 breeding pairs have been monitored annually since the 1990 breeding season. This annual breeder feeds on small burrowing petrels during the breeding season from October to March (Mougeot et al. 1998). Both species are loosely colonial and highly territorial and lay two eggs (Furness 1996). Site tenacity and mate fidelity are high (Ainley et al. 1990, Pietz and Parmelee 1993).

Monitoring procedures for banding and resighting were similar for the two species: all individuals were ringed with a stainless steel band and a plastic band engraved with a unique alphanumeric code. This allowed individual identification at a distance with binoculars. Every year, each partner of a breeding pair was identified at the time of the visits (four to eight) to the nests and territories during egg laying, incubation, and chick-rearing (from early November to early February). Groups of nonbreeding individuals occurring at both sites were also checked regularly for individual identification of ringed birds. Breeding performances were determined by checking the nest sites for the presence of eggs or young chicks, and nest surroundings for the presence of chicks. Chicks were ringed just before fledging. New individuals (breeders and nonbreeders) found in the territories and their surroundings were ringed each year.

Blood sampling

Skuas were captured using a nylon snare on the end of a fishing rod or using remote-controlled noose traps. South Polar Skuas ($n = 76$) were captured from 5 January to 7 February 2003 (32 males and 27 females), and from 17 December 2004 to 19 January 2005 (7 males and 10 females). In total, 13 were nonbreeders, 8 were incubating, and 55 were brooding. Brown Skuas (31 males and 37 females) were handled from 17 November to 9 December 2001. Among them, 11 were nonbreeders, 33 were incubating, and 24 were brooding. Among nonbreeders, 4 were not ringed and were thus not included in the CMR analyses.

Blood samples (1 mL) were taken immediately after capture from the alar vein with a heparinized 5-mL syringe and a 25-gauge needle. After centrifugation, plasma and blood cells were separated and stored at –20°C until assayed. In Great Skuas, blood is a good indicator of mercury intake during the breeding season (Bearhop et al. 2000).

Analysis of Hg concentrations and molecular sexing

Total Hg was measured at the laboratory Littoral ENvironnement et Sociétés (LIENSs) from lyophilized red blood cells in an Advanced Mercury Analyzer

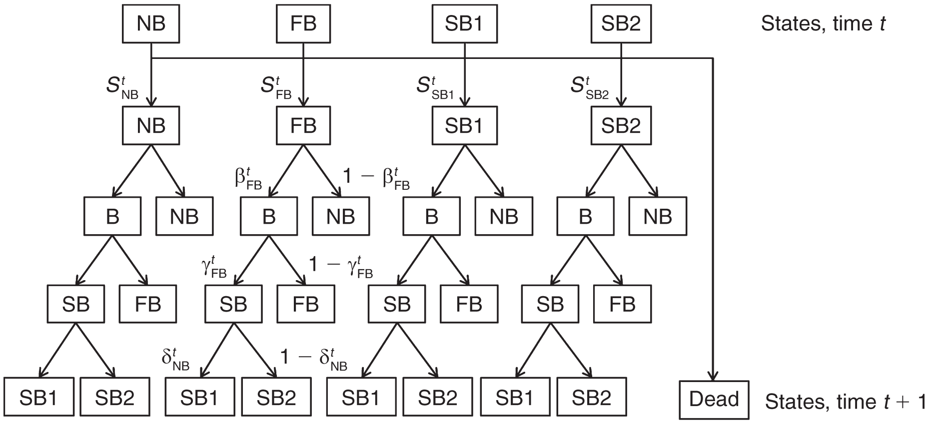

FIG. 1. A multinomial tree diagram describing the probability structure for multistate observations. Solid boxes indicate the states alive in state NB (nonbreeder), FB (failed breeder), B (breeder), SB1 (successful breeder with one chick), SB2 (successful breeder with two chicks), or dead. State transition probabilities were decomposed in a four-step process. The state transitions are S, apparent survival rate; β, breeding probability; γ, breeding success; and δ, probability of successfully brooding two chicks); states are defined in the *Methods* section.

spectrophotometer (Altec AMA 254, LECO, St. Joseph, Michigan, USA). At least two aliquots ranging from 5 to 10 mg dry mass were analyzed for each individual, and measurement quality was certified by reference material, as described by Bustamante et al. (2006). Molecular sexing was determined at the Centre d'Etudes Biologiques de Chizé (CEBC), by polymerase chain reaction (PCR) amplification of part of two highly conserved genes (CHD) present on the sex chromosomes, as detailed in Weimerskirch et al. (2005).

We used R software (R Development Core Team 2012) and generalized linear models (GLMs) with quasi-Poisson error distribution and a log-link function to test whether Hg levels were linked to current breeding status (nonbreeding, incubating, brooding), sex, and the interaction effect between breeding status and sex.

Estimating the effect of Hg on demographic parameters

We evaluated the effects of Hg concentrations on the demographic parameters through the capture–recapture data of sampled individuals from 2002 to 2011 for the South Polar Skua, and from 2001 to 2011 for the Brown Skua. We constructed a MSMR model common to both species. This model distinguished five states: nonbreeder (NB, defined as an individual that was not observed with an egg); failed breeder (FB, defined as an individual that was observed with one or two eggs, or one or two chicks but that failed to fledged a chick); successful breeder with one chick (SB1, defined as an individual that fledged one chick); successful breeder with two chicks (SB2, defined as an individual that fledged two chicks); and dead. The state "dead" was an absorbing state representing death or permanent emigration from the study areas. Models were parameterized in terms of the probability of survival (S), the probability of breeding (β), the probability of breeding successfully (γ), the probability of successfully raising two chicks (δ), and the detection probability (p). Transition probabilities between states were thus modeled with a four-step procedure where S, β, γ, and δ were considered as four successive steps in transition matrices. Fig. 1 presents a multinomial tree diagram describing the probability structure for multistate observations, and parameters of the model are defined in Table 1. We chose a MSMR approach because this allows taking into account the probability of detecting individuals given their return to the study sites. It also allows taking into account the previous breeding state of individuals, which might be important for obtaining unbiased estimates of demographic parameters (Lebreton and Pradel 2002).

Several constraints were made to ensure that the parameters of the model were estimable. Because the dead state was explicitly included in the model but was never encountered, transition probabilities from the dead state were fixed to 0 and capture probability was fixed to 0 (Pradel 2005, Choquet et al. 2009*a*). Our capture–recapture analyses relied on a limited number of individual capture histories (South Polar Skua, $n = 76$; Brown Skua, $n = 64$); thus parameters S, β, γ, and δ were constrained to be constant over time but state dependent. With this constraint, the initial model was full rank. Detection probability was time and state dependent to allow taking into account variations in detectability. Note that we ran a model where all demographic parameters were time and state dependent, but this model was highly rank deficient.

This MSMR model was parameterized by the survival–transition probabilities matrix:

$$\begin{array}{c c} & \begin{array}{ccccc} \text{NB} & \text{FB} & \text{SB1} & \text{SB2} & \text{Dead} \end{array} \\ \begin{array}{c} \text{NB} \\ \text{FB} \\ \text{SB1} \\ \text{SB2} \\ \text{Dead} \end{array} & \left[\begin{array}{ccccc} S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ S(1-\beta) & S\beta(1-\gamma) & S\beta\gamma(1-\delta) & S\beta\gamma\delta & * \\ - & - & - & - & * \end{array}\right] \end{array}.$$

TABLE 1. Definition of parameters used in the multistate mark–recapture model.

Parameter	Definition
S_s^t	Probability that an individual in state *s* at time *t* survives to time *t* + 1 and does not permanently emigrate from the study area.
β_s^t	Probability that an individual in state *s* at time *t* breeds at time *t* + 1, given that it survives to *t* + 1.
γ_s^t	Probability that an individual in state *s* at time *t* breeds successfully at time *t* + 1, given that it survives to and breeds at time *t* + 1.
δ_s^t	Probability that an individual in state *s* at time *t* raises successfully two chicks at time *t* + 1, given that it survives to and breeds successfully at time *t* + 1.
p_s^t	Probability that an individual in state *s* at time *t* is encountered at time *t* + 1.

Asterisks in the column for dead birds represent the complementary parameter (complement of the sum of positive row entries).

Because we were interested in testing for sex-specific effects of Hg on demographic parameters, we started from an initial model including an effect of sex (g) on each parameter. Model selection was first performed on detection probability by testing state dependency (difference between all states, between breeders and nonbreeders, or no difference) and time dependency. We then tested for state dependency (difference between all states, difference between breeders and nonbreeders, or no difference) for S, β, γ, and δ. Once we identified the best model structure for all parameters, we tested for an effect of breeding experience (number of previous breeding attempts) for South Polar Skuas on the demographic parameters (S, β, γ, or δ). Breeding experience data were not available for Brown Skuas. Then we tested for a linear or a quadratic effect of Hg on demographic parameters in the following year to test the hypothesis that contamination levels in one breeding season may influence the survival and breeding success of an individual in the following season. We did not test for an effect of Hg on current breeding success, because capture and blood sampling were mainly conducted during the chick-rearing period. We built MSMR models where each demographic parameter θ was modeled as a function of Hg using a logit link function: $\text{logit}(\theta) = a + b \times \text{Hg}_i$, where a is an intercept, b is a slope, and Hg_i is the Hg concentration for individual i. When $b < 0$, or $b > 0$, the covariate Hg has a negative or positive effect, respectively, on the demographic parameter. Individual covariates, breeding experience, and Hg were standardized. We tested the goodness of fit (GOF) of the time-dependent MSMR model using U-CARE (Choquet et al. 2009*b*).

Model selection was based on Akaike's information criterion corrected for small sample size, AIC_c (Burnham and Anderson 2002), and all models were run under program E-SURGE 1.8.5, allowing the splitting of transition probabilities between states (Choquet et al. 2009*a*).

Modeling population dynamics

To evaluate the population-level effects of Hg, we constructed population models using pre-breeding matrices (Caswell 2001) structured by age and reproductive status classes (Fig. 2). For South Polar Skuas, we built a female-only age- and stage-classified matrix population model, because Hg similarly affected the same demographic parameters of both sexes (see *Results*). Based on results from a detailed demographic study on South Polar Skuas (Ainley et al. 1990), the model consists of four immature (juvenile) age classes (first-year J_1, second-year J_2, third-year J_3, fourth-year J_4); five pre-breeder classes (from PB_5 to PB_9: individuals in this class are able to start breeding and are thus considered as pre-breeders); and two stage classes: breeder (B) and nonbreeder (NB). Parameters entering the model were adult survival rate of breeders and nonbreeders (S_{AB} and S_{ANB}); survival during the second and the third year (S_1 and S_2); the proportion of juveniles attempting to breed (pb_5 to pb_9), breeding probability of breeders and nonbreeders (β_B and β_{NB}), fecundity, and the proportion of immigrants (m). Fecundity was calculated as the product of clutch size (2), breeding success probability (γ), the probability of successfully raising two chicks (δ), the survival probability during the first year at sea (S_0), and assuming a 1:1 sex ratio.

For the Brown Skua, we built a two-sex age- and stage-classified matrix population model (Caswell 2001), because Hg concentrations affected the demographic parameters of males only (see *Results*). We used the same life cycle as the one used for South Polar Skuas, because Brown Skuas and South Polar Skuas are similar in size and other life history traits (Furness 1996). Moreover, to the best of our knowledge, there is no detailed demographic study on Brown Skuas. The two-sex model was thus parameterized with the same parameters as for the South Polar Skua, except for fecundity, which included the harmonic fertility function $n_{(f,m)}/(n_f + n_m)$, where n_f and n_m are the number of breeding females and males, respectively.

We first built deterministic matrix models with no stochasticity, which included the mean values of the demographic rates. Mean estimates of the demographic parameters used in the deterministic model (S_0, S_1, S_2, pb_5 to pb_9, and m) were obtained from Ainley et al. (1990) and from our MSMR model results (S_{AB}, S_{ANB}, β_B, β_{NB}, γ, and δ). From these matrix analyses, we estimated the deterministic growth rate (λ) and the sensitivities of λ to variations in demographic rates θ

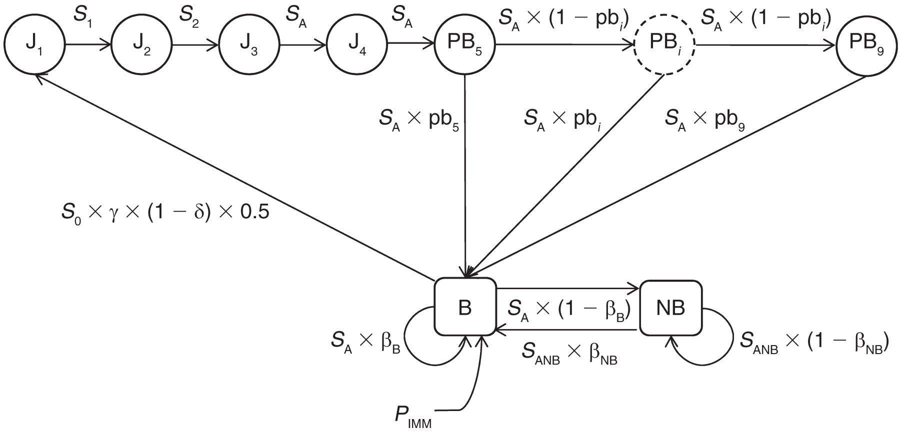

FIG. 2. Lifetime cycle graph for the Brown Skua and the South Polar Skua. J_i, juvenile of age class *i*; PB_i, pre-breeder of age class *i*; B, adult breeder; NB, adult nonbreeder; S_0, survival during the first year at sea; S_i, survival probability of age class *i*; S_A, adult breeder survival probability; S_{ANB}, adult nonbreeder survival probability; pb_i, proportion of pre-breeders of age class *i* attempting to breed for the first time; β_B, breeding probability of breeders; β_{NB}, breeding probability of nonbreeders; γ, probability of breeding successfully; δ, probability of successfully raising two chicks; P_{IMM}, immigration rate.

($\partial\lambda/\partial\theta$) (Caswell 2001). We then focused on stochastic matrix models to estimate the stochastic growth rate λ_{sto}. Environmental stochasticity was included in two different ways. When a vital rate had no significant relationship with Hg levels, its yearly values were sampled from a beta distribution (Morris and Doak 2002), with mean and variance equal to those estimated from the MSMR model selected or taken from Ainley et al. (1990). When a vital rate had a significant relationship with Hg levels, its value at year *t* (θ^t) was modeled as $\theta^t = \text{logit}^{-1}(a + b \times \text{Hg}^t)$, where Hg^t represents the mean Hg value. Hg values were sampled from a lognormal distribution for all individuals sampled. To assess the population-level effects of Hg concentrations, we estimated stochastic population growth rates according to changes in mean Hg levels within the range of observed Hg values.

We assessed the fit of our deterministic and stochastic population models by comparing the observed annual population growth rate (λ_{obs}) calculated as $(N_t/N_0)^{(1/t)}$ (Caughley 1977), based on the counts of the number of breeding pairs. The matrix population models were analyzed by Monte Carlo simulations (10 000 iterations) using package *popbio* (Stubben and Milligan 2007) implemented in program R (R Development Core Team 2012).

RESULTS

Effects of sex, current breeding status, breeding experience, and body conditions on Hg levels

Hg levels were around four times higher in Brown Skuas (8.22 ± 0.24 μg/g dry mass, mean ± SE) than in South Polar Skuas (2.15 ± 0.17 μg/g dry mass; $F_{1,140} = 381.07$, $P < 0.001$), even when considering only breeders ($F_{1,116} = 1162.00$, $P < 0.001$). Nonbreeders bore higher Hg levels than incubating and chick-rearing South Polar Skuas, without sex difference (Fig. 3A, Table 2). Nonbreeders had lower previous breeding experience than incubating and chick-rearing birds ($F_{2,68} = 4.908$, $P = 0.010$), and Hg levels decreased with increasing breeding experience in South Polar Skuas (Table 2). In

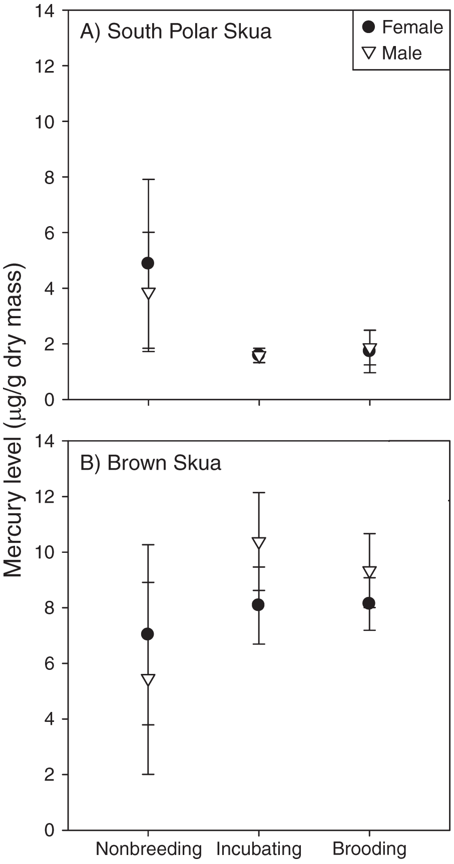

FIG. 3. Mercury (Hg) levels (mean ± SD) in nonbreeding, incubating, and brooding South Polar Skuas and Brown Skuas, by sex.

TABLE 2. Mercury (Hg) levels as a function of breeding status, sex, the interaction between breeding status and sex, and breeding experience in South Polar Skuas and Brown Skuas.

Independent variables (Hg is dependent)	South Polar Skua			Brown Skua		
	df	F	P	df	F	P
Breeding status	2, 71	30.986	<0.001	2, 65	8.612	0.001
Sex	1, 69	0.006	0.938	1, 64	7.760	0.007
Breeding status × sex	2, 67	0.280	0.757	2, 62	3.821	0.027
Breeding experience	1, 67	10.107	0.002			

Notes: Analysis was done using GLMs (quasi-Poisson error distribution and a log-link function). Breeding status (nonbreeding, incubating, brooding) was assessed in the year of blood sampling; breeding experience was prior to the year of blood sampling.

Brown Skuas, nonbreeding males had lower Hg levels than incubating and chick-rearing males, whereas Hg levels did not differ among females' breeding status (Fig. 3B, Table 2).

Long-term fitness consequences of Hg exposure

The GOF of the MSMR model was overall not significant for South Polar Skuas (males, $\chi^2 = 15.31$, df = 47, $P = 1.0$; females, $\chi^2 = 19.85$, df = 50, $P = 1.0$) and for Brown Skuas (males, $\chi^2 = 13.48$, df = 35, $P = 1.0$; females, $\chi^2 = 19.99$, df = 43, $P = 0.99$). For the two skua species, the best model according to $\mathrm{AIC_c}$ (model 9, Appendix) states that in year $t + 1$, individuals captured as breeders in year t had higher apparent survival rates, higher breeding probabilities, and higher detection probabilities than nonbreeders captured in year t, but did not differ in breeding success probabilities (Appendix and Table 3).

In South Polar Skuas, model 12 (Table 4A) was the best model according to $\mathrm{AIC_c}$; it suggested an effect of previous breeding experience on breeding probability. However, the parameter value (–0.05) and its wide confidence interval including 0 suggested that the effect was very weak. For the two species, Hg levels had no effect on apparent survival rate and breeding probability in the following year (Table 4A, B: models 15–18,). In South Polar Skuas, increasing Hg levels were linked to decreasing breeding success in the following year (model 19, Table 4A, Fig. 4A), but not to the probability of successfully raising two chicks in the following year (models 21 and 22, Table 4A). In Brown Skuas, breeding success in the following year was not related to Hg levels (models 19 and 20, Table 4B), but the probability of successfully fledging two chicks in the following year decreased with increasing Hg levels (Models 21–23, Table 4B). Specifically, model 23 suggested that the probability of successfully raising two chicks in the following year decreased with increasing Hg levels in male Brown Skuas (Fig. 4B). Model 23 had the lowest $\mathrm{AIC_c}$ and the confidence interval for the slope parameter did not contain 0 (Table 4B).

Hg and population growth rate

The deterministic population growth rate was 1.002 and 1.020 for South Polar Skuas and Brown Skuas, respectively, and the respective generation times were 19.4 and 23.5 years. Sensitivity analyses suggested that changes in adult survival of breeders will have the greatest effect on the population growth rate for both species, followed by changes in the probability of breeding, the probability of adult survival of nonbreeders, and the probability of juvenile survival in the South Polar Skua, and by changes in the probability of breeding, the probability of juvenile survival, and the probability of breeding successfully in the Brown Skua. In both species, changes in the probability of breeding successfully will have a greater effect on the population growth rate than will changes in the probability of fledging two chicks (ratio of elasticities 4.6 to 4.7).

Our stochastic population model predicted an increase in the numbers of breeding pairs of South Polar Skua ($\lambda_{\mathrm{sto}} = 1.001$) and Brown Skua ($\lambda_{\mathrm{sto}} = 1.009$), which were similar to the mean annual population growth rate observed from 2003 to 2012 ($\lambda_{\mathrm{obs}} = 1.015$) for South Polar Skuas and from 2001 to 2011 ($\lambda_{\mathrm{obs}} = 1.008$) for Brown Skuas. Population growth rates accounting for Hg effects from MSMR analyses were similar to the purely stochastic growth rate regardless of Hg effects

TABLE 3. Estimation of parameters (mean with 95% CI; all values are percentages) calculated from the best model (model 9) for South Polar Skuas and Brown Skuas.

Parameter	South Polar Skuas		Brown Skuas	
	Nonbreeders	Breeders	Nonbreeders	Breeders
S, apparent survival rate	83 [72–91]	93 [89–95]	80 [66–89]	95 [90–97]
β, breeding probability	60 [48–71]	85 [81–89]	37 [25–50]	87 [82–90]
γ, breeding success	74 [68–78]	74 [68–78]	84 [79–88]	84 [79–88]
δ, probability of successfully brooding two chicks	28 [23–34]	28 [23–34]	28 [23–34]	28 [23–34]
p, detection probability	59 [46–70]	100 [100–100]	41 [29–55]	100 [100–100]

TABLE 4. Modeling the effects of experience, Hg levels, and sex on demographic parameters of South Polar Skuas, and of Hg levels and sex on demographic parameters on Brown Skuas; effects are arranged from lowest to highest ΔAIC_c for each species.

Hypothesis, by species	Model no.	Rank	Deviance	ΔAIC_c	Slope [95% CI]
A) South Polar Skua					
Experience					
Effect on β	12	13	1537.71	0	−0.05 [−0.34, 0.24]
No effect on S, β, γ, δ	9	11	1543.36	1.42	
Effect on γ	13	12	1542.97	3.14	
Effect on δ	14	12	1543.34	3.51	
Effect on S	11	13	1549.40	11.69	
Mercury, Hg					
Effect (lin) on γ	19	13	1530.89	0	−1.92 [−3.40, −0.45]
Effect (quad) on γ	27	14	1530.26	1.51	
Effect (lin) on γ with Hg × sex effect	20	15	1530.39	3.77	
Effect (lin) on δ	21	13	1537.81	6.93	
Effect (quad) on γ with Hg × sex effect	28	17	1529.56	7.26	
No effect on S, β, γ, δ	9	11	1543.36	8.24	
Effect (lin) on δ	29	14	1537.12	8.37	
Effect (lin) on S with Hg × sex effect	16	18	1528.70	8.57	
Effect (lin) on δ with Hg × sex effect	22	15	1536.32	9.70	
Effect (quad) on δ with Hg × sex effect	30	17	1532.10	9.80	
Effect (quad) on β	25	17	1532.33	10.03	
Effect (quad) on β with Hg × sex effect	26	23	1521.53	12.42	
Effect (lin) on S	15	14	1541.22	12.47	
Effect (lin) on β with Hg × sex effect	18	18	1532.61	12.48	
Effect (lin) on β	17	14	1541.85	13.10	
Effect (quad) on S with Hg × sex effect	24	23	1524.11	14.99	
Effect (quad) on S	23	17	1539.27	16.97	
B) Brown Skua					
Mercury, Hg					
Effect (lin) of males on δ	23	14	1332.10	0	−1.70 [−3.34, −0.06]
Effect (lin) on δ	21	13	1335.54	1.29	−0.58 [−1.36, 0.20]
Effect (lin) on δ with Hg × sex effect	22	15	1331.74	1.80	males −1.70 [−3.33, −0.06]; females −0.40 [−1.72, 0.93]
Effect (quad) on δ	31	14	1335.50	3.40	
Effect (lin) of females on δ	24	14	1337.40	5.30	
No effect on S, β, γ, δ	9	11	1344.80	6.29	
Effect (quad) on S	25	17	1334.28	8.70	
Effect (quad) on δ with Hg × sex effect	32	17	1335.42	10.62	
Effect (quad) on γ	29	14	1343.00	10.90	
Effect (quad) on β	27	17	1337.01	11.42	
Effect (lin) on S	15	15	1342.40	12.46	
Effect (lin) on γ with Hg × sex effect	20	15	1343.69	13.75	
Effect (quad) on γ with Hg × sex effect	30	17	1340.57	14.98	
Effect (lin) on β with Hg × sex effect	18	19	1337.53	16.34	
Effect (lin) on S with Hg × sex effect	16	19	1338.52	17.33	
Effect (lin) on γ	19	13	1351.22	16.98	
Effect (quad) on S with Hg × sex effect	26	23	1330.83	18.57	
Effect (quad) on β with Hg × sex effect	28	23	1336.18	23.92	
Effect (lin) on β	17	15	1479.61	149.67	

Notes: The effects of standardized breeding experience were tested on each parameter. The effects of standardized Hg levels (lin, linear relationship; quad, quadratic relationship) were then tested on each parameter in the following year, with or without an interaction effect between Hg and sex.

(South Polar Skua, $\lambda = 1.006$; Brown Skua, $\lambda = 1.020$). According to our population modeling, Hg negatively affects population growth rate. Demographic decline ($\lambda < 1$) was predicted for mean Hg levels exceeding 2.8 μg/g dry mass in the South Polar Skua and 12 μg/g dry mass in the Brown Skua (Fig. 5).

DISCUSSION

Using long-term data sets and MSMR models, the present study indicates no effect of Hg accumulation on adult survival rate and breeding probability in the following year. However, Hg exposure decreased the probability of successfully raising at least one or two chicks, respectively, in the following year in the South Polar Skua and the Brown Skua. At the population level, this study suggested a slight demographic decline in response to increasing Hg levels.

Hg levels in Brown Skuas and South Polar Skuas

Hg levels found in adult Brown Skuas and South Polar Skuas were within the range of those measured in the blood of adult Great Skuas at northeast Atlantic colonies (from 3.49 ± 1.83 to 6.71 ± 3.08 μg/g dry mass, mean ± SE; Bearhop et al. 2000). South Polar Skuas

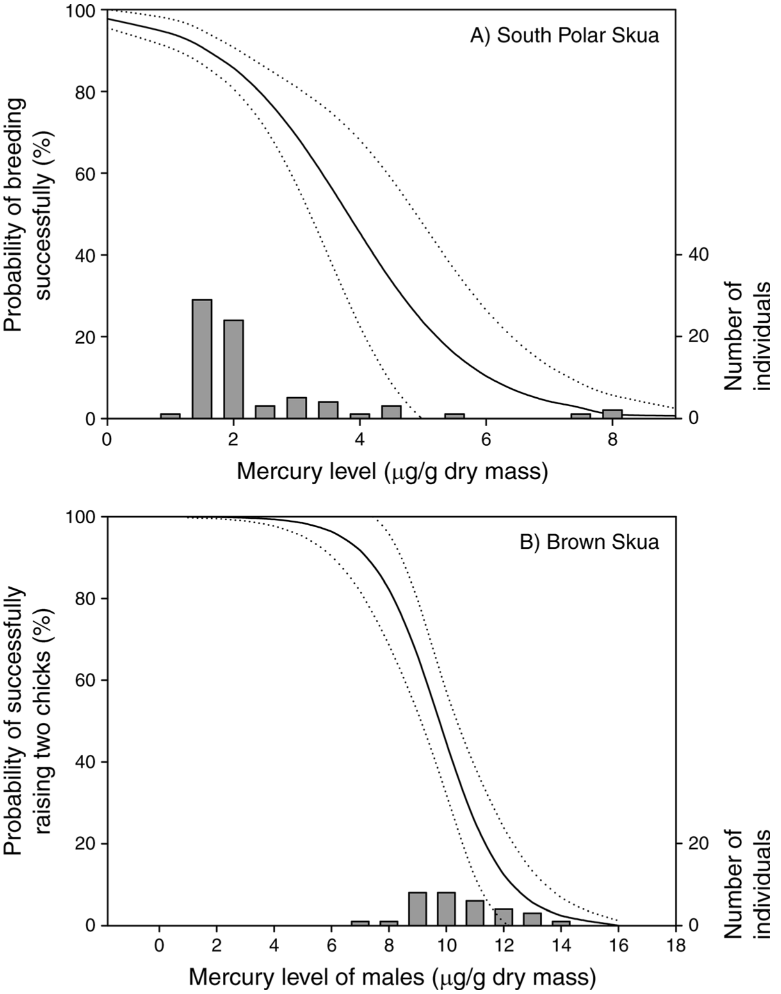

FIG. 4. Effects of Hg on (A) the probability of breeding successfully in the following year in South Polar Skuas (Table 4A: model 19) and (B) the probability of raising two chicks in the following year in Brown Skuas (Table 4A: model 23). The solid line is the mean probability; the dotted lines represent 95% confidence intervals estimated using the delta method (Seber 1982). Histograms represent the measured Hg levels in the sampled individuals (right axis).

were less contaminated than Brown Skuas, which could be attributed to a species-specific difference in diet and trophic level during the breeding season and/or during the wintering period. On the one hand, Brown Skuas breeding in the Kerguelen Islands feed primarily on adult Blue Petrels *Halobaena caerulea* (Mougeot et al. 1998), long-lived highly piscivorous seabirds (Cherel et al. 2002). On the other hand, South Polar Skuas breeding in Adélie Land rely on fish, as well as eggs and chicks of the Adélie Penguin *Pygoscelis adeliae*, a krill-eating seabird (Young 1963). The two species also differ in their migration pattern and wintering areas, with South Polar Skuas migrating farther north to Japan (CEBC [Centre d'Etudes Biologiques de Chizé], *unpublished data*) and the northern Atlantic and the northern Pacific Oceans (Kopp et al. 2011) than Brown Skuas, which migrate to Australia (CEBC, *unpublished data*) and between the Antarctic Polar Front and the Northern Subtropical Front (Phillips et al. 2007). Moreover, Hg levels decreased with previous breeding experience, and differed between breeders and nonbreeders in a species-specific manner. This could be due to a difference in foraging ecology between breeders and nonbreeders. Little is known about the foraging ecology of nonbreeders. Although it is conceivable that the most contaminated individuals were not functionally able to breed (Tartu et al. 2013), this was not supported by our MSMR analysis.

Long-term fitness consequences of Hg exposure

In the two skua species, adult survival rates of breeders were high and similar to those previously estimated for South Polar Skuas (89–96%; Ainley et al. 1990, Pietz and Parmelee 1993) and for Great Skuas (82–93%; Ratcliffe et al. 2002). Breeding probability was low in individuals previously observed as nonbreeders (37–60%) and high in breeders (~86%), as previously estimated (72–100% for mature South Polar Skuas;

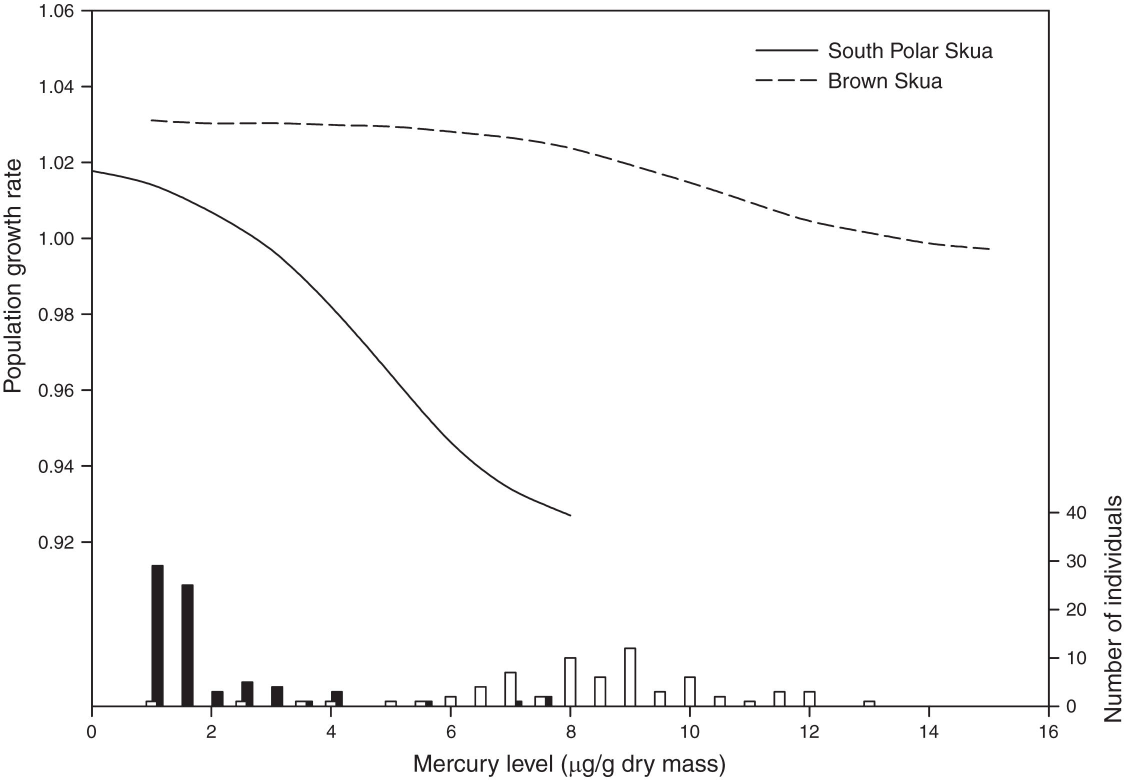

FIG. 5. Modeled population-level growth rate responses (curves) to an increase in mean Hg levels in South Polar Skuas and Brown Skuas. Histograms of the observed range of Hg levels in the sampled individuals (right axis) are given for South Polar Skuas (black bars) and for Brown Skusa (open bars).

Ainley et al. 1990). The probability of breeding successfully was higher in Brown Skuas (83.8%) than in South Polar Skuas (73.5%). The probability of successfully raising two chicks was low in the two skua species (~28%). Although experienced seabirds are known to breed more frequently than inexperienced ones (Desprez et al. 2011), we did not detect any strong effect of previous breeding experience on breeding parameters. This could be due to our relatively low sample size and/or to an effect of experience being restricted to the first reproductive attempts (Nevoux et al. 2007).

According to life history theory, environmental stressors should have the strongest effects on life history traits with the lowest sensitivity, e.g., traits with the lowest importance for population growth (Gaillard et al. 2000, Forbes et al. 2010). In long-lived species, adult survival rate has the highest elasticity and should be the least affected by environmental stressors, whereas breeding success has the lowest elasticity and should be the most sensitive to stressors (Gaillard et al. 2000, Gaillard and Yoccoz 2003), including toxic chemicals (Forbes et al. 2010). Our results partly supported this theoretical framework, because Hg burden did not jeopardize adult survival in the two skua species (which had the highest elasticity by far), thereby corroborating previous studies (Thompson et al. 1991, Mitro et al. 2008, Wayland et al. 2008, Hallinger et al. 2011). Moreover, the probability of remaining a breeder in the following year was not affected by Hg levels. In contrast, high Hg levels induced detrimental effects on the probability of successfully fledgling one or two chicks in the following year. The probability of successfully fledgling at least one chick had a higher elasticity than the probability of raising two chicks. This Hg-induced breeding failure was previously demonstrated in the current breeding attempt (Brasso and Cristol 2008, Burgess and Meyer 2008, Frederick and Jayasena 2010, Jackson et al. 2011), but not in the following year.

Although Brown Skuas exhibited much higher Hg levels than South Polar Skuas, Hg-induced effects in the following year were much stronger in the South Polar Skua and were only detected in male Brown Skuas. This study clearly highlights that closely related species did not respond similarly to toxic chemicals under natural conditions. This species difference could be attributed to environmental conditions, such as harsh weather, food availability, and/or the interaction with others pollutants. All of these environmental fluctuations may exacerbate or attenuate the Hg-induced effects on breeding success. Testing the combined effects of multiple stressors on survival and lifetime breeding performances is a challenging task that would require very large data sets.

PLATE 1. South Polar Skua *Catharacta maccormicki* displaying, Pointe Géologie Archipelago, Adélie Land, Antarctica. This individual is ringed with a stainless steel band and a plastic band engraved with unique alphanumeric code (H24). Photo credit: A. Goutte.

Hg and population growth rate

Anthropogenic Hg emissions are expected to rise worldwide in the next decades (Streets et al. 2009), probably resulting in growing Hg accumulation in Antarctic top predators. Our population models predicted that an increase of 1 μg/g dry mass in mean Hg levels would slightly decelerate the population growth rate of 1.51% in the South Polar Skua and 0.46% in the Brown Skua. An Hg increase of 0.6 μg/g dry mass in the South Polar Skua and of 3.8 μg/g dry mass in the Brown Skua would be enough to cause population declines. Hence, the South Polar Skua from Adélie Land appears to be more exposed to population decline in response to Hg contamination than is the Brown Skua from Kerguelen Island. These predictions could undoubtedly be worsened by other environmental perturbations. For instance, climate change is known to affect Hg distribution and exposure in polar ecosystems (Stern et al. 2012), and to trigger steep population declines in seabirds (Frederiksen et al. 2004, Jenouvrier et al. 2009, Barbraud et al. 2011). An additional harmful factor is the high levels of persistent organic pollutants (POPs: PCBs, pesticides) found in South Polar Skuas (Bustnes et al. 2007). In Glaucous Gulls *Larus hyperboreus*, the local survival rate was negatively affect by organochlorines and was only apparent among individuals with the highest levels of contamination (Erikstad et al. 2013). Hence, we urge future population modeling to take into account the coupled effects of climate change and anthropogenic pollution (heavy metal and POPs) to predict population-level responses to a wider range of environmental perturbations.

Translating individual-level effects of toxic chemicals to population-level processes is a crucial and ultimate goal of modern ecological research. By using recent and robust methodological approaches and long-term data sets, we showed a negative effect of Hg on breeding success in the following year in free-living top predators. An increase of Hg levels may result in a slight demographic decline, as highlighted by matrix population models.

ACKNOWLEDGMENTS

This project was supported by the French Polar Institute (IPEV, program 109, H. Weimerskirch), Agence Nationale de la Recherche (ANR PolarTop, O. Chastel), Terres Australes et Antarctiques Françaises, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE). Field procedures and blood sampling were authorized by the Ethics Committee of IPEV and by the Comité de l'Environnement Polaire. The authors thank G. Bouteloup, R. Bernard, F. Angelier, B. Moe, and all the wintering field-workers involved in the long-term monitoring programs for their help on the field, and D. Besson for managing the long-term data base.

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Supplemental Material

Appendix

Table presenting the effects of time and state on detection probability (p), and of state on the probabilities of survival (S), breeding (β), breeding successfully (γ), and successfully raising two chicks (δ) in South Polar Skuas and Brown Skuas (*Ecological Archives* E095-091-A1).