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Fishery discards do not compensate natural prey shortage in Northern gannets from the English Channel

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ABSTRACT

Fisheries modify ecosystem balance by harvesting through marine food webs and producing large amounts of discards subsidizing scavengers. Among them, seabirds are the most conspicuous and have been benefiting from anthropogenic food sources generated by fisheries. However, this modified feeding behaviour also exposes them to threats, such as accidental bycatch on fishing gear and ecological traps set by discards of lower nutritional value compared to seabird natural prey. Seabird-fishery interactions have been the focus of numerous studies, but very few integrative investigations tested multi-annual dynamics. To explore this temporal dimension, we performed stable isotopic and body condition analyses, as well as GPS-tracking in Northern gannets (*Morus bassanus*) over a 12-year period (2005–2017), during which they coexisted with fisheries in the English Channel. We demonstrate that gannets fed either on natural prey, or fishery wastes, but that discard consumption induced increased seabird foraging effort and reduced adult body condition. These changes are concomitant with reduced gannet reproductive success, and reduced growth rate of their breeding population. Our work provides essential, novel understanding of scavengers-fisheries interactions, by showing that fishery discards do not compensate natural prey shortage in the longer term. Altered gannet foraging and fitness strongly suggest pelagic fish depletion threatening Northern gannets in the English Channel. To improve gannet conservation in this ecoregion, fishery discards may be banned, but, efforts should in priority go towards rebuilding Northern gannet pelagic prey populations, particularly by strongly reducing fishing effort on North Atlantic mackerel.

1. Introduction

In addition to the harvest of marine resources, fisheries generate large volumes of discards. Those are defined as unwanted catches returned to the water dead or alive (Enever et al., 2007), representing an annual 10.3 million tons of discarded marine organisms worldwide (Pauly and Zeller, 2016). Discards are an unsustainable waste of resources, both from an economic and ecological point of view, and are incompatible with ecosystem-based approaches to fisheries (Bellido et al., 2011). Consequently, there are worldwide incentives to reduce, and ultimately ban discarding at sea (Condie et al., 2014). However, as the third anthropogenic food source for wildlife (Oro et al., 2013) discards subsidize organisms from the benthic fauna (Erzini et al., 2003) to marine mammals (Hill and Wassenberg, 2000; Luque et al., 2006) with an important part supplying seabirds (Depestele et al., 2016; Hudson and Furness, 1988). Therefore, and particularly for seabirds, a drastic reduction of discarded volumes rises concerns (e.g. Bicknell et al., 2013; Fondo et al., 2015) about negative conservation impacts on a short to medium-term (Veiga et al., 2016). On the other hand, scavenging can also be risky for seabirds. Foraging in the vicinity of fishing vessels exposes them to accidental mortality through interaction with fishing gear, a major threat for such long-lived species (Croxall et al., 2012; Lewison et al., 2004). Furthermore, fishery wastes can set ecological traps leading to reduced seabird reproduction rates when food quality is not adequate for chick nutritional needs (Grémillet et al., 2008) and lead to reduced fitness in the longer term (Cohen et al., 2014).

Indeed, seabirds are particularly sensitive to food availability and

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Table 1

Details of deployed GPS loggers on Northern Gannets from Rouzic Island, 2005–2017. *: in 2017, CatTraQ™ loggers were modified to double battery size.

Year	GPS logger	Company	Size (L × W × H; mm)	Mass (g)	Recording frequency	Deployed loggers (n)	Recaught loggers (n)	Number of individual first trip totally recorded (n)
2005	1-channel GPS data logger	NewBehaviour	95 × 48 × 24	65	1 s	21	21	20
	GPSlog	Earth and Ocean Technologies	96 × 39 × 26.5	75	2 min/1 s			
2010	Gipsy	Technosmart	95 × 40 × 27	60	1 s	38	35	22
2011	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	22	22	19
2012	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	27	23	19
2013	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	11	11	9
2014	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	20	19	19
2015	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	21	19	19
2016	CatTraQ™	Catnip Technologies	47 × 30 × 13	20	30s	20	19	19
2017	CatTraQ™*	Catnip Technologies	57 × 35 × 18	30	30s	12	11	11

quality during the breeding season, when energy demand and intraspecific competition are highest. Food shortage may lead to brood neglect (Lewis et al., 2004) and reduced breeding success, or breeding failure (Ponchon et al., 2014), or even to diminished adult body condition (Grémillet et al., 2016), with consequences at the population level (Becker et al., 2007; Bolnick et al., 2002). Generalist seabirds should be able to cope with short-term resources fluctuations (Courbin et al., 2018) through foraging plasticity, by switching prey types or foraging areas (Montevecchi et al., 2009; Pettex et al., 2012), but subsidized prey of lower quality, like discards, may reverse the benefit in the longer term (Cohen et al., 2014).

Seabird - fishery interactions have been studied extensively (reviewed in Le Bot et al., 2018), with recent electronic tracking technologies enabling crucial insights into the behavioural responses of seabirds to fishing activities (e.g. Votier et al., 2010; Weimerskirch et al., 2017). This includes long-term studies which investigated temporal changes in fishery wastes consumption (e.g. Arcos and Oro, 2002) or single year studies focusing on the effects of such consumption (e.g. Bartumeus et al., 2010). However, very few integrative studies have assessed impacts of discard consumption on seabird foraging behaviour, diet, body condition and reproductive performance over multiple years (e.g. Cohen et al., 2014).

We performed such investigations in Northern gannets (*Morus bassanus*), largest of all seabirds in the North Atlantic. Gannets are known for their dietary flexibility (Garthe et al., 2007; Pettex et al., 2012), and are considered as particularly resilient to marine environmental changes (Grandgeorge et al., 2008). Specifically, their diet has been shown to match pelagic prey availability (Garthe et al., 2014; Montevecchi et al., 2009), with an extensive use of fishery discards (Depestele et al., 2016; Hudson and Furness, 1988; Votier et al., 2010). Overall, Northern gannet populations have been increasing over the past 70 years (Eveillard-Buchoux et al., 2017; Wanless et al., 2005), presumably due to protection of their breeding sites and high availability of discards across their range.

In the Eastern North Atlantic, this subsidized nutritional status might be changing with the implementation of the new common fishing policy of the European Union. Planned since 2015 (Borges, 2015), it specifically aims at reducing, and ultimately supressing, all discards (Catchpole et al., 2017). Pre-existing knowledge concerning Northern gannets in the Eastern North Atlantic (Grémillet et al., 2006; Hamer et al., 1997; Votier et al., 2010; Wanless et al., 2005), indicate that discards constituted a significant part of the birds' diet during their breeding season in the Western English Channel and that a discard reform should reduce prey diversity and availability.

On the basis of such previous information, we hypothesized that fishery discards are the preferred prey of Northern gannets, allowing them to ensure body maintenance and reproductive performance, and to maintain breeding colony size. We tested this premise through a unique longitudinal study of the diet, trophic status, foraging effort, and fitness proxies (adult body condition and reproductive performance) in Northern gannets coexisting with intense fishing activities in the English Channel. Marine fisheries and seabirds occur worldwide, and lessons learnt in the English Channel are therefore widely applicable.

2. Materials and methods

Fieldwork was carried out during the early chick-rearing phase of the gannet breeding season (June–July) between 2010 and 2017 on Rouzic Island (48°54′0″N, 3°26′11″W) in the Sept-Iles archipelago located in the Western part of the English Channel, Brittany (France). This gannet breeding colony hosts ca. 20,000 breeding pairs and is the southernmost European nesting site for the species, with the exception of isolated breeding attempts in the Mediterranean. Additional data from a previous study performed in 2005 at the same breeding site were added to extend the study period (Grémillet et al., 2006). Over a 12 yr period, we assessed foraging behaviour using GPS tracking, determined diet using stable isotope analyses, and collected data on individual fitness proxies as well as population size and breeding success. All experiments were performed under permits issued by the French Direction des Services Vétérinaires (N° 34-369) and the Comité d'Ethique Régional Languedoc-Roussillon (N°1110).

2.1. Assessing foraging behaviour using GPS tracking

We tracked breeding gannets throughout their at-sea foraging trips using GPS tags in 2005 (Grémillet et al., 2006) and 2010–2017 (details in Table 1). Gannets were equipped from mid-June to mid-July each year, while they were raising 2 to 6 week-old chicks and both parents were relaying each other to either take care of their single chick at the nest or collect food at sea. We caught them at the nest, almost exclusively on nest reliefs (i.e. we targeted birds that were leaving their nests after the arrival of their partner), using a telescopic carbon fiber pole fitted with a metal crook, and attached devices to their lower back with white Tesa© tape. Great care was given to minimize disturbance to the birds: each bird was handled in < 15 min, in silence and in the shade to avoid stress, particularly overheating. Birds were recaptured and devices recovered when they came back to feed their chick after at least one foraging trip at sea. We only considered foraging trips lasting > 40 min (Warwick-Evans et al., 2016) and excluded locations within 500 m of the colony to exclude movements linked to nest maintenance, as well as bathing and rafting in the vicinity of the colony (Carter et al., 2016). We only kept the first foraging trip (> 40 min) when several were recorded. Trip duration in hours and foraging range in km^2 were used as an index of foraging effort. Foraging range was estimated, through a kernel analysis, using the adehabitatHR package in R (Calenge, 2006), over a grid of 4 km^2 cells. The smoothing parameter was calculated as a function of the standard deviation of gannet GPS coordinates and their number, following methods recommended by Calenge et al. (2015). Surface areas corresponding to the 95% kernel utilization distributions (kernel UDs, km^2) were calculated for each individual and the 25%, 50%, 70% and 95% average kernel UDs of all individuals were mapped for each study year.

2.2. Assessing diet using stable isotope analyses

Stable isotope analyses (SIA) is a biochemical technique, which relies on the measurement of the differential between stable isotopes for carbon ($\delta^{13}C$), and nitrogen ($\delta^{15}N$). It provides indirect information on fish or seabird feeding ecology. Nitrogen ratios mainly reflect individual trophic levels, and carbon ratios are linked to their at-sea habitats and varies between benthic/pelagic and coastal/oceanic environments (McKechnie, 2004).

Adult gannets tend to regurgitate stomach contents spontaneously when handled. In 2011–2017, we collected, froze and stored these samples (in a −20 °C freezer) whenever GPS-tracked birds regurgitated during handling. Prey items were later identified to the lowest taxon. Using those collected regurgitates, we sampled fish muscle from the four species or taxa of fish most frequently ingested by gannets (garfish, *Belone belone*; mackerel, *Scomber* sp.; gurnard, *Triglidae*; whitefish, Gadiforms). Overall, we found that these four types of prey represented 85% of the ingested fish prey biomass.

Additionally, in 2011–2017, we sampled 0.2–0.5 ml of blood from the tarsal vein of each bird tracked by GPS upon device recovery ($n = 137$), using a 23-gauge needle. To increase sample size, blood samples from Gannets caught for another study were added ($n = 44$). Red blood cells (RBC) and plasma were separated by centrifugation (10 min at 13500 RPM) within 60 min of collection and stored frozen at −20 °C. SIA were performed on plasma samples, which integrate information on bird diet across 2–5 days before sampling (Mariano-Jelicich et al., 2014). Prior to all analyses, gannet plasma ($n = 181$) and fish muscle ($n = 22$) samples were freeze-dried for 48 h, homogenized, and delipidized (in a 2:1 chloroform:methanol solution for plasma and in cyclohexane for prey muscle, Cherel et al., 2018). About 0.4 mg of sample was then encapsulated in tin capsules before $\delta^{13}C$ and $\delta^{15}N$ were measured by mass spectrometry at the LIttoral ENvironnement et Sociétés (LIENSs) Stable Isotope platform.

2.3. Assessing fitness proxies

The body mass of each adult gannet equipped with GPS (181 individuals) was recorded with a hand-held scale to the nearest 50 g at capture and recapture. To minimize biases due to the variation in stomach fullness, we only kept mass measurements at capture, when birds had been on the nest for extended periods and were assumed to have fed their chick and digested most of the remaining stomach content. Additionally, in 2011–2016, we measured the thickness of their pectoral muscle to the nearest 0.1 mm (112 individuals) following Lindstrom et al. (2000). We used a TITAN© portable ultrasound system (Sonosite, Inc. USA) with a HST/10–5 MHz broadband transducer. Pectoral muscle thickness is considered as an indicator of body condition in birds (Lindstrom et al., 2000).

2.4. Assessing population size and breeding success

Each year in early June, from 1939 to 2017, the total number of apparently occupied nests (AON, sensu Nelson, 2002) was determined using direct counts and/or aerial photographs following Siorat and Rocamora (1995). Counts were performed at irregular time intervals from 1939 to 1955, then nearly every year after 1955. Information for the 1939–2005 period has been previously published (Grémillet et al., 2006) and we updated it for the 2005–2017 period. Breeding success (1991–1997; 2002; 2013–2017) was monitored daily throughout the breeding season (from May to October) on a sample of 100 AONs using a remote-controlled camera permanently installed on the colony following recommendations by the Groupement d'Intérêt Scientifique Oiseaux Marins (Cadiou, 2010, unpublished report). For each AON, the dates of laying, presence of egg, chick and chick age were documented until either breeding failure (egg broken or missing, chick dead or missing) or breeding success (fully feathered chick ready to fledge).

2.5. Statistical analyses

Stable isotope ratios for bird plasma were analyzed using the SIBER package in R in order to investigate the isotopic niche of Northern gannets and its temporal changes (Jackson et al., 2011). To this end, standard ellipse areas corrected for small sample sizes (SEAc), which include about 40% of individuals within a group based on bivariate normal distributions, were calculated for each year. The posterior estimates of the Bayesian standard ellipse area (SEAB, posterior draws = 10^6) were then used to test for inter-annual differences in bird isotopic niches (using MANOVA and ANOVA).

Isotopic measurements on the four major prey of gannets were first used to test for an inter-annual variation of the gannet population's isotopic signature (ANOVA). Second, they were incorporated in a Bayesian stable isotope mixing model to estimate the overall composition of individual gannet diets. More specifically, the relative contribution of each prey was estimated using the SIMMR package in R (Parnell et al., 2013). We used trophic enrichment factors of 2.25‰ (± 0.61) for nitrogen and 0.24‰ (± 0.79) for carbon between prey muscle and gannet plasma, as previously used in Northern gannets (Stauss et al., 2012). In order to evaluate the importance of fishery wastes in the gannet diet, gurnards and whitefish were grouped as "discards". In this context, it is important to note that gurnards and whitefish are demersal species, which only become accessible to gannets when discarded by fishing vessels. Conversely, garfish and mackerel are pelagic species which are caught naturally by gannets; however, the second is also an important target for pelagic trawlers and may be discarded. Therefore, we possibly underestimated the proportion of anthropogenic prey by considering mackerel as a natural prey only, while it could be a potential discard. For each year, we present the estimated distribution of the proportion of discards, mackerel and garfish in the diet.

For foraging trip duration, foraging range, body mass and pectoral muscle size, we tested for inter-annual differences with ANOVAs, using year as factor and pairwise multiple *t*-test. We then explored the influence of discard consumption on those foraging and body condition variables using a bootstrap procedure. Indeed, discard proportion in the diet was estimated for grouped individuals per year (see above) because estimating individual values would have brought too much uncertainty. Therefore, for each individual, we randomly drew a discard proportion value in the estimated distribution for the corresponding year, creating an individual discard variable. We then calculated a Pearson rank correlation between this discard variable and each foraging and body condition variable, to evaluate their relationship. To account for within-year variability in discard consumption, we re-iterated all calculations 10,000 times, estimating the distribution of the correlation between the proportion of discard in the diet and the individual foraging and condition variables. We considered that the effect of discard consumption was significant when the 95% confidence interval of the correlation distribution did not overlap with zero. All analyses were performed in R version 3.2.3 (R Core Team, 2015).

3. Results

3.1. Stable isotope analyses

Northern gannet isotopic signatures significantly varied between years (MANOVA; Wilk's lambda; $F_{12,348} = 14.01$; $p < 0.001$; Fig. 1.a), both in terms of $\delta\,^{15}N$ (ANOVA; $F_{6,174} = 2.61$; $p = 0.019$) and of $\delta\,^{13}C$ ($F_{6,174} = 33.59$; $p < 0.001$). Furthermore, temporal changes in SEAB

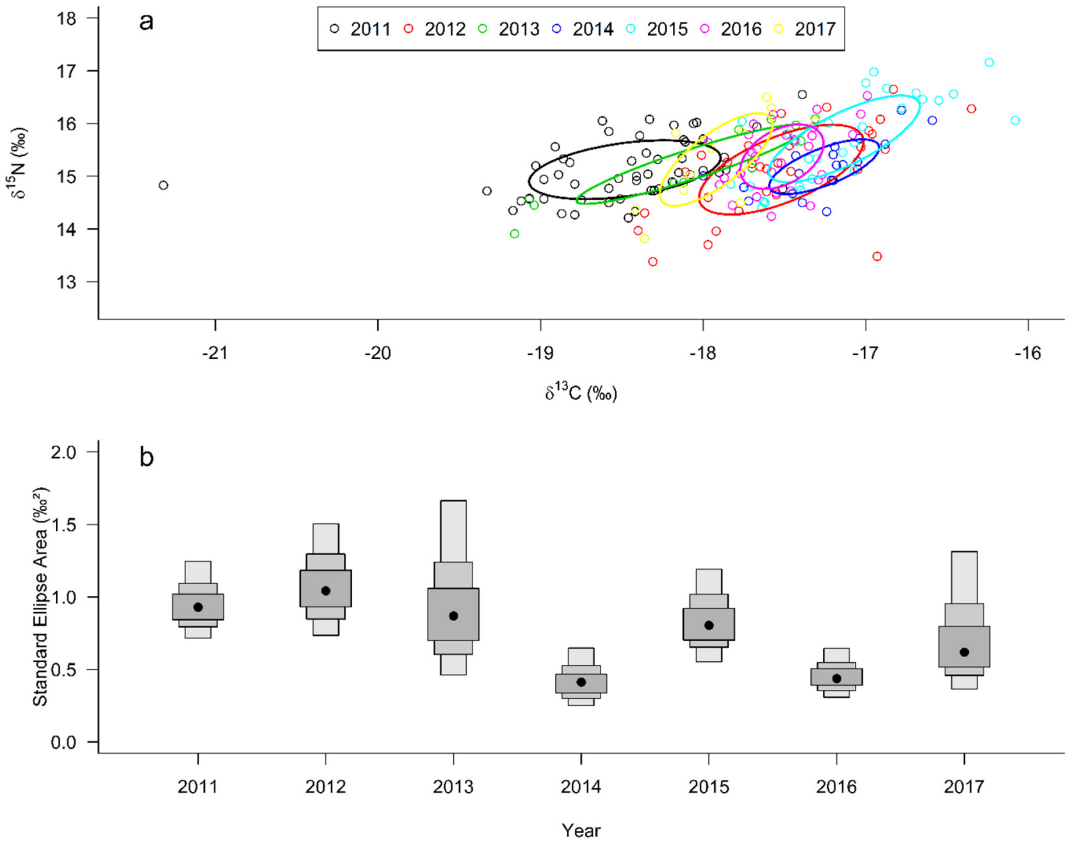

Fig. 1. Stable isotopic analysis: a. δ^{13}C and δ^{15}N signature of Northern gannets from Rouzic Island grouped by year from 2011 to 2017 ($n = 52$ in 2011, $n = 31$ in 2012, n = 11 in 2013, $n = 19$ in 2014, $n = 28$ in 2015, $n = 29$ in 2016, $n = 11$ in 2017). Isotopic area occupied each year are represented by standard ellipse area corrected for small sample sizes (SEAc; solid lines) b. Posterior estimates of the Bayesian standard ellipse area (SEAB) for Northern Gannets from Rouzic Isand by year.

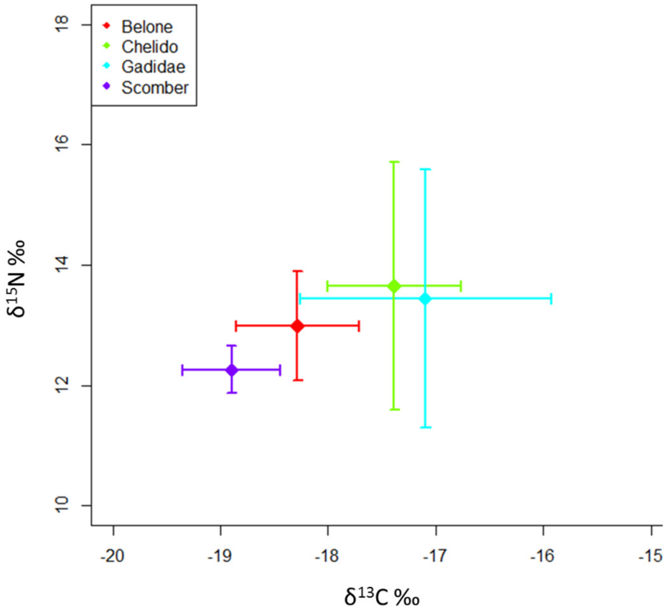

Fig. 2. δ^{13}C and δ^{15}N signature of Northern gannets main regurgitated prey; Belone: garfish (*Belone belone*), Scomber: Mackerel (*Scomber* sp.), Chelido: Gurnards (*Chelidonidae*), Gadidae: Whitefish (Gadiforms).

values revealed a contraction of the isotopic niche of the Rouzic gannets over time ($p < 0.001$, $R^2 = 0.21$; Fig. 1.b). δ^{15}N and δ^{13}C values of the four main prey (Fig. 2) were significantly different (respectively $p < 0.05$ and $p < 0.001$), and consistent in time with no effect of the year. Gurnards and gadiforms had similar isotopic signatures; we therefore grouped these two benthic prey species into a “discards” group. The respective mean values of $\delta\ ^{15}$N and $\delta\ ^{13}$C for discards, mackerel and garfish were used in the stable isotope mixing models.

SIMMR mixing models revealed a strong variation in gannet diet over years (Fig. 3). Particularly, a drop-off of mackerel proportion was observed in recent years (from 55% ± 8 in 2011 to 10% ± 6 in 2015), concurrently with peaks of discards proportion (from 14% ± 5 in 2011 to 67 ± 7 in 2015). In general, mackerel proportion in the diet exhibited the reverse pattern of the discards proportion, while the garfish proportion remained stable over years (Fig. 3).

3.2. Inter-annual variations in foraging behaviour

We observed significant inter-annual variations in trip duration (Fig. 4.a; ANOVA; F = 2675; $p < 0.01$), with longer trips in 2014 and 2015 ($p < 0.05$) and smaller in 2005 and 2017 ($p < 0.01$). Variations between years were also observed in foraging range (Fig. 4.b and Fig. 5; ANOVA; F = 2449; $p < 0.05$) with a significantly bigger range in 2015 ($p < 0.05$) and significantly smaller ranges in years 2005, 2013 ($p < 0.05$) and 2017 ($p < 0.01$).

3.3. Inter-annual variation in body condition

Body mass showed significant inter-annual variation (ANOVA; $F_{8,174} = 6{,}37$; $p < 0{,}001$; Fig. 4.3) with recorded weights falling under 3000 g since 2011, with significantly heavier individuals in 2005 ($p < 0.05$) and 2010 ($p < 0.0001$). Pectoral muscle thickness showed a constant decrease after 2011 (ANOVA; $F_{5,106} = 5241$, $p < 0.001$; Fig. 4.4), with markedly thicker muscles in 2011 ($p < 0.001$) and

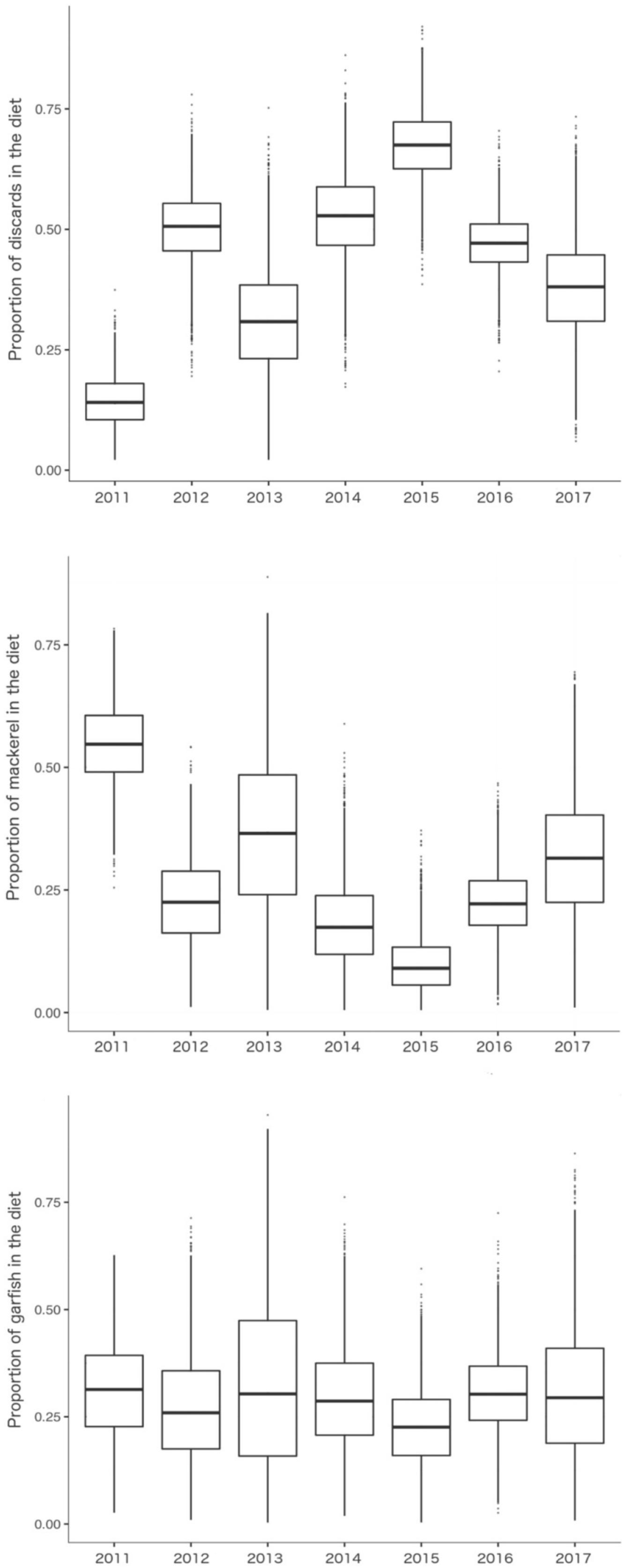

Fig. 3. Proportion of the different prey types in Northern Gannets diet from 2011 to 2017, as estimated by stable isotope mixing models.

thinner one in 2011 ($p < 0.01$).

3.4. Population size and breeding success

After a constant but moderate increase from its foundation in 1939, the population size exhibited a period of steep growth from 1981 to 2011, until it stabilized around 20,000 breeding pairs with a slight tendency to decrease in recent years, and especially low counts in 2013 and 2017 (Fig. 6.b). From 2005 to 2011, the mean annual growth rate was +4.25% while it was −2.56% from 2011 to 2017. From 1991 to 2017, egg laying was observed in at least 80% of the monitored occupied nests (Fig. 6.a). Until 2002, the proportion of produced fledgling per laid egg remained stable at ∼90% before falling down to 47% in 2013 and 38% in 2017. From 2013 onwards, the observation protocol made it possible to distinguish between primary (failure during the incubation stage) and secondary failure (during the chick rearing stage). Secondary failure remained relatively stable, between 18% (2013) and 31% (2016), contrary to primary failure which showed strong inter-annual variations with peaks in 2013 (40%) and 2017 (53%).

3.5. Linking estimated discard proportions in Northern gannet diet with individual foraging trip characteristics and body condition

Discard consumption had a significant positive effect on foraging trip duration (Fig. 7.a) and foraging trip range (Fig. 7.b) in Northern gannets. Gannets feeding more intensively on discards travelled further away from the colony and for longer periods. Individuals exhibiting a higher proportion of discards in their diet had thinner pectoral muscles (Fig. 7.d) but did not exhibit significantly lower body masses (Fig. 7.c).

4. Discussion

Using an integrative multi-year study, we reject the hypothesis that fishery discards are a beneficial long-term feeding resource for Northern gannet in the English Channel. Our results highlight alarming trends for seabird conservation in this area. Notably, we observed an important fluctuation of the main natural prey, mackerel, in gannet diet, replaced by discards in years of food shortage. Concurrently, in years of high discard consumption, adult gannets increased their foraging effort and had lower body condition. Across the 2011–2017 study period, reproduction performance was generally low and the study colony declined in terms of nests observed as active during the breeding season, indicating generally unfavourable feeding conditions.

4.1. Fishery discards do not compensate natural prey shortage

Our reconstruction of gannet diet over the 2011–2017 period showed marked alternations from natural to anthropogenic food. We are aware that the isotopic signature of specific prey can change with time (Phillips et al., 2014) and that averaging trophic values across years may blur patterns. We therefore took great care to examine year-specific trophic signatures, and validated the fact they did not differ for single prey between years, but differed consistently between prey types. Moreover, the stable isotope mixing models which we used integrate year- and prey-specific information, to model overall trends in trophic niche (Parnell et al., 2013; Phillips et al., 2014). Further inherent variability to diet reconstruction models comes from the choice of the trophic enrichment factor (TEF), i.e. the difference between the isotopic value of a predator and its prey. Here we used values which had already been implemented in Northern gannets (Stauss et al., 2012) and this inherent variability is also taken into account in model estimations (Parnell et al., 2013; Phillips et al., 2014). We are therefore confident that observed gannet diet fluctuations are not a measurement artefact. Uncertainty also exists about the origin of the mackerels ingested by Northern gannets and whether they are natural prey, or discards.

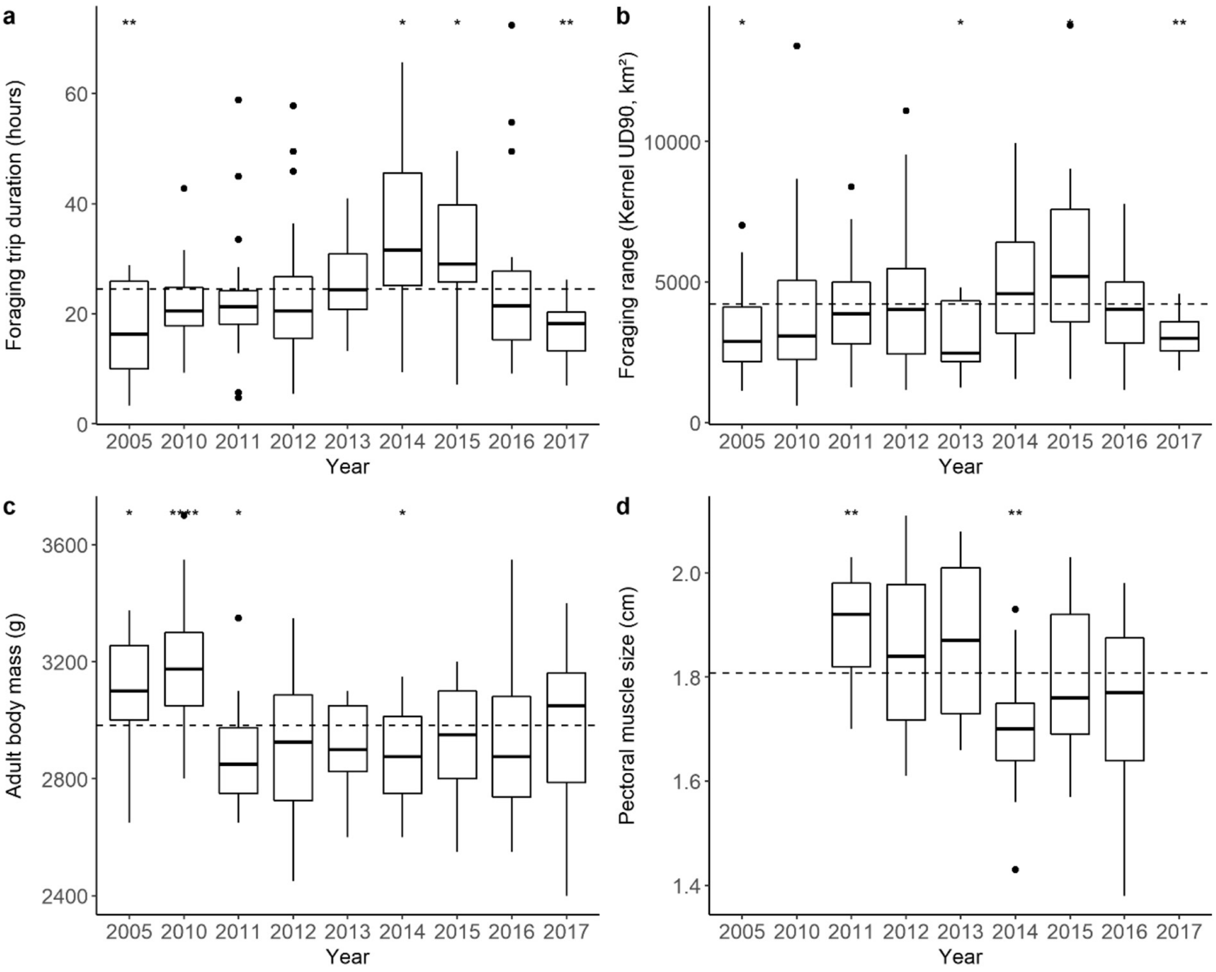

Fig. 4. Annual distributions of foraging trip and body condition characteristics of Northern Gannets from Rouzic Island, 2005–2017. Dotted line gives the mean over the sampled years. Years significantly different to this mean are given by * ($p < 0.05$), ** ($p < 0.01$) and **** ($p < 0.0001$). a. Foraging trip duration (hours). b. Foraging range (kernel UD95, km^2). c. Adult body mass (g). d. Pectoral muscle size (cm).

However, reports and studies of discarding practices in EU waters show that mackerels (a valued item on the seafood market) represent a minute fraction of the overall discarded biomass, whereas gadiforms and gurnards (*Triglidae*) are between the most commonly dumped fish, and major food subsidies to gannets and other seabirds (Depestele et al., 2016; Enever et al., 2007; Uhlmann et al., 2013). Also, the changes in foraging behaviour depending on the mirrored presence of mackerel and discards in the gannet diet comfort our interpretation of mackerels as natural gannet prey.

Surprisingly, Northern gannets increased their foraging effort in terms of trip duration and foraging range as they increased their discard consumption (Fig. 7). This is contrary to the junk-food hypothesis (Grémillet et al., 2008), which posits that discards are easier to access than natural prey for seabirds. This result also contradicts previous studies performed in the same ecoregion, which showed that discards were easier to target for foraging gannets, as birds cue on operating fishing vessels (Patrick et al., 2015; Votier et al., 2010). However it may be explained by two non-exclusive hypotheses: 1) Northern gannet initially prospect for their natural prey before falling back on discards, thereby increasing their foraging range and time at sea. 2) Increased intraspecific competition for discards in the context of rarefied natural prey limit the access to this anthropogenic prey and lengthens foraging time. As a consequence, it is noticeable that across our study period, birds spent more time searching for less profitable food, with a rather logical negative impact on their body condition.

Our results are consistent with previous investigations, which showed that a diet based on discards affects seabird fitness proxies, even when compensated by lower foraging effort (Grémillet et al., 2008). Crucially, we demonstrated that even if adult body mass showed no statistically significant relationship with discard consumption, bird pectoral muscle was impacted significantly (Fig. 7.d). It is, to the best of our knowledge, the first demonstration of the impact of ‘junk food’ on a mass-independent fitness proxy in seabirds. This trend is extremely serious, as adult gannets are considered to be particularly resilient, due to their strong dietary plasticity and their capacity to store body reserves outside of the breeding season (Nelson, 1978). Reduced muscle mass is an indication that birds have already exhausted all fat reserves, and start catabolizing proteins, a process which may lead to irreversible starvation (Le Maho et al., 1981). These results are consistent with Lindstrom et al. (2000), which also used echography to demonstrate pectoral muscle mass variation in waders, in relation to their nutritional status during migration.

Beyond adult body condition, reproductive success, another fitness proxy, may also be affected by discard consumption. Indeed, feeding chicks with fishery waste may impact their growth and fledging success, as demonstrated in closely-related Cape gannets *Morus capensis* (Grémillet et al., 2008). Furthermore, increased foraging effort and deteriorated condition may lead adults to favour their own survival to the detriment of their offspring's (Lewis et al., 2004). This may explain the recently observed drop in the colony breeding success (Fig. 6.a). Specifically, since 2012, the reproductive success of Brittany's Northern gannets has been consistently < 50%, this figure being extremely low

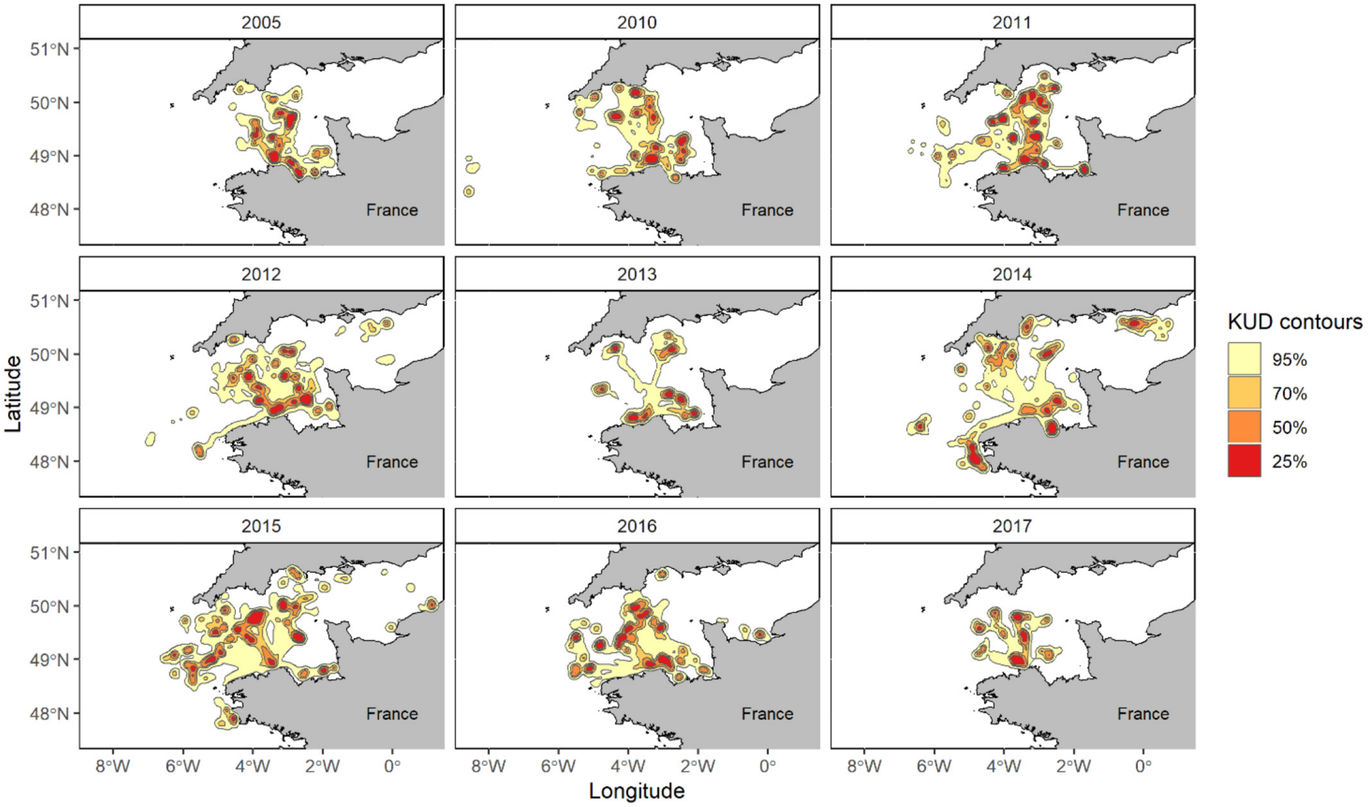

Fig. 5. Foraging range density estimated from kernel density algorithms in Northern Gannets from Rouzic Island, 2005–2017.

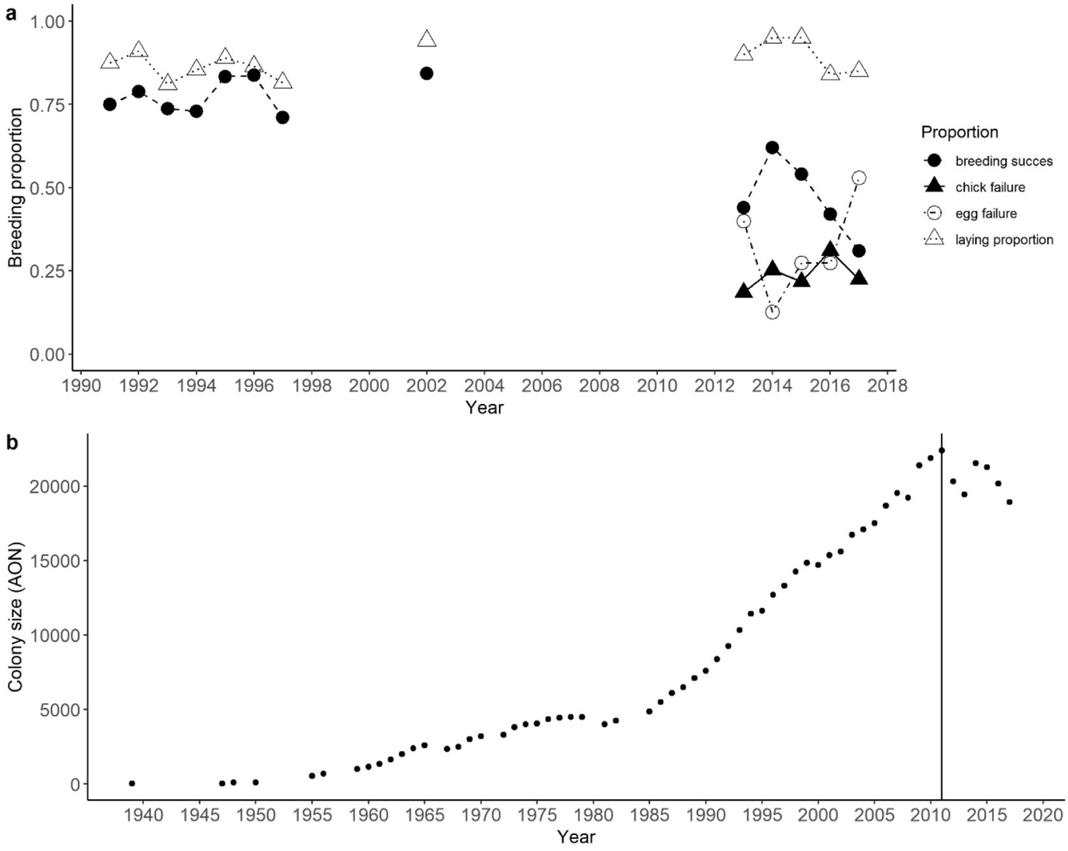

Fig. 6. Population monitoring of Northern gannets from Rouzic Island (1939–2017). a. Trends in breeding success parameters; laying proportion, breeding success, egg failure and chick failure. b. Trend in colony size (apparently occupied nests, AON); a vertical line has been added for the year 2011.

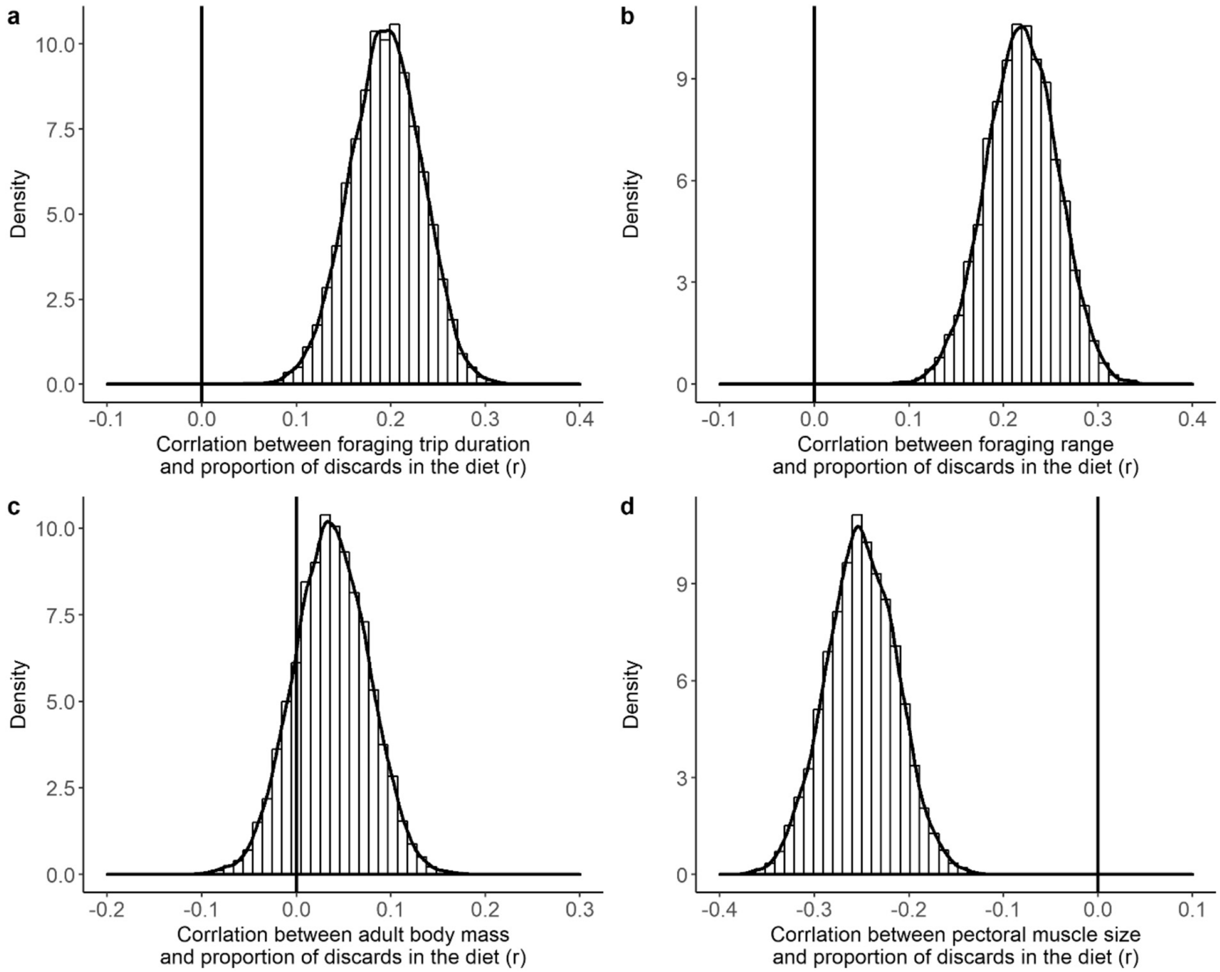

Fig. 7. Correlation between discard proportion in the diet and a) foraging trip duration (hours), b) foraging range (kernel UD90, km^2), c) adult body mass (g) and pectoral muscle thickness (cm) in Northern gannets from Rouzic Island during the 2011–2017 period.

and comparable to drastic breeding performance of conspecifics from the Northwest Atlantic (Franci et al., 2015). It is also important to note that the foraging behaviour and the reproductive performance studies were performed on two different population fractions. Indeed, we only equipped with GPS birds which were successful at the time of chick-rearing, therefore excluding individuals that had already failed. Consequently, GPS-tracked birds might be considered as higher quality individuals compared to the overall population, and effects of marine resource scarcity might actually be stronger at the colony level.

Overall, despite the availability of discards, Northern gannets give a strong signal of food shortage, coherent with multi-decadal competition between seabirds and fisheries on a worldwide scale (Grémillet et al., 2018). A reduction in pelagic fish availability to gannets may be partly due to competition with fisheries (Smith et al., 2011; Pikitch, 2015). Indeed, forage-fish fisheries have boomed in the last two decades to support aquaculture expansions (Froehlich et al., 2018). Mackerel stocks have not been spared, and their North-eastern Atlantic population has declined over our study period, falling under sustainability thresholds (ICES, 2018). This notably led the Marine Stewardship Council to withdrawing its 'Sustainable Fishery' certificate for the Eastern Atlantic Mackerel fishery in March 2019. Also, regional environmental changes, notably the consequences of global warming (Molinero et al., 2013), may act synergistically with fisheries damages, and reduce Mackerel availability to Northern gannet in their southern range (Essington et al., 2015).

4.2. Conservation implication

The fate of the Rouzic breeding colony is emblematic because of the highly charismatic status of Northern gannets, and because of the message they convey about the state of the marine environment (Lescroël et al., 2016). Our findings therefore go far beyond a case study of Northern gannet foraging ecology. They specifically call for an improved management of the marine environment across the ecoregion. Importantly, they underpin the need to reduce fishing pressure on seabird pelagic prey, in a context of synergetic impact with global warming (Essington et al., 2015). Specifically, we support the advice of ICES expert panel to strongly reduce the fishing effort on North Atlantic Mackerel, not only towards a monospecific maximum sustainable yield threshold, but towards ecosystem-based thresholds taking into account the needs of seabirds (Cury et al., 2011) and other marine top-predators.

To conclude, our study points that if fishery discards are to be banned worldwide, marked efforts should also go towards rebuilding pelagic prey populations, which are essential both to apex predators such as seabirds, and more generally to the functioning and viability of marine food webs and of economic activities.

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