No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation

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Abstract

Seabirds are one of the most threatened of all bird groups, with a marked community-wide decline across the last decades. Yet, some seabird species are more resilient than others, and it is essential to study under which conditions even these highly resilient organisms are affected by global changes. Using global location sensors (GLS), demographic and stable isotope analyses, we performed a long-term study of the migration biology and inter-annual survival of northern gannets (*Morus bassanus*) breeding on Rouzic Island in Brittany, France. Across 2006-2015, our analyses showed that the birds spent the inter-breeding period off Western Europe, in the Mediterranean or off West Africa. There were no inter-annual trends in the use of these different areas, but isotopic analyses suggested food competition between gannets and industrial-scale fisheries. Crucially, we found a precipitous decline in the return rates of birds equipped with GLS, from 90% in 2006-2007 to less than 10% after 2015. This decline was consistent with a marked decrease in inter-annual survival probabilities for ringed adult gannets, from >90% in 2014-2015 to <60% in 2018-2019, and with a population decline of the Rouzic gannet breeding colony in recent years. Strong ecological signals provided by northern gannets point to critical marine ecosystem perturbation in the Eastern Atlantic, and the decline of this resilient and emblematic species should lead to the urgently needed transformation of marine policies.

Keywords: Bycatch, CMR, GLS, Marine conservation, Marine predator, Overfishing, Population dynamics, Stable isotope analysis, West Africa

Introduction

Seabirds are, together with parrots, the most threatened of all bird groups, with marked community-level population decline across the second half of the 20th century **(Paleczny et al. 2015)**. The main reasons for this downward trend are predation by invasive species on islands, bycatch on fishing gear and the consequences of climate change **(Dias et al. 2019)**. A recent analysis also showed persisting worldwide food competition between seabirds and fisheries **(Grémillet et al. 2018)**. Specific seabird groups are far more affected than others, with albatrosses, petrels, penguins and terns being particularly vulnerable **(Dias et al. 2019)**. At the other end of the spectrum, some seabird species are notoriously resilient, with overall population sizes showing positive trends even in highly anthropized marine areas. This is very much the case for northern gannets (*Morus bassanus,* hereafter 'gannets') in the Eastern Atlantic. The gannet is the heaviest (3 kg) and largest (1.8m wingspan) of all seabirds in the North Atlantic. These morphological characteristics, combined with aggressive behaviour and a 10cm, razor-sharp beak, allow gannets to dominate multi-species seabird feeding aggregations at sea, being on live prey or on fishery waste dumped behind vessels **(Garthe and Hüppop 1994)**. Through highly diversified diet **(Hamer et al. 2000)** and the capacity to catch fish within the first 20m of the water column **(Garthe et al. 2000)**, they also outcompete most other North Atlantic seabirds in terms of foraging niche breadth. This is further reinforced by their flight technique, which combines flapping and gliding flight and allows them to achieve a daily foraging range of hundreds of kilometers **(Hamer et al. 2000)**. Marked gannet resilience was summarized as follows by the late Bryan Nelson **(Nelson 1978)**: "*It takes a lot to starve a gannet*".

Gannets, as all seabirds, were hunted heavily until the 20th century, but from the 1950s efficient protection of their breeding sites, followed by the European birds directive of 1979,

allowed population recovery across the Eastern Atlantic **(Grandgeorge et al. 2008)**. Still across 1969-1970 to 2013-2014, the UK gannet populations had a remarkably consistent average annual growth rate of 3.7% **(Murray et al. 2015)**. This general positive trend seems unaffected by marked global changes in the Eastern North Atlantic; gannets even thrive in the North Sea, arguably one of the most anthropized marine areas of the planet **(Lozán 1990)**. There, while global changes led to marked population declines for other seabirds in Scotland, Orkney and Shetland **(Mitchell et al. 2004)**, gannet colonies keep on growing, with the largest in the world (Bass Rock, >75,000 pairs; **(Murray et al. 2015)**) facing the North Sea near Edinburgh.

Yet, at the southern margin of their distribution range in the Eastern North Atlantic, gannets recently displayed worrying ecological signals. Specifically, long-term monitoring of their southernmost breeding location on Rouzic Island (Brittany, France) in the Western English Channel demonstrated that, after 70 years of population growth, breeding numbers stagnated around 20,000 pairs from the early 2010s, to then decline gradually **(Le Bot et al. 2019)**. This trend was observed even though there is still abundant available breeding space for gannets on Rouzic, and in the absence of noticeable disturbance or predation by invasive species at this protected breeding site embedded into the National Natural Reserve of the Sept-Iles archipelago. Fifteen years ago, we noticed that gannet foraging effort at Rouzic was disproportionately large for a colony of this size **(Grémillet et al. 2006)**. This already pointed to food limitation. More recently, it has been proposed that the EU ban on the disposal of fishery wastes at sea would deprive scavenging seabirds, including gannets, from an essential food source **(Bicknell et al. 2013)**. Using Rouzic gannet body condition measurements, stable isotope analyses of their trophic status and GPS-tracking of their movements at sea across 2005-2017 **(Le Bot et al. 2019)**, we demonstrated that gannets fed either on natural prey or fishery wastes, but that discard consumption induced increased seabird foraging effort and

92 reduced adult body condition. From 2015, a drop-off of natural prey (mackerel; *Scomber sp.*)
93 proportion was observed, concurrently with peaks of discards proportion. These changes were
94 concomitant with reduced gannet reproductive success. Thereby, we showed that fishery
95 discards do not compensate shortage in gannet natural prey, and that the latter seem to be
96 depleted in the English Channel.
97 Food scarcity is therefore strongly suspected to be a potential driver of local population
98 decline in Rouzic gannets, especially since the International Council for the Exploration of the
99 Sea **(ICES 2018)** recently admitted that mackerel had been overharvested in the Eastern
100 Atlantic. This notably led the Marine Stewardship Council to withdraw its 'Sustainable Fishery'
101 certificate for the Eastern Atlantic Mackerel fishery in March 2019 **(Le Bot et al. 2019)**.
102 However, seabird population trends are not only affected by conditions during the
103 reproductive season, but also during the inter-breeding period. Those impact gannet fitness
104 directly through inter-breeding mortality, and via carry-over effects of inter-breeding
105 conditions on summer survival and reproduction **(Williams 2013)**. Electronic tracking showed
106 that gannets use a wide range of inter-breeding habitats, ranging from the Northern North
107 Sea to West African coastal waters **(Fort et al. 2012)**. Since West Africa is currently the main
108 hotspot for Illegal Unreported and Unregulated (IUU) fisheries **(Pauly et al. 2014)**, we warned
109 that those fisheries may have a significant impact on gannet inter-breeding survival, through
110 food competition, accidental bycatch but also intentional harvest of seabirds for illegal export
111 to Eastern Asian markets **(Grémillet et al. 2015)**.
112 Building up on these advances, we present the first long-term analysis of gannet inter-
113 breeding movements followed using Global Location Sensors (GLS) across 2006-2015. This
114 spatial analysis performed for gannets breeding on Rouzic Island, was combined with stable
115 isotope analyses on feathers of birds equipped with GLS, which provided information on their

trophic status and potential for food competition with fisheries. Crucially, we also established a mark-recapture study which enabled us to calculate the first estimates of inter-annual survival rates for Rouzic gannets. These three complementary approaches allowed us to test for inter-annual trends in gannet migratory biology in the context of global changes, and to assess conservation consequences **(Montevecchi et al. 2011)**.

Methods

Northern gannets were studied on Rouzic Island (48°54'0''N, 3°26'11''W), Brittany, France, during the chick-rearing period (June-August).

- Mark-recapture analysis

Between 2014 and 2019, we fitted 91 adult breeding gannets with a Darvic ring on the right tarsus, engraved with a code consisting of three letters (black on a white background). Birds were simultaneously ringed with a Darvic, and a metal ring, and observations and recapture showed that Darvic ring loss was <1% over five years. Ringed birds were resighted for 10-15 days each year in June-July, with X10 binoculars or a spotting scope equipped with a X25-50 zoom, from a blind and at a maximum distance of 150m. We analysed mark-recapture data with Cormack-Jolly-Seber (CJS) models **(Lebreton et al. 1992)** using MARK 6.2 **(White and Burnham 1999)**. We fitted 9 different models that were the combination of three models on survival probability and three on resighting probability. Survival probability was modeled constant, time-varying or with a linear (on logit-scale) trend over time. Resighting probability was modeled constant, time-varying or depending on field effort (number of days dedicated to resightings). Models were ranked using AICc **(Burnham and Anderson 2002)**. We performed a goodness-of-fit test with U-care **(Choquet et al. 2009)**. The overall test was not significant

(chi2=16.15, dl=12, p=0.18), showing no significant departure from the CJS model assumptions.

- Geolocation

From 2006 to 2016, we deployed geolocators (Earth and Ocean Technologies, BAS MK5 or Lotek Wireless LAT250A) on 172 chick-rearing adults (Table 1) attached to polypropylene leg rings. Attachment mass did not exceed 0.4% of adult body mass and was unlikely to have any adverse effects. Eighty-nine equipped birds were recaptured after 1-5 years (52% of equipped birds), and 82 tags were successfully downloaded (92%). Among the 82 tags successfully downloaded, 4 loggers stopped recording prematurely (2-3 months) or failed to estimate locations (LOTEK algorithms), and 3 loggers produced erroneous locations. It resulted in GLS tracks recorded for 75 individuals between 2006 and 2016.

British Antarctic Survey (BAS) geolocators store raw light data and geographical positions were estimated twice per day **(Wilson 1992)** using the TransEdit and BirdTracker softwares (British Antartic Survey, Cambridge). Twilight transitions were defined with a user-defined light threshold (16) and inspected visually in TransEdit. The transition file was then imported to BirdTracker for geolocalisation. The sun elevation parameter was set for each logger by fitting the estimated locations of the calibration period to its reference geographical position (range: -4 to -2). Unlike BAS geolocators, the Lotek geolocator model used in this study estimates positions using onboard algorithms that apply fixed threshold and sun angle values and provide only one estimated location per day (raw light data were not recorded). After eliminating outliers and equinox periods, we determined the core areas used by each gannets during the inter-breeding period (mid-October to mid-January; **Fort et al. 2012**) using kernel density distributions (**Wood et al. 2000**) with smoothing factor equal to 1 decimal degree to

account for geolocation error (Phillips et al. 2006). Core areas were considered to be the polygons corresponding to 25% KUD (Kernel Utilisation Density) contours. KUD polygons (25%) were used to calculate the proportion of individuals wintering in the 4 main wintering areas for each year (2006-2014). Thereby, we excluded data for four years because sample sizes were too limited (2012 n=3; 2013 n=2; 2015 n=2; 2016 n=4). We used the 'adehabitatHR' package **(Calenge 2006)** to generate the KUD and maps were generated using the packages 'sf' **(Pebesma 2018)** and 'tidyverse' **(Wickham et al. 2019)** in R version 3.6.1 (R Core team 2019).

- Resigthing rate of GLS

Beyond recovering GLS attached to the birds, we also recorded each year the number of GLS-equipped birds which were resighted, but could not be recaught. We used this second metric because it better reflected the number of GLS-equipped birds which came back to the Rouzic colony, in comparison with the (lower) number of GLS-equipped birds recaught each year. We then modeled the percentage of GLS resighted in the field using generalized linear models (GLM) with a binomial distribution and a logit link function. More specifically, the response variable was the number of GLS resighted during a specific year against the number of GLS deployed the years before (for instance the number of GLS deployed in 2006 and resighted in 2007). As there was slight overdispersion in the residuals of the model (c-hat=1.6) we used a quasibinomial distribution. The independent variables included the additive effects of the year of deployment, the number of years since deployment and the field effort (in days). GLM were fitted in R version 3.2.3 (R Development Core Team, 2015).

- Stable Isotope Analyses (SIA)

Nitrogen ratios mainly reflect bird diet and trophic status, and carbon ratios are an indicator of at-sea habitats **(Kelly 2000)**. When performed on inert tissues such as feathers, SIA provide information upon the individual feeding ecology during tissue synthesis **(Le Bot et al. 2018)**, hence during the inter-breeding period for northern gannet primary feathers **(Nelson 1978)**. From 2010 and for all recaptured birds, we sampled the upper tip of the 4^{th} (in 2010) or 6^{th} (from 2011) primary feather for stable isotopic analyses (SIA). To increase our sample size, we also included samples from birds caught between 2011 and 2016 for another study **(Le Bot et al. 2019)**. Prior to isotopic analyses, samples were washed in a chloroform-methanol (2:1) solution in an ultrasonic bath for three minutes, rinsed two times in a methanol solution, dried for 48h at 45°C and homogenized. Stable isotope analyses were then performed on a subsample of 0.4 mg of homogenized feather loaded in a tin capsule, using an elemental analyzer (Flash EA 1112, Thermo Fisher) coupled in continuous flow mode to an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher, Bremen, Germany). Analyses were performed at the Littoral Environnement et Sociétés (LIENSs) institute. Results for carbon and nitrogen isotopic ratios are presented as δ-values of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ and expressed in ‰. We tested for inter-annual differences in isotopes values with MANOVAs, using year as a factor, followed by Tukey post-hoc multiple comparison tests (HSD). All analyses were performed in R version 3.2.3 (R Development Core Team, 2015).

Results

- Inter-breeding survival

The two best models included a linearly decreasing trend of survival probabilities over the years while the resighting probability was either constant or dependent of the field effort

(Table 2). Mean resighting probability was estimated to 0.81 [0.72-0.88 95% CI] in the best model and varied between 0.72 [0.52-0.86] and 0.86 [0.74-0.96] in the second best model. From the best model, the survival probability was estimated to 0.93 [0.84-0.97] the first year of the study and linearly decreased to 0.56 [0.41-0.69] the last year (Figure 1).

- Resigthing rates of GLS

The effect of field effort on the GLS tags resighting rate was not significant ($F=1.34$, $df=1$, $p=0.37$) while the effects of the number of years since deployment as well as the year of deployment were significant ($F=243.95$, $df=1$, $p<0.001$ and $F=30.79$, $df=1$, $p<0.001$ respectively). The resighting rates of GLS decreased sharply with the number of years elapsed since deployment; it also strongly decreased with the year of deployment (Figure 1).

- Geolocation

GLS data showed that northern Gannets from Rouzic Island used a wide range of inter-breeding habitats (Fig. 2). Their inter-breeding distribution stretched from the North Sea to the coast of Mauritania and from the Canary Islands to the Eastern Mediterranean, with the remarkable presence of an individual over three consecutive years off Lebanon (Fig.2). No bird was recorded in the Mediterranean during the 2006/2007, 2011/2012 and 2014/2015 inter-breeding periods. The use of European and African waters fluctuated over time, with no clear preference of one area to the detriment of another.

- Stable Isotope Analyses (SIA)

No difference was observed between feathers stable isotope signatures for birds which spent the inter-breeding period in different areas (MANOVA: $F_{2, 44} = 0.907$, $p = 0.4633$). Significant inter-annual variations were detected ($F_{6, 187} = 4.18$, $p < 0.001$) explained by variations in $\delta^{13}C$

229 (ANOVA: $F_{6, 187} = 3.91$, $p < 0.001$; Figure 3) but not in $\delta^{15}N$ ($F_{6, 187} = 2.068$, $p = 0.06$; Figure 3).
230 Even though there were inter-annual differences, Post hoc Tukey's multiple comparison tests
231 indicated no temporal trend in carbon stable isotope signatures, with only significantly lower
232 $\delta^{13}C$ values for the 2013/2014 interbreeding period compared to 2010/2011 ($p < 0.001$).

233

234 Discussion

235 Our long-term analyses challenge the general perception of gannets as highly resilient
236 seabirds, and demonstrate that the inter-breeding phase can lead to high mortality rates in
237 this emblematic species. These results point to critically perturbed marine environments
238 across gannet home ranges.
239 Specifically, we used multi-year geolocation of gannet inter-breeding movements, stable
240 isotope analyses (SIA) of their feathers, and mark-recapture techniques, and showed that
241 Rouzic gannets spent the inter-breeding season in a variety of oceanic habitats but mostly in
242 productive waters over continental shelves, from the North Sea to West Africa and the
243 Mediterranean (Figure 2). SIA of gannet feathers also showed signatures compatible with the
244 consumption of small pelagic fish (Figure 3, and see details in **Le Bot et al. 2019**) across the
245 study period and independently of their wintering grounds, thereby pointing to the potential
246 concurrent use of this resource with industrial fisheries. Crucially, we found exceptionally
247 strong declines in the recapture rates of gannets equipped with geolocators across 2006-2017,
248 as well as an equally strong decline in estimated inter-year survival rates of ringed gannets
249 across 2014-2019 (Figure 1). The CMR methods we used explicitly aim at dealing with variation
250 of recapture probability, to yield unbiased survival probabilities. In our model, recapture
251 probabilities were best assessed using a constant parameter over years or with an effect of

252 the field effort. Survival estimations are thus robust to variations in recapture probabilities.
253 Those survival trends are consistent with recent declines in gannet breeding numbers at
254 Rouzic Island, and concomitant with declines in their reproductive rates **(Le Bot et al. 2019)**.
255 In long-lived seabirds such as gannets, adult inter-annual survival probabilities of ca. 95% are
256 expected **(Deakin et al. 2019)**. For a colony of ca. 40,000 breeding adults such as Rouzic, this
257 means that each year, ca. 2000 adults will not come back to their nest site in the spring. Yet,
258 according to our CMR analysis, only 81% of all adults, on average, came back to breed each
259 year across our 2014-2019, corresponding to ca. 7600 annual casualties. In the last year of our
260 study, inter-annual survival even fell to 56%, corresponding to a staggering 17600 missing
261 individuals. To our knowledge, such low survival probabilities had never been recorded in
262 breeding gannets. Those do not translate linearly into a population decline at the Rouzic
263 breeding site (if so, the colony would be eradicated in two to three years), potentially because
264 there is a very large number of adult and sub-adult non-breeders, which replace breeding
265 adults as they vanish. Also, there is some uncertainty around our estimates, which indicates
266 that these figures do not have to be used to the dot, but rather as an indication of a very
267 substantial decline in survival probabilities.
268 Survival probabilities integrate mortality factors across the year cycle. They are calculated
269 from ring resightings performed during one breeding season (i.e. during early chick-rearing in
270 Rouzic gannets) to the resightings performed in the following season during the same time
271 period. Between these two sighting sessions, gannets which vanished may either have died,
272 skipped a breeding season, or dispersed to another breeding site. Yet, adult gannets are
273 extremely philopatric and do not skip years once they start breeding at a given colony **(Nelson**
274 **1978)**, which was the case for all the birds ringed at Rouzic. Hence, dispersal is probably
275 negligible as a factor contributing to inter-annual survival probability. Abnormally low survival

276 probabilities recently observed for Rouzic gannets are therefore most probably linked to
277 additional mortality. In gannets, such mortality may be due to oiling and winter storms,
278 diseases, starvation, accidental bycatch, intentional harvest, or a combination of these
279 potential causes.

280 Oiling and winter storms: The temperate Eastern Atlantic hosts some of the busiest shipping
281 routes in the world, linked to major oil spill hotspots **(Vieites et al. 2004)**. Historically, oiling
282 has been a major cause of gannet inter-breeding mortality in Europe, but this has declined
283 strongly in recent years (see Supplementary material 1). Oil spills are often linked with winter
284 storms, which may also directly cause seabird mass mortality, yet gannets are rated as less
285 sensitive to winter storms and oiling than other European seabirds, especially alcids **(Wiese**
286 **and Robertson 2004)**.

287 Pathogens and parasites: Seabird population dynamics can be strongly affected by diseases
288 **(Gamble et al. 2020)**, and gannets have been shown to carry Newcastle Disease Virus **(Wilson**
289 **1950)** and Meningoencephalitis **(Spalding et al. 2002)**. No major gannet dye-off has ever been
290 recorded in Europe, and no suspicious chick or adult carcass has been collected at the Rouzic
291 colony. Yet, pathogens and parasites cannot be completely excluded as a cause of the
292 observed decline in survival probability for Rouzic gannets.

293 Starvation: Previous studies demonstrated that Rouzic gannets struggle to find food during
294 the breeding season **(Grémillet et al. 2006)**, leading to declining fitness as assessed through
295 body condition analysis **(Le Bot et al. 2019)**. Geolocation also showed significant spatial
296 overlap between inter-breeding gannets and fisheries off West Africa, while SIA suggested
297 that non-breeding gannets fed to some extent on small pelagic fish all along the study period.
298 This pointed to concurrent use of these resources by the two parties **(Grémillet et al. 2015**;
299 this study). Yet, unlike in closely-related Cape gannets (*Morus capensis*), for which food

competition with fisheries demonstratively led to starvation **(Grémillet et al. 2016)**, we do not know whether Rouzic gannets are food deprived across their entire year cycle. Also, in addition to competition with fisheries, gannets may face the consequences of a northwestward shift in Mackerel populations induced by climate change **(Hughes et al. 2014)**. Such a shift is predicted to push mackerel stocks away from coastal areas of Western Europe, notably from the Western English Channel **(Bruge et al. 2016)**. The similar isotopic signatures observed all along the study period nonetheless suggest that inter-breeding gannet trophic status did not change markedly.

Accidental bycatch and intentional harvest: These two mortality causes seem far more likely. As we demonstrated (Fig. 2), some Rouzic gannets spend the inter-breeding period in the Canary current off West Africa, which notoriously hosts the most severe IUU fisheries of the planet **(Cabral et al. 2018)**. Gannets are also vulnerable to bycatch in the Mediterranean **(Cortés et al. 2017)**. In this context, the strikingly low recent return rates of gannets equipped with geolocators, as well as low survival probabilities calculated via CMR analysis, are typical of seabird bycatch, as recorded for albatrosses and petrels of the Southern Ocean across the 1990s **(Tuck et al. 2003)**.

We cannot attribute the decline of the Rouzic gannet colony to a single, well-identified cause or period, yet we may hypothesize that competition with fisheries and bycatch, both on their breeding and inter-breeding grounds, might be the main driving forces. However, this observed population decline is puzzling when compared to the dynamics of most other gannet colonies of the Eastern Atlantic. Indeed, especially around the British Isles, all colonies show persistent positive trends **(Murray et al. 2015)**. Further, detailed demographic analyses at colonies closest to Rouzic (British Channel Islands and Wales) show adult survival estimates close to 95% **(Warwick-Evans et al. 2016, Deakin et al. 2019)**, the expected value for adult

long-lived seabirds. Since those gannet populations broadly share the same inter-breeding areas as Rouzic gannets **(Veron and Lawlor 2009)**, and also forage in the Western English Channel and the Irish Sea during the breeding season **(Soanes et al. 2013)**, their positive dynamics seem hard to reconcile with the local decline of the Rouzic population. These contrasts clearly deserve further investigations, but they may be due to the fact that the trends we observe at Rouzic are extremely recent, and may have remained unnoticed at other breeding sites. Also, the only difference between Rouzic gannets and birds from other colonies, is that significant numbers of Rouzic birds spend the inter-breeding period in the Mediterranean. Since seabird bycatch can be extremely severe in some parts of the Mediterranean **(Afán et al. 2019)**, this may partly explain the lower survival rates of Rouzic gannets.

Further, even though declining trends seem unusual at European gannet colonies, they are consistent with marked population declines in closely-related Cape gannets, which also compete with fisheries **(Sherley et al. 2019)**, and with declining northern gannet populations in Eastern Canada. There, long term monitoring showed that gannet populations and the individual fitness of adults declined markedly from the early 2010s **(Franci et al. 2015)**. These declines were attributed to poor feeding conditions, due to a shifting prey base driven by global warming **(Montevecchi et al. 2013)**.

Overall, our work stresses that even one of the most resilient seabirds of the world is likely affected by man-made constraints upon its populations. The Rouzic gannet colony is a major emblem of French metropolitan biodiversity, with constant media attention. We therefore anticipate that our work will contribute to foster a sense of common destiny between seabirds and humans in coastal marine ecosystems severely affected by global change, leading to the urgently needed transformation of marine policies **(Lescroël et al. 2016)**. Notably, we are

currently using scientific evidence gathered through the long-term monitoring of the Rouzic colony to promote the establishment of a marine extension to the National Nature Reserve of the Sept-Iles archipelago, and to warn the European Union for the consequences of its fishing activities off West Africa **(Ramos and Grémillet 2013)**. Similar science-to-policy strategies using seabirds as flagship species are being increasingly employed on a world-wide scale, notably for the establishment of large marine protected areas. This is the case for the 500,000 km^2 marine extension to the nature reserve of the French Sub Antarctic territories, established in 2015 upon long-term monitoring of 10 seabird species **(Delord et al. 2014)**.

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525

526

527 Tables

528 Table 1. GLS deployment and recapture. For each recapture year, the number of birds
529 resighted with a GLS is given, followed (in brackets) by the number of birds which were
530 resighted, but not recaught. Hence, if a year is noted 5(3), this means that five birds were seen
531 with a GLS, of which three could not be recaught.

		Year of recapture/resighting													
Year equipped	**Equipped per year**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**Total retrieved**
2006	10	10		0	0	0	0	0	0	0	0	0	0	0	10
2007	0														0
2008	39				22	8	5(5)	3(2)	1(1)	1(1)	0	0	0	0	31
2009	0														0
2010	37					24	5(5)	3(2)	2(2)	1	1(1)	2(2)	0	0	26
2011	20						7	2(2)	3(2)	2	0	0	0	0	10
2012	0														0
2013	0														0
2014	21									14(6)	2(2)	0	0	0	8
2015	23										6(4)	1(1)	1	1(1)	3
2016	22											8(7)	3(1)	1	4
total	172														89

532

533

534 Table 2. Model selection for the modeling of survival probability. Phi is the survival, p the
535 resighting probability. '.' means constant, "t" means time-varying, "trend" mean a linear trend
536 over years and "effort" mean "linear relationship with field effort".

537

Model	Nb param	AICc	DeltaAICc	AICweight
Phi(trend) p(.)	3	324.86	0.00	0.33
Phi(trend) p(effort)	4	325.23	0.37	0.28
Phi(t) p(.)	6	327.20	2.34	0.10
Phi(.) p(t)	6	327.43	2.57	0.09
Phi(trend) p(t)	7	327.51	2.65	0.09
Phi(t) p(effort)	7	327.78	2.93	0.08
Phi(t) p(t) PIM	9	330.48	5.62	0.02
Phi(.) p(effort)	3	332.92	8.06	0.01
Phi(.) p(.)	2	337.34	12.49	0.00

538

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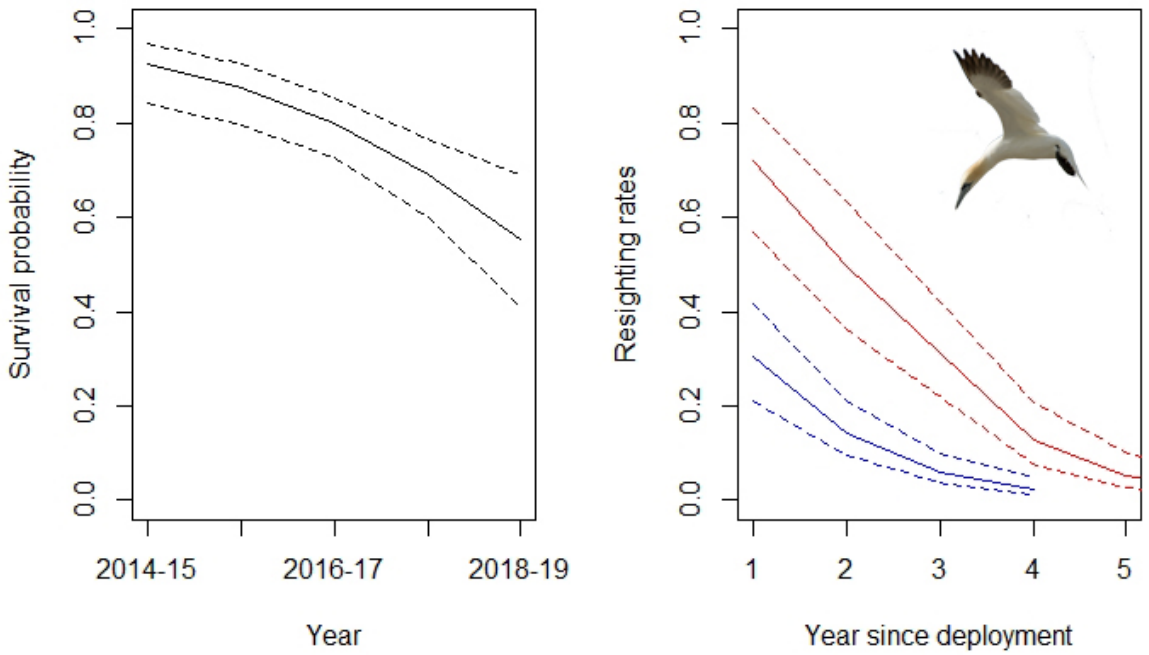
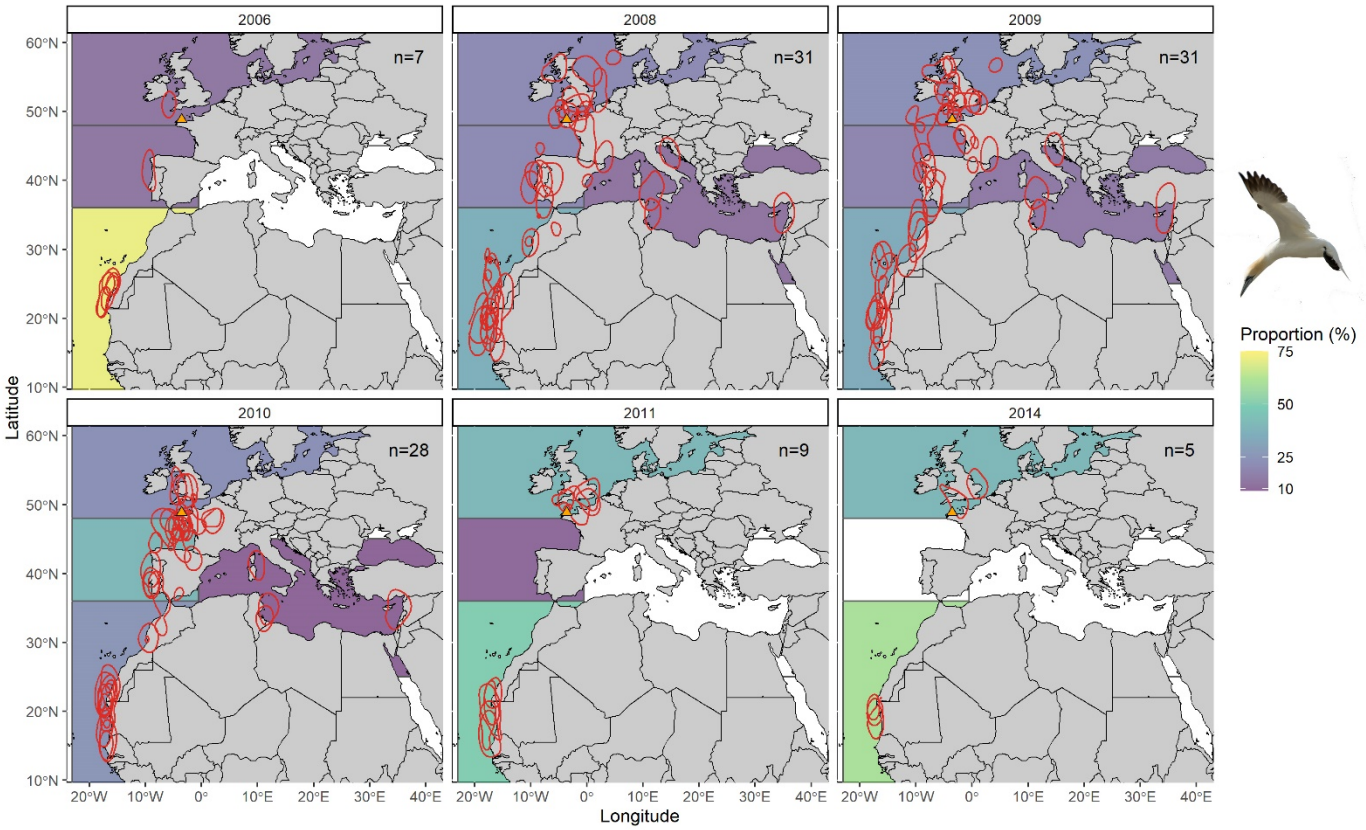


Figure 1. Survival probability estimates (left panel) depending on the year. GLS resighting rates estimates (right panel) depending on the number of years elapsed since deployment and on the year of deployment (red line for 2006 and blue line for 2015). Dotted lines are 95% confident interval of estimates.

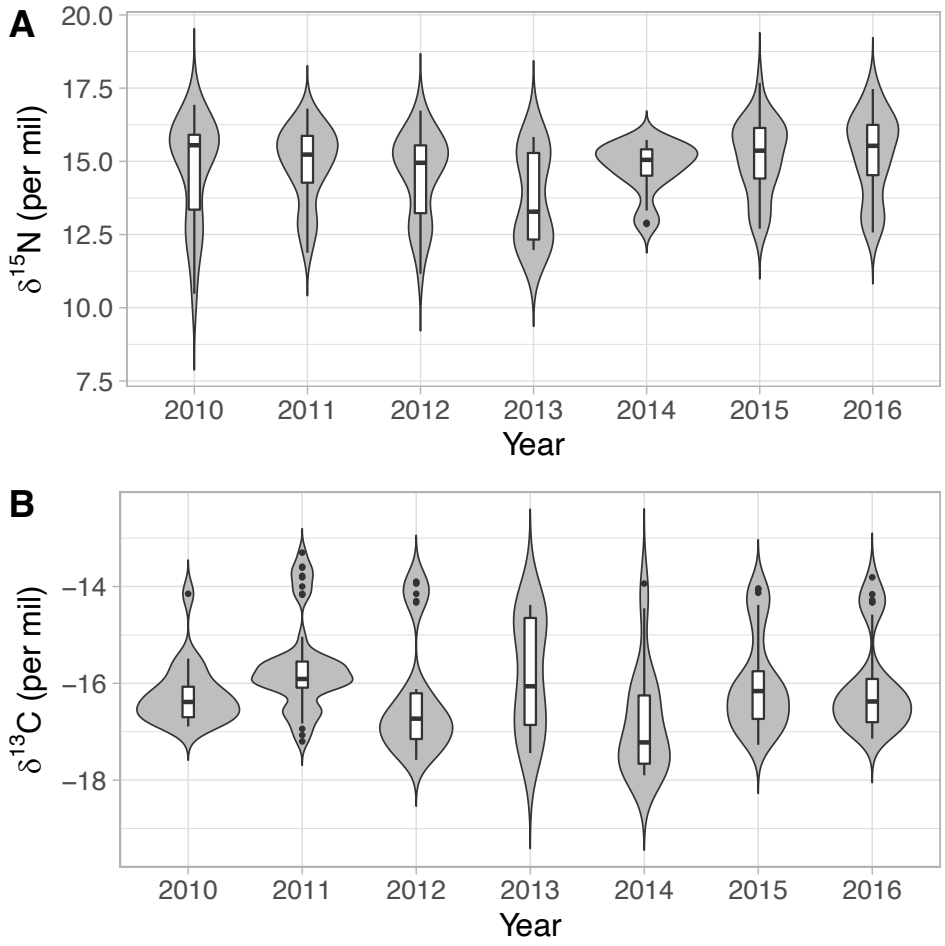


548

549 Figure 2. Inter-breeding habitat use in Northern gannets from Rouzic Island (yellow triangle
550 on the top-left map). Red lines delineate individual core wintering areas (15th October to 15th
551 January, 25% Kernel Usage Density contours). Colour gradients (scale to the right of the maps,
552 zero is white) show, for each map, the proportion of birds using one the following maritime
553 regions: Northern Western Europe (North of Brest in Brittany), Atlantic waters between Brest
554 and Gibraltar, Mediterranean waters, West African waters. The number of individuals
555 successfully tracked in each year is given in the top-right corner of each map. Note that the
556 total sample size for this analysis (n=111) is higher than the total number of tracked gannets
557 because some individuals were tracked over multiple years.

558

559



560

561 Figure 3. Stable isotopic signatures of feathers of chick-rearing northern gannets. Violin plots
562 show the median (horizontal line), interquartile range (box height) and frequency (shaded
563 kernel density plot) of δ13C (A) and δ15N (B) isotopic signatures during the 2008-2010 to
564 2015-2016 interbreeding periods.

565

Supplementary material 1: Total number of oiled northern gannets (*Morus bassanus*) hosted per year at the wildlife care center of the Station Ornithologique de l'Île Grande, which is the major seabird care center in Brittany (France). The incidence of the 1999-2000 Erica oil spill is clearly visible, with comparatively lower numbers of oiled gannets recorded from 2010 (Source: Ligue pour la Protection des Oiseaux).