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Author for correspondence:

Aurélie Goutte

e-mail: agoutte@gmail.com

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Demographic consequences of heavy metals and persistent organic pollutants in a vulnerable long-lived bird, the wandering albatross

Aurélie Goutte^{1,2}, Christophe Barbraud¹, Alizée Meillère¹, Alice Carravieri¹, Paco Bustamante², Pierre Labadie³, Hélène Budzinski³, Karine Delord¹, Yves Cherel¹, Henri Weimerskirch¹ and Olivier Chastel¹

¹Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372, CNRS-Université de La Rochelle, Villiers-en-Bois 79360, France

²Littoral Environnement et Sociétés (LIENSs), UMR 7266, CNRS-Université de La Rochelle, 2 rue Olympe de Gouges, La Rochelle 17000, France

³UMR 5805 EPOC-LPTC, Université Bordeaux, 351 Cours de la Libération, Talence Cedex 33405, France

Seabirds are top predators of the marine environment that accumulate contaminants over a long life-span. Chronic exposure to pollutants is thought to compromise survival rate and long-term reproductive outputs in these long-lived organisms, thus inducing population decline. However, the demographic consequences of contaminant exposure are largely theoretical because of the dearth of long-term datasets. This study aims to test whether adult survival rate, return to the colony and long-term breeding performance were related to blood mercury (Hg), cadmium (Cd) and persistent organic pollutants (POPs), by using a capture–mark–recapture dataset on the vulnerable wandering albatross *Diomedea exulans*. We did not find evidence for any effect of contaminants on adult survival probability. However, blood Hg and POPs negatively impacted long-term breeding probability, hatching and fledging probabilities. The proximate mechanisms underlying these deleterious effects are likely multifaceted, through physiological perturbations and interactions with reproductive costs. Using matrix population models, we projected a demographic decline in response to an increase in Hg or POPs concentrations. This decline in population growth rate could be exacerbated by other anthropogenic perturbations, such as climate change, disease and fishery bycatch. This study gives a new dimension to the overall picture of environmental threats to wildlife populations.

1. Introduction

Free-living animal populations are affected by a wide range of anthropogenic pressures. Chronic exposure to metallic and organic pollutants may compromise survival and long-term fecundity, thereby leading to population decline. For instance, mercury (Hg) is a globally distributed heavy metal of particular concern for aquatic biota, because of the harmful effects of its organic form (methyl-Hg) on embryo development, neurology, immune system, physiology and behaviour [1–3]. Another ubiquitous heavy metal, cadmium (Cd), causes irreversible renal tubular damage, leading to reduced skeletal calcium content [4]. Persistent organic pollutants (POPs), such as organochlorine pesticides (HCB, HCH, DDE, DDD and DDT), polychlorinated biphenyls (PCBs) and brominated diphenyl ethers (BDEs), can persist in the environment for decades and trigger a suite of detrimental effects in vertebrates, including endocrine disruption, immunotoxicity, embryo mortality and behavioural impairments [5–7].

Although toxic effects of heavy metals and POPs have been well described at the individual level and under controlled laboratory conditions, their population-level effects have been virtually neglected in free-living vertebrates because of the

dearth of long-term datasets. In aquatic birds, there is no evidence of an impact of heavy metals on adult mortality [8,9]. In two *Catharacta skua* species, breeding failure in the following year, but not adult survival rate, was positively related to Hg exposure [10], as highlighted by the use of long-term datasets and multi-state mark–recapture models (MSMR [11]). Concerning POPs, very high concentrations of organochlorine compounds were related to increased mortality in the glaucous gull *Larus hyperboreus* [12], but their effects on long-term fecundity were not explored in that study.

The present study aimed to relate demographic parameters to pollutants in wandering albatrosses *Diomedea exulans*. The effects of Hg and Cd in red blood cells and Σ POPs in plasma on apparent probabilities of adult survival, return to the breeding colony, breeding, hatching and fledgling, were investigated by using a MSMR approach. According to recent studies on long-lived seabirds [10,12], a deleterious effect of Hg was expected on long-term breeding performances and a possible lethal effect of POPs was expected in the most contaminated wandering albatrosses. Then, population-level responses to an increase in Hg and POPs levels were assessed by establishing a life cycle for the wandering albatross and by including Hg- or POP-dependent demographic traits in the matrix population models [13].

Despite high pollution burdens in albatrosses [14–16], the effects of contaminants on demographic parameters and population growth rate are unknown. Albatrosses are among the most highly endangered of the world's birds, with 18 of 22 species considered as threatened and the remaining four species considered as near threatened [17]. In this population of wandering albatrosses, population growth rate remained relatively stable during the 1960s (about 850 breeding pairs), before a first decline between the early 1970s and 1986, and a second decline since 2003 down to 380 breeding pairs [18]. Causes of decline in albatross populations have been attributed to fishery bycatch, climate change and disease [19]. This study thus gives a new dimension to the overall picture of environmental threats in albatross populations.

2. Material and methods

(a) Study area and species

The study was conducted at Ile de la Possession in the Crozet Archipelago (46° S, 52° E), Southern Indian Ocean, where 300–400 pairs of wandering albatrosses nest each year. Adults return to their breeding grounds in December and females lay a single egg in late December–early January. Both parents incubate alternately until hatching in March and most young are fledged in November. Up to 6% of the birds that fledged a chick bred again in the following year, and the wandering albatross is considered to be a quasi-biennial breeding species [20]. Approximately 80% of birds that failed to breed in the previous year engage in another breeding attempt in the following year. All wandering albatrosses had been ringed and sexed as part of a long-term mark–recapture programme [21]. In December, pre-breeding adults are controlled over the whole island. From mid-January to mid-February, at least three visits are carried out every 10 days at each nest to determine the identity and breeding status (egg laid/egg hatched) of each individual. In mid-April, June and August, all nests are checked to monitor the chicks' survival.

(b) Blood sampling

From 21 December 2007 to 04 March 2008, 147 sexually mature adults (i.e. observed as incubating or chick-rearing at least once before or during the current breeding season) were captured.

A sample of venous blood was taken from the tarsus with a 1-ml heparinized syringe and a 25-gauge needle. Only one bird was sampled per nest. The volume of the blood draws never exceeded 0.05% of the bird's body mass (8–12 kg).

(c) Laboratory analyses

Hg and Cd were analysed in red blood cells at the Littoral Environnement et Sociétés (LIENSs), La Rochelle, France. POPs (PCBs: CB-28, -52, -101, -118, -138, -153 and -180; organochlorine pesticides: HCB (hexachlorobenzene), Gamma HCH (hexachlorocyclohexane), Heptachlore, 2,4' DDE (dichlorodiphenyldichloroethylene), Cis-chlordane, trans-nonachlor, 4,4' DDD (dichlorodiphenyldichloroethane), 2,4' DDT (dichlorodiphenyltrichloroethane), 4,4' DDT, Mirex; and BDE-47) were analysed in plasma at the EPOC-LPTC, Bordeaux, France. Further details about analyses are reported in the electronic supplementary material.

(d) Estimating the effects of blood heavy metals and persistent organic pollutants on breeding output during the year of sampling

Generalized linear models (GLMs) with binomial error distribution and a logit link function were used to test whether breeding success in 2007–2008 was linked to blood Hg, Cd or POP levels in individuals sampled as breeders in 2007–2008. Breeding success was coded as 1 for birds that successfully fledged a chick, and as 0 for those that failed at the egg or chick stage. Analyses were performed using R [22].

(e) Estimating the effects of blood heavy metals and persistent organic pollutants on demographic parameters

The capture–recapture data of sampled individuals from 2008 to 2012 were used to evaluate the effects of blood Hg, Cd and POPs on demographic parameters.¹ A MSMR model was constructed, as developed by Pardo *et al.* [23,24], and included eight states: dead, failed breeder on egg (FBE, defined as an individual that was observed with one egg that failed to hatch), failed breeder on chick (FBC, defined as an individual that was observed with one chick but that failed to fledge the chick), successful breeder (SB, defined as an individual that fledged one chick), observable non-breeder (ONB, defined as an individual that was observed at the colony but that was not observed with an egg or a chick) and three unobservable states (UNB) consisting of non-breeders that were observed at the colony during the previous breeding attempt (PONB), non-breeders whose previous breeding attempt failed (PFB) and non-breeders whose previous breeding attempt was successful (PSB). The state coded as 'dead' (†) absorbed all those individuals that had either died or permanently emigrated from the study areas. The UNBs account for temporary absence, corresponding to birds that skip breeding in one year after breeding unsuccessfully or successfully during the previous year.

Models were parametrized in terms of the probability of survival (s), the probability of returning to the colony given survival (r), the probability of breeding given return to the colony (β), the probability of successful hatching given breeding (ω), the probability of successful fledgling given hatching (γ) and the detection probability (p). Transition probabilities between states were thus modelled with a five-step procedure where s , r , β , ω and γ were considered as five successive steps in transition matrices. Parameters of the model are defined in the electronic

supplementary material. We chose a MSMR approach as this allows us to take into account the probability of detecting individuals given their return to the study site, as well as the

previous breeding state of individuals in order to obtain unbiased estimates of demographic parameters [11].

This MSMR model was parametrized by the survival-transition probabilities matrix

	FBE	FBC	SB	ONB	PFB	PSB	PONB	†
FBE	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	$s(1-r)$	---	---	*
FBC	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	$s(1-r)$	---	---	*
SB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	$s(1-r)$	---	*
ONB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	---	$s(1-r)$	*
PFB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	---	---	*
PSB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	---	---	*
PONB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	---	---	*
†	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	---	---	---	*

Several constraints were made to ensure that the parameters of the model were estimable. The state 'dead' being explicitly included in the model but never being encountered, initial state probability was fixed at 0, transition probabilities from the state 'dead' to the other states were fixed at 0 and capture probability was fixed at 0 [25,26]. The probability of seeing individuals in UNBs and transitions between UNBs was constrained to 0. Since some individuals were observed breeding in the year consecutive to a successful breeding event [20], β_{SB} was not constrained to 0. To limit redundancy in survival parameters, models where survival probabilities all varied separately were not considered [27]. Because of the limited number of individual capture histories, the limited number of recapture occasions and the relatively large number of UNBs, we constrained (i) all parameters to be constant over time, (ii) r to be identical for ONB, PFB, PSB and PONB and (iii) β to be identical for PFB, PSB and PONB. With these constraints, the initial model was full-rank. Note that the model where all demographic parameters were time- and state-dependent was highly rank deficient.

Once the best model structure was identified (Model 21, electronic supplementary material), effects of blood Hg, Cd and POPs were tested on demographic parameters to investigate whether contamination levels in one breeding season may influence the long-term survival and breeding outputs of an individual over the four following years. MSMR models were built where each demographic parameter θ was modelled as a function of an individual covariate C (standardized level of Hg, Cd or sum of POPs (log-transformed)) using a logit link function: $\text{logit}(\theta) = a + b \times C_i$, where a is an intercept, b is a slope and C_i is the covariate for individual i . When $b < 0$, or $b > 0$, C has a negative or positive effect on θ , respectively.

The effect of C was first tested on each demographic parameter separately and for different states. Because some parameters were estimated as 100% [100–100%] (electronic supplementary material), we did not test the effects of C on the return probability of males previously observed as (FBE and FBC) or as (ONB, PFB, PSB and PONB), and on the breeding probability of unobservable non-breeders. The 95% confidence interval (CI) of the slope parameters was used, as well as Akaike's information criterion corrected (AICc) for small sample size [28] for inference. We considered a contaminant's effect to be statistically supported when 0 was outside the 95% CI of the mean of the slope of the relationship [29]. A composite model was then constructed by combining all the covariates that were detected to have an effect on demographic parameters. Composite models were constructed for heavy metals and POPs separately, as sample sizes differed. In composite models, an effect was not supported if the 95% CI of the slope parameter included 0 [29].

We tested the goodness-of-fit (GOF) of the time-dependent MSMR model using U-CARE [30]. All models were run under program E-SURGE 1.8.5 allowing splitting transition probabilities

between states [26]. To avoid estimating parameters at a local minimum of the likelihood function, each model was run five times with random initial values.

(f) Modelling population dynamics

To evaluate the population-level effects of contaminants, we constructed population models using pre-breeding matrices [13] structured by age and reproductive status classes. We built a two-sex age- and stage-classified matrix population model [13], because Hg and POPs concentrations affected the demographic parameters of males and females differently (see §3). Based on a detailed demographic study on wandering albatrosses [31], the model consists of five juvenile age classes, one pre-breeder class and seven stage-classes according to the breeding status (SB, FBE, FBC, ONB, PSB, PFB and PONB). Parameters entering the model were the recruitment probability, s of adult males, females and juveniles, r of SB and other states, β of SB, FB, ONB and UNB for males and females separately, ω and γ of breeders and non-breeders. We assumed a 1:1 sex ratio.

We first built a deterministic matrix model with no stochasticity, which included the mean estimates of the demographic parameters from our MSMR model results and from Barbraud *et al.* [31] for juvenile survival and recruitment probability. From these matrix analyses, we estimated the deterministic population growth rate [13]. We then focused on stochastic matrix models to estimate the stochastic growth rate. Environmental stochasticity was included in two different ways. When a vital rate had no significant relationship with levels of contaminant (C), its yearly values were sampled from a beta distribution [32], with mean and variance equal to those estimated from the MSMR model selected. When a vital rate had a significant relationship with C levels, its value was modelled as $\theta = \text{logit}^{-1}(a + b \times \bar{C})$, where \bar{C} is the mean value of the contaminant levels for all individuals. C values were sampled from a log-normal distribution for all individuals sampled. The values of a and b were recalculated for non-standardized C values representing the absolute values for Hg and log-transformed values for Σ POPs. To assess the population-level effects of C , we estimated stochastic population growth rates according to changes in mean C levels within the range of observed C values. The matrix population models were analysed by Monte Carlo simulations (10 000 iterations) using package popbio [33] implemented in R [22].

3. Results

(a) Effects of blood heavy metal and persistent organic pollutants on current breeding output

Blood levels of contaminants are given in the electronic supplementary material. When considering only breeders in 2008,

Table 1. Modelling the effects of standardized blood heavy metals levels (*a*, Hg; *b*, Cd; and *c*, composite model) on demographic parameters ($N = 147$ individuals). The estimated slope and 95% CIs for models with a lower AICc than the intercept model (Hg0 and Cd0) are given.

hypothesis	model	rank	deviance	Δ AICc	slope (CI−; CI+)
<i>(a) effect of blood Hg on demographic parameters</i>					
breeding probability of females previously in state ONB	Hg10	24	1442.026	0	−2.141 (−4.267; −0.014)
hatching probability of individuals previously in states FB or SB	Hg3	24	1444.431	2.405	−0.659 (−1.271; −0.047)
fledging probability of individuals previously in states FB or SB	Hg1	24	1444.560	2.533	−0.844 (−1.659; −0.029)
breeding probability of males previously in states FBE or FBC	Hg5	24	1446.133	4.107	1.569 (−0.307; 3.445)
intercept model: no effect	Hg0	23	1449.217	4.946	
breeding probability of females previously in states FBE or FBC	Hg6	24	1448.236	6.210	
breeding probability of females previously in state SB	Hg8	24	1448.881	6.854	
return probability of individuals previously in state SB	Hg12	24	1448.955	6.929	
hatching probability of individuals previously in states ONB or UNB	Hg4	24	1449.035	7.009	
breeding probability of males previously in state SB	Hg7	24	1449.159	7.133	
fledging probability of individuals previously in states ONB or UNB	Hg2	24	1449.208	7.182	
survival rate of females	Hg14	24	1449.209	7.183	
breeding probability of males previously in state ONB	Hg9	24	1449.215	7.189	
survival rate of males	Hg13	24	1449.216	7.190	
breeding probability of females previously in states PFB, PSB or PONB	Hg11	24	1449.217	7.191	
<i>(b) effect of blood Cd on demographic parameters</i>					
return probability of individuals previously in state SB	Cd12	24	1445.909	0	−0.350 (−0.758; 0.058)
hatching probability of individuals previously in states ONB or UNB	Cd4	24	1446.645	0.735	0.520 (−0.204; 1.243)
intercept model: no effect	Cd0	23	1449.217	1.063	
fledging probability of individuals previously in states ONB or UNB	Cd2	24	1447.314	1.405	
breeding probability of females previously in state ONB	Cd10	24	1447.905	1.996	
breeding probability of females previously in state SB	Cd8	24	1448.247	2.338	
breeding probability of females previously in states FBE or FBC	Cd6	24	1448.730	2.820	
hatching probability of individuals previously in states FB or SB	Cd3	24	1448.744	2.835	
survival rate of females	Cd14	24	1448.794	2.885	
survival rate of males	Cd13	24	1449.048	3.139	
probability of males previously in states FBE or FBC	Cd5	24	1449.054	3.145	
fledging probability of individuals previously in states FB or SB	Cd1	24	1449.129	3.220	
breeding probability of males previously in state SB	Cd7	24	1449.159	3.250	
breeding probability of males previously in state ONB	Cd9	24	1449.215	3.306	
breeding probability of females previously in states PFB, PSB or PONB	Cd11	24	1449.217	3.307	
<i>(c) effect of blood heavy metals on demographic parameters</i>					
composite model (Hg10, Hg3, Hg1)	Hg15	26	1433.319	0	(cf. S3(b))
intercept model: no effect	Hg0	23	1449.217	9.131	

current breeding success was not related to Hg (d.f. = 1,105, $\chi^2 = 0.126$, $p = 0.723$), Cd (d.f. = 1,105, $\chi^2 = 0.008$, $p = 0.929$) or Σ POPs concentrations (d.f. = 1,81, $\chi^2 < 0.001$, $p = 0.993$).

(b) Demographic consequences of blood heavy metal levels

The GOF of the MSMR model was overall not significant (males: $\chi^2 = 16.327$, d.f. = 22, $p = 0.799$ and females: $\chi^2 = 7.078$, d.f. = 16, $p = 0.972$). The effects of sex and states on demographic parameters and the estimation of parameters are detailed in the electronic supplementary material.

Model selection and slope estimates suggested negative effects of Hg on the breeding probability of females previously in state ONB, and on hatching probability and fledging probability of individuals previously in states FB and SB (table 1*a*). There was no detectable effect of Cd on demographic parameters (table 1*b*). Slope estimates obtained from the composite model (table 1*c*) were −2.114 (95% CI: (−4.213; −0.015)), −0.620 (−1.234; −0.005) and −0.807 (−1.645; 0.032) for the effects of Hg on breeding probability of females previously in state ONB (figure 1*a,c*), hatching probability of individuals previously in states FB and SB (figure 1*b,c*) and fledging probability of individuals previously in states FB

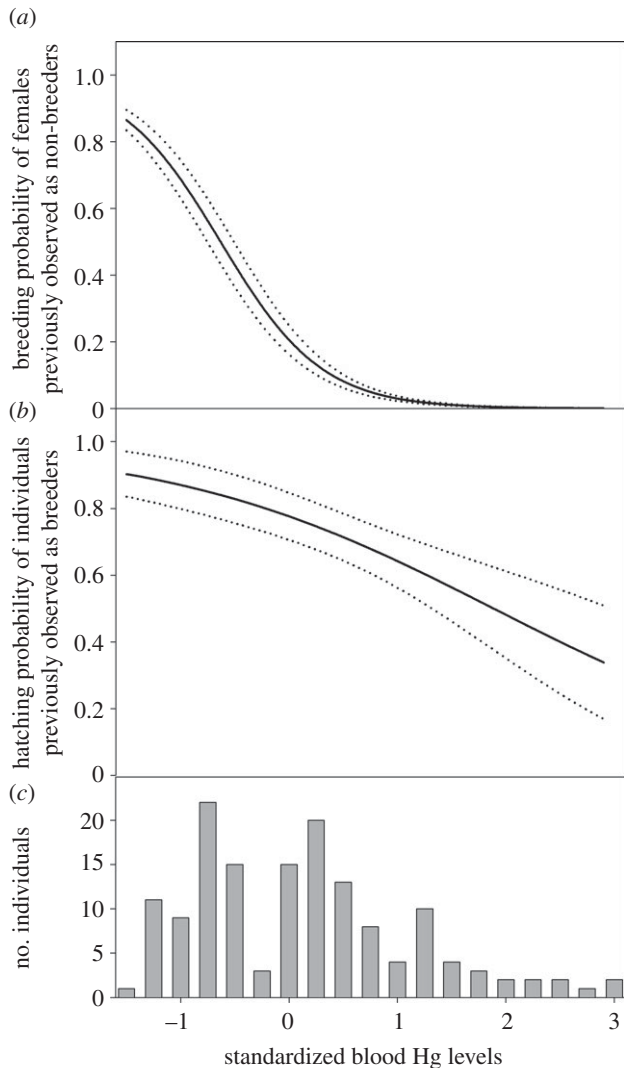


Figure 1. Effect of standardized blood Hg levels on (a) breeding probability of females previously observable as non-breeders (ONB), and (b) hatching probability of individuals previously observed as breeders. Dotted lines represent 95% CIs estimated using the delta method [34]. Histograms represent the measured blood Hg levels (c).

and SB, respectively. The last effect was not supported, because 95% CI included 0 in the composite model.

(c) Demographic consequences of blood Σ POP levels

Model selection and slope estimates suggested a negative effect of Σ POPs on fledging probability of individuals previously in states ONB or UNB and on breeding probability of females previously in state ONB (table 2). Other models were not supported, because 95% CI of slope parameter values included 0 (table 2). Slope estimates obtained from the composite model were -0.976 (-1.917 ; -0.035) and -0.812 (-1.551 ; -0.072) for the effects of Σ POPs on breeding probability of females previously in state ONB (figure 2a,c) and on fledging probability of individuals previously in states ONB or UNB (figure 2b,c), respectively.

(d) Modelling population dynamics

The deterministic population growth rate was 1.038, and the respective generation time was 23.8. The stochastic population growth rates were 1.008 when accounting for mean Hg effects from MSMR analyses, 1.002 when accounting for mean POPs

effects and 0.991 when accounting for both mean Hg and POPs effects (figure 3). A doubling in mean Hg concentration would decelerate the population growth rate of 0.68%. A doubling in mean Σ POPs concentration would decelerate the population growth rate of 0.11%. Doublings in mean Hg and Σ POPs concentrations would decelerate the population growth rate of 1.31% (figure 3).

4. Discussion

Using a unique long-term dataset and MSMR models, this study explores the demographic effects of both metallic and organic pollutants in a wild vertebrate population. Contaminant levels were associated with a lower breeding probability, a higher hatching failure and a higher fledgling failure, but not with adult survival rate in the wandering albatross. At the population level, a demographic decline was projected in response to increasing Hg and Σ POP levels.

(a) Effects of contaminants on current breeding output

Contrary to previous studies [1,2,5,7], no negative effect of blood Hg, Cd and Σ POPs was detected on breeding success at the year of sampling. The lack of relationship is probably due to the sampling protocol, since blood sampling was mainly conducted during the incubating period. Some effect of contaminants on early nest desertion and skipped breeding [3] may have been missed.

(b) Survival and contaminants

Estimated demographic parameters were similar to those previously estimated in the same population using all ringed individuals [20,24]. The survival rate of wandering albatrosses was not jeopardized by Hg, Cd and POPs. An effect of POPs was detected on survival rate in one of the most polluted seabirds, the glaucous gull breeding in the Norwegian Arctic, but only the most contaminated individuals had lower survival [12]. Concerning heavy metals, these findings corroborate previous studies that did not evidence an effect of Hg and Cd on adult mortality in birds [8–10]. However, our study did not exclude the possibility that contaminants could jeopardize the survival rate of immature wandering albatrosses, as they have a higher pollution burden [16] and a lower survival rate [31] than sexually mature adults.

(c) Long-term fecundity and heavy metals

A negative effect of blood Hg was detected on breeding probability of females observed as non-breeders. Concerning the proximate mechanisms, Hg, in its methylated form, is known to disrupt reproductive hormones [1] such as the luteinizing hormone, a key pituitary hormone for the onset of breeding [3].

As found in two southern *Catharacta skua* species [10], Hg negatively impacted hatching probability of albatrosses, but only in individuals previously observed as breeders. Energetic and time-dependent costs of reproduction may have downstream consequences for reproductive investment during the following breeding season (carry-over effect [35]). Hence, Hg load may have exacerbated these carry-over effects in individuals that previously bred. Concerning the possible proximate mechanisms, Hg may have caused long-term endocrine disruption of the reproductive system and behavioural

Table 2. Modelling the effects of blood Σ POP levels (log-transformed and standardized) on demographic parameters ($N = 115$ individuals). The estimated slope and 95% CIs for models with a lower AICc than the intercept model (POP0) are given.

hypothesis	model	rank	deviance	Δ AICc	slope (CI-; CI+)
breeding probability of females previously in state SB	POP8	24	1129.266	0	2.763 (-0.205; 5.731)
composite model (POP2, POP10)	POP15	25	1127.642	0.716	(cf. S3(c))
fledging probability of individuals previously in states ONB or UNB	POP2	24	1130.764	1.498	-0.878 (-1.641; -0.114)
hatching probability of individuals previously in states ONB or UNB	POP4	24	1131.111	1.845	0.841 (-0.036; 1.719)
fledging probability of individuals previously in states FB and SB	POP1	24	1131.312	2.046	1.226 (-0.075; 2.527)
hatching probability of individuals previously in states FB and SB	POP3	24	1131.434	2.168	1.006 (-0.116; 2.127)
breeding probability of females previously in state ONB	POP10	24	1131.826	2.560	-0.964 (-1.870; -0.058)
intercept model: no effect	POP0	23	1135.079	3.488	
breeding probability of females previously in states PFB, PSB or PONB	POP11	24	1133.513	4.247	
breeding probability of males previously in state SB	POP7	24	1133.847	4.581	
breeding probability of males previously in states FBE or FBC	POP5	24	1134.095	4.829	
survival rate of males	POP13	24	1134.313	5.047	
breeding probability of females previously in states FBE or FBC	POP6	24	1134.808	5.542	
return rate of individuals previously in state SB	POP12	24	1135.034	5.768	
survival rate of females	POP14	24	1135.035	5.769	
breeding probability of males previously in state ONB	POP9	24	1135.093	5.827	

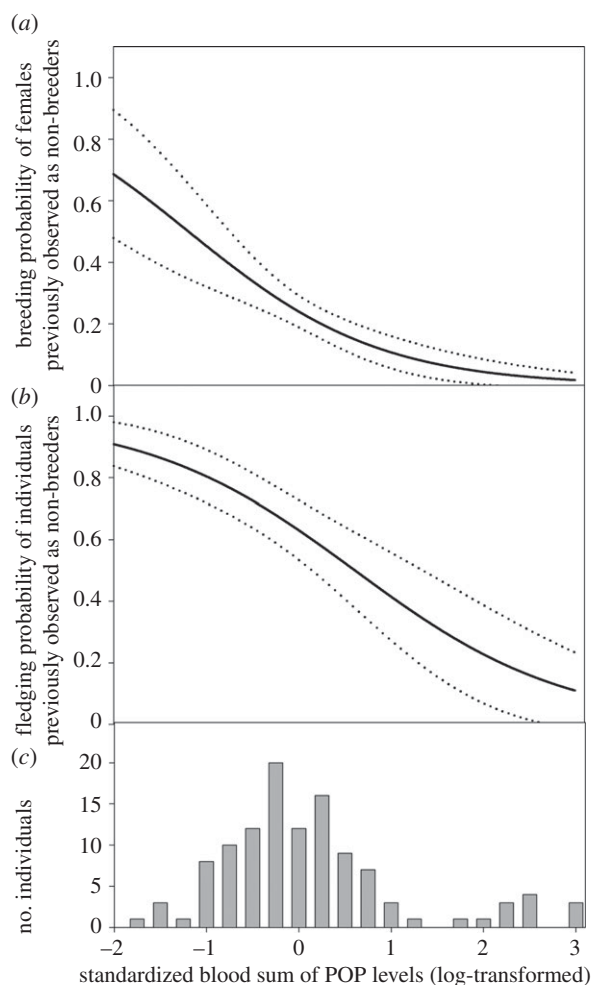


Figure 2. Effect of standardized blood Σ POPs (log-transformed) on (a) breeding probability of females previously observed as non-breeders, and (b) fledging probability of individuals previously observed as non-breeders or unobserved. Dotted lines represent 95% CIs estimated using the delta method [34]. Histograms represent the measured blood Σ POP levels (c).

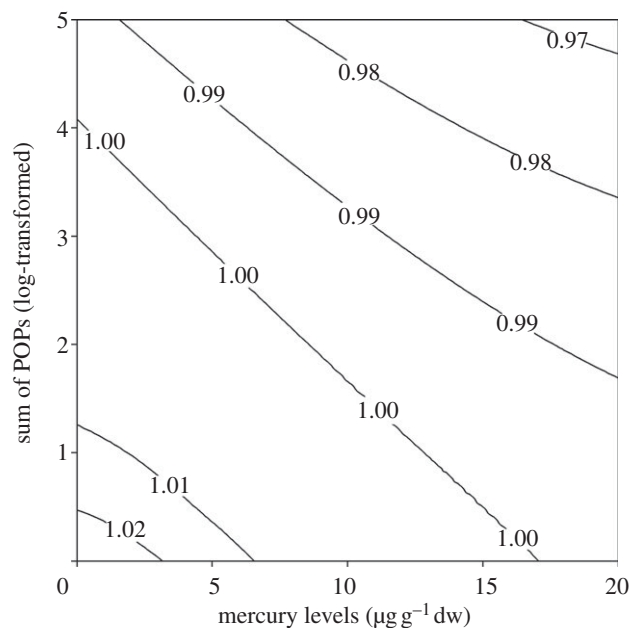


Figure 3. Isoclines of population growth rate in wandering albatrosses as projected with the population models, which included the responses to blood Hg levels and blood Σ POPs (log-transformed) within the range of observed Hg and Σ POP levels.

impairments [1,2]. In addition, the maternal transfer of Hg into the egg may have altered embryo development [36].

(d) Long-term fecundity and Σ POPs

POP burdens reduced the long-term breeding probability of females previously observed as non-breeders and fledging probability of individuals that were previously non-breeders. Interestingly, POPs appeared to mostly affect albatrosses that skipped the preceding breeding attempt, suggesting a possible

segregation of foraging areas between breeders and non-breeders. Alternatively, non-breeding females may suffer from higher deleterious effects of POPs on long-term fecundity, because their loads of POPs were not eliminated through the egg.

During the incubating and chick-rearing periods, POPs may weaken the secretion of prolactin, a hormone closely involved in the mediation of parental care, as shown in glaucous gulls [37]. In turn, a durable Hg-induced attenuation of prolactin release may result in fledgling failure.

The link between contaminants and reduced fecundity could be a by-product of age-dependant mechanisms. However, in this population, fecundity declined in the oldest individuals (35+ years old [24,38]), while Hg levels tended to decrease with age [16] and POP levels were unrelated to age (data not shown). Moreover, age (6–48+ years old) did not affect humoral immunity, oxidative stress, antioxidant defences or hormone levels in wandering albatrosses [38]. Hence, it is unlikely that age was a confounding factor in the correlation between contaminants and physiological mechanisms underlying breeding performance.

(e) Modelling population dynamics

Translating individual-level effects of contaminants to population-level processes is a crucial and ultimate goal of modern ecological research. Our population models suggested that the actual Hg and POPs levels could decelerate the population growth rate (0.991), whereas the population growth rate would increase (1.027) with zero concentrations of blood Hg and POPs. In addition, doublings in mean blood Hg and POPs levels would decelerate the growth rate of this wandering

albatross population by 1.31%. These predictions could undoubtedly be worsened by other anthropogenic perturbations. For instance, climate change can impact transport, distribution, bioavailability, bioaccumulation and effects of pollutants [39–41] and triggers steep population declines in albatrosses [19]. In that respect, a future avenue for ecotoxicological and conservation research could be dedicated to evaluating and predicting the coupled effects of climatic and chemical perturbations on wildlife population viability.

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Endnote

¹Dataset: demographic consequences of heavy metals and POPs in a vulnerable long-lived bird, the wandering albatross. Aurelie Goutte, Christophe Barbraud, Alizée Meillère, Alice Carravieri, Paco Bustamante, Pierre Labadie, Hélène Budzinski, Karine Delord, Yves Chereh, Henri Weimerskirch, Olivier Chastel. figshare (<http://dx.doi.org/10.6084/m9.figshare.947689>).

References

- Tan SW, Meiller JC, Mahaffey KR. 2009 The endocrine effects of mercury in humans and wildlife. *Crit. Rev. Toxicol.* **39**, 228–269. (doi:10.1080/10408440802233259)
- Frederick P, Jayasena N. 2010 Altered pairing behaviour and reproductive success in white ibises exposed to environmentally relevant concentrations of methylmercury. *Proc. R. Soc. B* **278**, 1851–1857. (doi:10.1098/rspb.2010.2189)
- Tartu S *et al.* 2013 To breed or not to breed: endocrine response to mercury contamination by an arctic seabird. *Biol. Lett.* **9**, 20130317. (doi:10.1098/rsbl.2013.0317)
- Larison JR, Likens GE, Fitzpatrick JW, Crock JG. 2000 Cadmium toxicity among wildlife in the Colorado Rocky Mountains. *Nature* **406**, 181–183. (doi:10.1038/35018068)
- Barron MG, Galbraith H, Beltman D. 1995 Comparative reproductive and developmental toxicology of PCBs in birds. *Comp. Biochem. Physiol.* **112**, 1–14. (doi:10.1016/0742-8413(95)00074-7)
- Vos JG, Dybing E, Greim HA, Ladefoged O, Lambré C, Tarazona JV, Brandt I, Vethaak AD. 2000 Health effects of endocrine-disrupting chemicals on wildlife, with special reference to the European situation. *Crit. Rev. Toxicol.* **30**, 71–133. (doi:10.1080/10408440091159176)
- Bustnes JO, Erikstad KE, Skaare JU, Bakken V, Mehlum F. 2003 Ecological effects of organochlorine pollutants in the Arctic: a study of the glaucous gull. *Ecol. Appl.* **13**, 504–515. (doi:10.1890/1051-0761(2003)013[0504:EEOPI]2.0.CO;2)
- Wayland M, Drake KL, Alisauskas RT, Kellett DK, Traylor J, Swoboda C, Mehl K. 2008 Survival rates and blood metal concentrations in two species of free-ranging North American sea ducks. *Environ. Toxicol. Chem.* **27**, 698–704. (doi:10.1897/07-321.1)
- Hallinger KK, Cornell KL, Brasso RL, Cristol DA. 2011 Mercury exposure and survival in free-living tree swallows (*Tachycineta bicolor*). *Ecotoxicology* **20**, 39–46. (doi:10.1007/s10646-010-0554-4)
- Goutte A, Bustamante P, Barbraud C, Delord K, Weimerskirch H, Chastel O. 2014 Demographic responses to mercury exposure in two closely-related Antarctic top predators. *Ecology* **95**, 1075–1086. (doi:10.1890/13-1229.1)
- Lebreton J-D, Pradel R. 2002 Multistate recapture models: modelling incomplete individual histories. *J. Appl. Stat.* **29**, 353–369. (doi:10.1080/02664760120108638)
- Erikstad KE, Sandvik H, Reiertsen TK, Bustnes JO, Strøm H. 2013 Persistent organic pollution in a high-Arctic top predator: sex-dependent thresholds in adult survival. *Proc. R. Soc. B* **280**, 20131483. (doi:10.1098/rspb.2013.1483)
- Caswell H. 2001 *Matrix population models: constructions, analysis and interpretation*, 2nd edn. Sunderland, MA: Sinauer Associates.
- Finkelstein M, Keitt BS, Croll DA, Tershy B, Jarman WM, Rodriguez-Pastor S, Anderson DJ, Sievert PR, Smith DR. 2006 Albatross species demonstrate regional differences in North Pacific marine contamination. *Ecol. Appl.* **16**, 678–686. (doi:10.1890/1051-0761(2006)016[0678:ASDRD]2.0.CO;2)
- Anderson ORJ, Phillips RA, Shore RF, McGill RAR, McDonald RA, Bearhop S. 2010 Element patterns in albatrosses and petrels: influence of trophic position, foraging range and prey type. *Environ. Pollut.* **158**, 98–107. (doi:10.1016/j.envpol.2009.07.040)
- Tavares S, Xavier JC, Phillips RA, Pereira ME, Pardo MA. 2013 Influence of age, sex and breeding status on mercury accumulation patterns in the wandering albatross *Diomedea exulans*. *Environ. Pollut.* **181**, 315–320. (doi:10.1016/j.envpol.2013.06.032)
- IUCN (2009). 2009 *IUCN Red List of threatened species*. See <http://www.iucnredlist.org>.
- Delord K, Besson D, Barbraud C, Weimerskirch H. 2008 Population trends in a community of large Procellariiforms of Indian Ocean: potential effects of environment and fisheries interactions. *Biol.*

- Conserv.* **141**, 1840–1856. (doi:10.1016/j.biocon.2008.05.001)
19. Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H. 2012 Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Mar. Ecol. Prog. Ser.* **454**, 285–307. (doi:10.3354/meps09616)
 20. Barbraud C, Weimerskirch H. 2012 Estimating survival and reproduction in a quasi-biennially breeding seabird with uncertain and unobservable states. *J. Ornithol.* **152**, 605–615. (doi:10.1007/s10336-011-0686-1)
 21. Weimerskirch H, Brothers N, Jouventin P. 1997 Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biol. Conserv.* **79**, 257–270. (doi:10.1016/S0006-3207(96)00084-5)
 22. R Core Team., and 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org/>.
 23. Pardo D, Weimerskirch H, Barbraud C. 2013 When celibacy matters: incorporating non-breeders improves demographic parameter estimates. *PLoS ONE* **8**, e60389. (doi:10.1371/journal.pone.0060389)
 24. Pardo D, Weimerskirch H, Barbraud C. 2013 Females better face senescence in the wandering albatross. *Oecologia* **173**, 1283–1294. (doi:10.1007/s00442-013-2704-x)
 25. Pradel R. 2005 Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* **61**, 442–447. (doi:10.1111/j.1541-0420.2005.00318.x)
 26. Choquet R, Rouan L, Pradel R. 2009 Program E-SURGE: a software application for fitting multievent models. In *Modeling demographic processes in marked populations* (eds DL Thomson, EG Cooch, MJ Conroy), pp. 845–865. New York, NY: Springer.
 27. Hunter CM, Caswell H. 2009 Rank and redundancy of multistate mark-recapture models for seabird populations with unobservable states. In *Modeling demographic processes in marked populations* (eds DL Thomson, EG Cooch, MJ Conroy), pp. 797–825. New York, NY: Springer.
 28. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
 29. Grosbois V, Gimenez O, Gaillard J-M, Pradel R, Barbraud C, Clobert J, Møller AP, Weimerskirch H. 2008 Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* **83**, 357–399. (doi:10.1111/j.1469-185X.2008.00047.x)
 30. Choquet R, Lebreton J-D, Gimenez O, Reboulet AM, Pradel R. 2009 U-CARE: utilities for performing goodness of fit tests and manipulating capture–recapture data. *Ecography* **32**, 1071–1074. (doi:10.1111/j.1600-0587.2009.05968.x)
 31. Barbraud C, Tuck GN, Thomson R, Delord K, Weimerskirch H. 2013 Fisheries bycatch as an inadvertent human-induced evolutionary mechanism. *PLoS ONE* **8**, e60353. (doi:10.1371/journal.pone.0060353)
 32. Morris WF, Doak DF. 2002 *Quantitative conservation biology: the theory and practice of population viability analysis*. Sunderland, MA: Sinauer Associates.
 33. Stubbén C, Milligan B. 2007 Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.* **22**, 1–23. See <http://www.jstatsoft.org/v22/i11/paper>.
 34. Seber GAF. 1982 *The estimation of animal abundance and related parameters*. New York, NY: MacMillan.
 35. Catry P, Dias MP, Anthony Phillips R, Granadeiro J. 2013 Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* **94**, 1230–1235. (doi:10.1890/12-2177.1)
 36. Kenow KP, Meyer MW, Rossmann R, Gendron-Fitzpatrick A, Gray BR. 2011 Effects of injected methylmercury on the hatching of common loon (*Gavia immer*) eggs. *Ecotoxicology* **20**, 1684–1693. (doi:10.1007/s10646-011-0743-9)
 37. Verreault J, Verboven N, Gabrielsen GW, Letcher RJ, Chastel O. 2008 Changes in prolactin in a highly organohalogen contaminated Arctic top predator seabird, the glaucous gull. *Gen. Comp. Endocrinol.* **156**, 569–576. (doi:10.1016/j.yggen.2008.02.013)
 38. Lecomte VJ *et al.* 2010 Patterns of aging in the long-lived wandering albatross. *Proc. Natl Acad. Sci. USA* **107**, 6370–6375. (doi:10.1073/pnas.0911181107)
 39. Noyes PD, McElwee MK, Miller HD, Clark BW, Van Tiem LA, Walcott KC, Erwin KN, Levin ED. 2009 The toxicology of climate change: environmental contaminants in a warming world. *Environ. Int.* **35**, 971–986. (doi:10.1016/j.envint.2009.02.006)
 40. Stern GA *et al.* 2012 How does climate change influence arctic mercury? *Sci. Total Environ.* **414**, 22–42. (doi:10.1016/j.scitotenv.2011.10.039)
 41. Cossa D. 2013 Marine biogeochemistry: methylmercury manufacture. *Nat. Geosci.* **6**, 810–811. (doi:10.1038/ngeo1967)