Local depletion by a fishery can affect seabird foraging

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Summary

1. Long-term demographic studies show that seabird populations may suffer from competition with fisheries. Understanding this process is critical for the implementation of an ecosystem approach to fisheries management (EAF). Existing studies rely mostly on indirect clues: overlaps between seabird foraging and fishing areas, comparing fish catches by seabirds and vessels.

2. The study is based on a GPS tracking experiment performed in 2007 on one of the main guano-producing seabird species, the Peruvian booby, breeding on an island near the major port for anchovy landings in Peru. The fishery, which is entirely monitored by a Vessel Monitoring System, opened the day we began the tracking experiment, providing a unique opportunity to examine the day-to-day effects of an intense fishing activity on seabird foraging behaviour.

3. We observed a significant increase in the range of the daily trips and distances of the dives by birds from the colony. This increase was significantly related to the concomitant fishing activity. Seabirds progressively became more segregated in space from the vessels. Their increased foraging effort was significantly related to the growing quantity of anchovy removals by the fishery. In addition, daily removals by the fishery were at least 100 times greater than the daily anchovy requirement of the seabird colonies. We conclude that seabirds needed to forage farther to cope with the regional prey depletion created by the intensive fishing behaviour of this open access fishery.

4. *Synthesis and applications.* We show that the foraging efficiency of breeding seabirds may be significantly affected by not only the global quantity, but also the temporal and spatial patterns of fishery removals. Together with an ecosystem-based definition of the fishery quota, an EAF should limit the risk of local depletion around breeding colonies using, for instance, adaptive marine protected areas.

Key-words: competition for prey, fishery management, guano-producing seabirds, Peruvian anchovy

Introduction

The Humboldt Current System (HCS) off the coast of Peru hosts important and iconic guano-producing seabird populations, including Peruvian booby *Sula variegata*, Guanay cormorant *Phalacrocorax bougainvillii* and Peruvian pelican *Pelecanus thagus*, together with one of the biggest forage fish populations (Peruvian anchovy, *Engraulis ringens*) and the world-leading monospecific fishery in terms of landings (>5 millions of metric tons year^{-1} on average since 1960). The HCS also experiences high environmental variability, including El Niño events (e.g. Chavez *et al.* 2008). Guano bird abundance oscillated between 3 and 8 million individuals between the first decade of the twentieth century and 1940s (Jordan & Fuentes 1966), increasing

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up to 16–28 million individuals in 1954–1955 (Jordan 1967; Tovar, Guillén & Cabrera 1987; Jahncke 1998; Tovar & Cabrera 2005) with the implementation of protected nesting areas in 1946 (Duffy 1983a). The industrial anchovy fishery began in the late 1950s. In 1972–1973, the combination of overfishing, the onset of decadal environmental conditions less favourable to anchovy and a dramatic El Niño event caused a collapse in the anchovy stock (Alheit & Niquen 2004; Bertrand *et al.* 2004), and in the dependent seabirds and fishery (Schaefer 1970; Paulik 1971; Tovar 1983; Tovar, Guillen & Nakama 1983). Since then, both the anchovy population and the fishery have recovered, while seabird populations now oscillate at lower levels (0·5–4 million individuals, J. D. Agrorural, personal communication). The fishery has been suspected to be the main driver maintaining the lower seabird population levels than those observed before the development of the industrial fishery (Jahncke 1998; Tasker *et al.* 2000; Jahncke, Checkley & Hunt 2004). Understanding the exact processes by which fisheries affect seabirds is critical for the implementation of an ecosystem approach to fisheries management (EAF).

Seabirds and fisheries may interact in a variety of ways (e.g. Tasker *et al.* 2000; Boyd, Wanless & Camphuysen 2006; Wagner & Boersma 2011). Off the coast of Peru, lethal interaction in accidental bycatch is not a prominent cause of the decline in seabird numbers (Duffy 1983b). Seabirds scavenging on fishery discard, and possibly suffering from a junk food effect (Grémillet *et al.* 2008; Österblom *et al.* 2008; Mullers *et al.* 2009), is also unlikely to be relevant here because (i) seabirds do not generally scavenge on fishing vessel discards in the HCS (Weichler *et al.* 2004; unpublished observation from IMARPE and fishing companies) and (ii) the industrial Peruvian purse seine fishery targets anchovy, the main natural seabird prey. However, as both seabirds and the fishery are active during the daytime in Peru (75% of the fishing sets performed between 07:00 and 14:00 h), seabirds may use local enhancement by fishing vessels to locate prey aggregations. In such cases, birds may even be driven outside their optimal feeding grounds (Bartumeus *et al.* 2010; Votier *et al.* 2010), which may have critical effects, especially during the breeding season.

Direct competition between fisheries and seabirds for fish prey is another type of interaction that has been suspected to influence seabird populations in a number of cases (e.g. Tasker *et al.* 2000; Furness & Tasker 2000; Furness 2006). Reproductive success, rather than direct adult mortality, is the parameter immediately affected by competition with the fisheries (e.g. Cairns 1987; Crawford 2007). In Peru, Furness & Monaghan (1987) mentioned that the anchovy fishery removes the superabundance of food on which the seabirds depend to cope with the recurring crashes induced by oceanographic perturbations like El Niño events. Duffy (1983b) stated that 'commercial fishing competed, not for subsistence food for adults, but for the extra food necessary to successfully raise young'. Understanding the precise mechanisms by which competi-

tion with fisheries may alter seabird reproductive success is a critical question for proposing mitigation measures and implementing an EAF.

Most of the work investigating competition between fisheries and seabirds (e.g. Croll & Tershy 1998; Okes *et al.* 2009; Pichegru *et al.* 2009) relied on the estimation of (i) the overlap of the foraging range envelopes and (ii) respective prey requirements. These estimates provide an indication of the 'potential' for competition; however, they do not describe the precise mechanisms for the interaction between seabirds and the fishery. Seabirds may, over certain ranges in prey availability, develop compensatory strategies (e.g. Kitaysky *et al.* 2000) and mitigate relationships between prey availability and reproductive success through variation in foraging effort (Piatt *et al.* 2007). The critical question for an EAF is therefore to quantify the ranges of prey availability that do not cause a decline in seabird reproductive success. Breeding seabirds have high energetic demands for feeding the chicks and are limited in their foraging range (owing to nest attendance). So prey availability is a matter of regional abundances rather than of global stock biomass. Localized depletions by fisheries, even if performed under a reasonable global catch quota, may be a threat to seabird reproductive success. As such, the fine-scale spatial pattern of the fishing activity is a critical aspect.

The Peruvian anchovy purse seiners fleet has increased from *c.* 400 units in the 1980s up to *c.* 1200 units in 2007 (Fréon *et al.* 2008), with a relatively stable global quota since 1993 (*c.* 6 million tons, except for a reduced quota during El Niño years 1997–1998). This led to a critical fleet overcapacity and a drastic reduction in the fishing season (200 days in 2002, 48 days in 2007). As the fishing season overlaps with the seabird breeding period, such a concentration in the timing of fish removals by the fishery may become critical for seabirds. Using tracking data from fishing vessels and seabirds, we propose to evaluate the extent to which local enhancement by fishing vessels and/or direct competition for prey influence foraging behaviour of breeding seabirds, and whether seabirds develop compensatory strategies when facing reduced prey availability.

The study is based on a GPS tracking experiment performed in 2007 on Peruvian boobies breeding on an island located off the most important port for anchovy landings in Peru. The fishery, entirely monitored by a Vessel Monitoring System (VMS), opened the day we began the tracking study on foraging boobies, providing a unique opportunity to examine day by day the potential effects on seabird foraging behaviour of an intense fishing activity. Specifically, we examine two alternative hypotheses: (i) Seabirds are attracted to clusters of fishing vessels, using local enhancement to find their prey aggregations. In this case, we should observe a constant or growing spatial association between seabirds and vessel foraging areas, and variation in seabird foraging effort should be related to the proximity of the fishing fleet to the breeding colony. (ii) Seabirds need to adjust their foraging effort

because of competition for the prey with the fishery. Under this hypothesis, we should observe a spatial dissociation between seabirds and fishing vessels, and an increase in the seabird foraging effort to buffer to some extent the food shortage created by the fishery removals (Cairns 1987).

Material and methods

SEABIRD DATA

The study was carried out between the 14th and the 28th November 2007 on Isla Guañape Sur (08°33′57S; 78°57′56W), one of the major Peruvian guano bird breeding colonies located 12·1 km off the coast. Isla Guañape lies in the northern region of Peru where the main anchovy fishery ports are located, one of which is Chimbote (137·6 km from Isla Guañape Sur). Peruvian boobies feed almost exclusively on Peruvian anchovy (Jahncke, Checkley & Hunt 2004) and are potentially very sensitive to a reduced availability of this prey. About 172 480 Peruvian boobies were breeding at the time of the study (Agrorural, personal communication, together with *c.* 112 000 Guanay cormorants and *c.* 12 800 Peruvian pelicans), mainly rearing small to large chicks. We fitted miniaturized GPS devices (GipSy GPS, 25–30 g; Technosmart, Rome, Italy) to 59 Peruvian boobies (average mass 1780 g). The birds were sexed by vocal call (when captured, males have a higher pitched call than females; Nelson 2005). The GPS recorded locations at 1, 30 or 60 s intervals and were attached with Tesa® tape on the tail feathers for few days (usually 1 or 2). From the recorded data, foraging trips were reconstructed. Some of the trips were incomplete because of battery limitations (for tags remaining more than 1 day on the animal) and were removed from the analyses. For each complete foraging trip ($n = 49$), we computed the following foraging effort indices: total distance travelled (D, km), maximum distance to the colony, that is, foraging range, (D_{max}, km), time at sea (T, h), sinuosity of the path (S, defined as the ratio $D/2*D_{max}$), average flight speed (FS, km h^{-1}) and proportion of time spent flying (TF, %).

A number of birds (26 individuals) were also fitted with Time Depth Recorders (TDR, G5, 3 g, CEFAS Technology, UK), attached to a metal leg band with Tesa® tape. TDR were programmed to record depth at 1 s interval, and at 0·1 s intervals when submerged. Hydrostatic pressure data were corrected for surface drift and analysed using the IKNOS-Dive program (Y. Tremblay, unpublished data). A dive was deemed to occur whether it lasted at least 2 s and reached a maximum depth of at least 1 m. For each trip, we determined the number of dives (*numD*) and, for each dive, the maximum depth (D_{maxd}, m), and the dive duration (Dd, s). Merging TDR and GPS data enabled identification of the position of the dives and computation of their distance to the breeding colony (D_{dist}, km).

Using these variables to characterize foraging trips and diving performance, we report general patterns of seabird foraging effort (see Appendix S1, Supporting Information for details on statistical analyses).

FISHERY DATA

The anchovy fishery management in Peru is based, among other things, on closures with the aim of protecting both reproduction and recruitment processes of anchovy (e.g. Chavez *et al.* 2008).

These closures separate two main fishing seasons each year, around April–June and November–December. A total allowable catch (TAC) is given separately for each season and the fishery is closed when the TAC is fulfilled. Until 2008, the fishery was open access and fleet overcapacity resulted in a competitive race for fish (Fréon *et al.* 2008). When the fishing season was declared open, a very large fleet arrived on the anchovy fishing grounds within a few hours, and vessels competed to catch as many fish as possible in the shortest time. The second fishing season in 2007 began the day we collected the first tracks from boobies (Fig. 1).

Two types of data were used to describe the deployment of the fishery activity in the Guañape area (defined as a 2° longitude*3° latitude rectangle around the island, i.e. an area of *c.* 74 000 km^2), both data sets are managed by IMARPE. First, we used VMS data describing the vessel movements for the entire anchovy industrial fleet. We used methods described by Bertrand *et al.* (2005) to identify fishing trips from the bulk of VMS positioning data. We estimated the fishing set locations in the tracks using a neural network approach extensively described by Bertrand, Díaz & Lengaigne (2008) and Joo *et al.* (2011). To better visualize the areas of intense fishing activity, we computed a kernel density surface from the fishing set positions (function *kde2d*, 'MASS' library, R). From these data, we computed the distance between fishing sets and the seabird breeding colony. As a daily index of proximity of fishing sets to the colony (FS_{dist}), we used the 0·25 quantile of those distances. Second, we used landing data from each port, available on a daily basis (*catch*). We also computed a daily cumulated catch (*cum.catch*) as this should better represent the effects of fishery removals through erosion of the quantity of prey available in the breeding seabird foraging area.

We quantified the spatial association between fishing sets and seabird dive positions (*clust*) using an approach based on the bivariate Ripley's K-function (Ripley 1976, 1979; Dixon 2002; see Appendix S1, Supporting Information). We investigated the relationships between seabird foraging and fishing activity using nonparametric smoothing regression techniques (GAM and GAMM, see Appendix S1, Supporting Information).

ESTIMATING FISH REMOVALS BY SEABIRDS AND THE FISHERY

To illustrate the magnitude of anchovy removals by the fishery in comparison with those by the seabirds, we first computed the daily anchovy biomass requirements for the multispecific seabird colony present at Guañape Sur at the time of our study. Numbers of breeding and nonbreeding birds for Peruvian boobies,
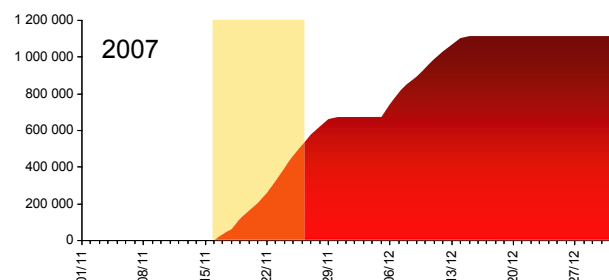

Fig. 1. Daily cumulated landings by the fishery in the studied area. Seabird tracking experiments periods are indicated with yellow bar.

guanay cormorants and Peruvian pelicans were estimated on 30 November 2007 by the island warden from Agrorural. Based on four different allometric energetic equations, Laugksch & Duffy (1984) provided four estimates of daily energetic expenditure (DEE) for adult individuals of all three species. For each species, we used the average DEE value from the four energetic equations, which was converted into wet weight of anchovy (Table S1, Supporting Information). Above their own daily energy needs, breeders also need to deliver energy to their chicks. To take that into account, we first computed the mean species-specific brood size, which was calculated as the mean species-specific clutch size multiplied by the mean species-specific hatching success (Nelson 2005). We then computed the average DEE (and wet weight of anchovy) for chicks of each species using the same method as for adults and considering that the average chicks' weight was $\approx 0\cdot5$ that of adults (Table S2, Supporting Information).

Second, we estimated the available anchovy biomass in the study area. IMARPE usually performs a routine spring (November–December) acoustic survey providing detailed biomass estimates, but this survey could not be performed in 2007 because the scientific vessel was not available. However, 2007 was not an outlier year in term of anchovy biomass (the global fishing quota for Peru was comparable to those of 2000–2006, $c.$ $6\cdot10^6$ t) so we used the average anchovy biomass from 2000 to 2006 as a first approximation of prey fish available in 2007.

Results

GENERAL PATTERNS OF FORAGING TRIPS

Basic statistics of seabird foraging trips are reported in Table 1. We found no significant differences in the GPS foraging variables between males and females. Seabirds performed mostly one trip per day, covering on average 120-km long paths, extending an average of 44 km from the colony, for trips of 3·11 h. Three trips lasted ≥ 6 h, which has been reported to be indicative of food shortage (Vogt 1942). The farthest trip reached 90·5 km from the colony. Flying occupied 86% of the trip duration, at an average speed of 47 km h^{-1}. Females dived slightly deeper than males but there were no other significant differences in the diving parameters between sexes.

DAY-TO-DAY VARIATION IN SEABIRD FORAGING TRIPS AND IN FISHING ACTIVITY

Day by day sequences (Fig. 2) illustrate how breeding seabirds and fishing vessels shared the same fishing grounds at the regional scale. At the local scale, seabirds foraged both in the heart of the fishing aggregations (e.g. 19 November 2007) and outside (26 November 2007). The locations of seabird feeding and fishing spots were highly variable between days, suggesting a highly mobile prey field or, more probably, a fast removal of the prey clusters by the fishery which meant that both predators needed to switch to new prey clusters on a daily basis. The daily changes in the seabird foraging and fishing activity variables are presented in Fig. 3. D_{max}, D and D_{dist} exhibited a shift, switching from no significant trend (17–23 Novem-

ber) to a significant increase (23–27 November; D_{max}: $R^2 = 0\cdot27$, $F_1^{18} = 6\cdot54$, $P = 0\cdot02$; D: $R^2 = 0\cdot26$, $F_1^{18} = 6\cdot38$, $P = 0\cdot02$; D_{dist}: $F_1^{273} = 61\cdot56$, $P < 0\cdot0001$). No significant trend was observed in T or in D_{dur}, while S showed a decrease with time ($R^2 = 0\cdot16$, $F_1^{37} = 7\cdot32$, $P = 0\cdot01$). The clustering index (*clust*) decreased from the 19 November ($R^2 = 0\cdot48$, $F_1^6 = 5\cdot568$, $P = 0\cdot05$) indicating a spatial dissociation between seabird dives and fishing sets during the period. Daily catches increased during the study period ($R^2 = 0\cdot63$, $F_1^8 = 13\cdot5$, $P = 0\cdot01$).

RELATIONSHIPS BETWEEN SEABIRD FORAGING EFFORT AND FISHING ACTIVITY

Results from the GAM and GAMM are presented in Table 2 and Fig. 4. D_{max} significantly increased, while S significantly decreased with the daily cumulated catches. Decreased sinuosity was consistent with the fact that seabirds travelled to remoter areas but their trips did not last longer. The strongest signal was evident for the distance of the dives from the colony (Table 2), significantly explained by *clust* and *cum.catch*. Seabirds dived closer to the colony while they were associated with fishing vessels (Fig. 4d), and the farthest dives from the colony occurred when the seabirds were spatially disconnected from fishing vessels. This suggest that seabirds may have used local enhancement by fishing vessels to some extent, but this was not obligatory and was not the reason why boobies tended to forage farther from the colony during the second period. The model showed also a significant positive relationship between the distance of the dives from the colony and the cumulated catches by the fishery. The more the fishery reduced the quantity of prey fish available in the area, the farther the breeding seabirds needed to forage from the colony to get their food. This trend was especially clear after the fishery removed 350 000 tonnes of anchovy in the Guañape area (Fig. 4).

RESPECTIVE DAILY PREY REMOVALS BY SEABIRDS AND THE FISHERY

We estimated the daily consumption of anchovy by the guano seabird populations from Guañape Sur to have been $c.$ 213·5 metric tons day^{-1} during our study period (Tables S1 and S2, Supporting Information). During the same period, within the same area, the fishery removed an average of 52 000 metric tons day^{-1} (min = 29 000; max = 72 000 tons day^{-1}), that is, 244 times more than seabirds from Guañape Sur. Even if we double the daily removals by seabirds to take into account the neighbouring colonies from Guañape Norte, daily fish removal by the fishery was still more than a hundred times greater than the seabirds.

Spring surveys over the 2000–2006 period estimated anchovy biomasses to 1·771 10^6 ± 0·320 10^6 tons for the study area (7°–10°S). During the 2007 spring fishing season (17 November–15 December), the fishery extracted

Table 1. Basic statistics of the seabird foraging trips by sex; 24 birds with GPS and TDR (Time Depth Recorders), 15 birds with GPS only; results are given as mean ± 1 SD, with the range in parenthesis

|	Total	Female	Male	Sex difference
Number of foraging trips	$N = 49$	$N = 25$	$N = 24$	$N = 49$ (39 for trips per day)
Number of trips per day	$1 \cdot 2 \pm 0 \cdot 22$ (1–2)	$1 \cdot 35 \pm 0 \cdot 41$ (1–2)	$1 \cdot 02 \pm 0 \cdot 06$ (1–2)	GLM with log link and Poisson error $P = 0.495$ (d.f. = 38)
Total distance travelled (D, km)	$119 \cdot 00 \pm 46 \cdot 54$ (45·07–241·90)	$121 \cdot 40 \pm 51 \cdot 06$ (45·07–241·90)	$116 \cdot 20 \pm 41 \cdot 80$ (50·31–195·30)	$W = 224\ P = 0 \cdot 351$
Maximum distance to the colony (D_{max}, km)	$43 \cdot 65 \pm 17 \cdot 48$ (17·91–90·49)	$45 \cdot 96 \pm 19 \cdot 27$ (20·34–90·49)	$41 \cdot 04 \pm 15 \cdot 21$ (17·91–79·31)	$W = 25\ P = 0 \cdot 095$
Trip duration (T, h)	$3 \cdot 11 \pm 1 \cdot 47$ (1·23–8·32)	$3 \cdot 28 \pm 1 \cdot 66$ (1·32–8·32)	$2 \cdot 93 \pm 1 \cdot 22$ (1·23–5·63)	$W = 233 \cdot 5\ P = 0 \cdot 227$
Sinuosity [$S = D/(2*D_{max})$]	$1 \cdot 38 \pm 0 \cdot 23$ (1·08–2·38)	$1 \cdot 33 \pm 0 \cdot 17$ (1·08–1·73)	$1 \cdot 44 \pm 0 \cdot 27$ (1·20–2·38)	$W = 147\ P = 0 \cdot 235$
Flight speed (FS, km h^{-1})	$46 \cdot 48 \pm 3 \cdot 10$ (40·64–51·61)	$47 \cdot 42 \pm 2 \cdot 95$ (41·52–51·61)	$45 \cdot 42 \pm 2 \cdot 97$ (40·64–50·39)	$W = 252\ P = 0 \cdot 084$
% Time flying ($TF\%$)	$85 \cdot 73 \pm 14 \cdot 82$ (23·77–99·75)	$82 \cdot 49 \pm 17 \cdot 53$ (23·77–98·92)	$89 \cdot 40 \pm 10 \cdot 17$ (65·31–99·75)	$D = 0 \cdot 247\ P = 0 \cdot 463$
Dives merged with GPS	$N = 598$	$N = 300$	$N = 298$	$N = 598$ (32 for dives per trip)
No. of Dives per trip ($numD$)	$18 \cdot 12 \pm 13 \cdot 97$ (3–53)	$16 \cdot 67 \pm 13 \cdot 41$ (3–53)	$18 \cdot 62 \pm 15 \cdot 17$ (3–52)	GLM with log link and Poisson error $P = 0.15$ (d.f. = 31)
Dive max depth (D_{maxd}, m)	$3 \cdot 55 \pm 1 \cdot 65$ (1·0–8·9)	$4 \cdot 06 \pm 1 \cdot 58$ (1–8·9)	$3 \cdot 04 \pm 1 \cdot 56$ (1–7·4)	$t = -3 \cdot 18\ P = 0 \cdot 0043$
Dive duration (D_d, s)	$5 \cdot 48 \pm 2 \cdot 72$ (2–22)	$5 \cdot 76 \pm 2 \cdot 86$ (2–22)	$5 \cdot 20 \pm 2 \cdot 55$ (2–21)	$t = -0 \cdot 78\ P = 0 \cdot 445$
Bottom time (s)	$1 \cdot 82 \pm 2 \cdot 25$ (0–15·90)	$1 \cdot 93 \pm 2 \cdot 47$ (0–15·30)	$1 \cdot 72 \pm 2 \cdot 01$ (0–15·90)	$t = -0 \cdot 54\ P = 0 \cdot 5936$
Dive distance to colony (D_{dist}, km)	$42 \cdot 24 \pm 22 \cdot 13$ (0·85–128·20)	$45 \cdot 88 \pm 27 \cdot 92$ (0·85–128·20)	$38 \cdot 59 \pm 13 \cdot 15$ (0·26–63·70)	$t = -1 \cdot 18\ P = 0 \cdot 2484$

FS, flight speed.
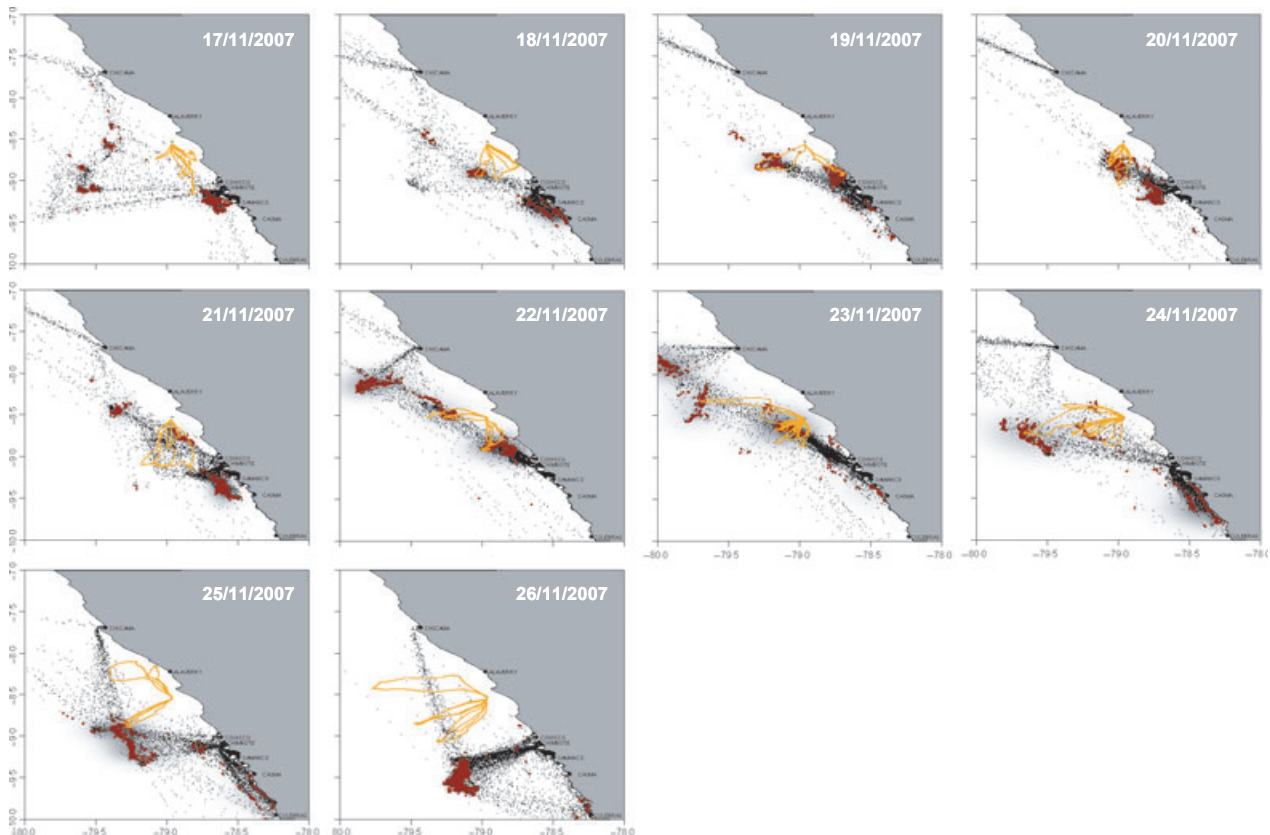
Fig. 2. Overlaid tracks of boobies fitted with GPS (orange lines) and fishing vessel tracks from Vessel Monitoring System (VMS) (black dots) in 2007 around Guañape Sur Island. Fishing set positions estimated from neural network are plotted in red. The grey shade gives a kernel representation of the fishing sets positions.

1 115 424 tons of anchovy (519 121 tons during the tracking experiment, 17 November–27 November) in the study area. We can estimate that the fishery removed *c.* 30% of the available anchovy biomass during the tracking experiment and 63% during the entire fishing season. In comparison, during the tracking experiment, seabirds extracted 0·12% of the available fish biomass.

Discussion

Breeding boobies in Guañape Sur travelled longer distances, for more time and to more distant foraging areas from the colony than previously reported for this species (Duffy 1983c, 1987; Ludynia, Garthe & Luna-Jorquera 2009; Zavalaga *et al.* 2010). Ludynia, Garthe & Luna-Jorquera (2009) and Zavalaga *et al.* (2010) worked, respectively, at the southern and northern limits of distribution of the Peruvian booby, on islands situated further offshore than Guañape Sur (12 km offshore). Anchovy are distributed from the shoreline out to 200 km offshore (Simmonds *et al.* 2011), so there is no obvious reason why seabirds from Guañape Sur should develop a higher foraging effort. What really differs between Guañape Sur and the other study islands is that it lies in the core of the latitudinal distribution of both the Peruvian anchovy (Simmonds *et al.* 2011) and the associated fishery. Although

prey is more abundant and pervasive, competition between conspecifics, with other seabirds and with the fishery is much more important. Competition between seabirds (conspecific and sympatric) possibly creates a zone of food depletion in the surroundings of large seabird colonies, producing the so-called Ashmole's halo (Ashmole 1963). Nevertheless, in our case study, the pelagic character of the prey, and the unbalanced pattern of prey sharing between seabirds and the fishery (two orders of magnitude in favour of the fishery) points more towards competition with the fishery than towards the predominance of such halo effect.

Taking advantage of monitoring seabird behaviour at the opening of a fishing season, we observed daily changes in seabird foraging effort. In particular, a shift in the range of the trips and the distance of the dives to the colony occurred. While presenting no trend in the first period (17–23 November), trip range and distance continuously and significantly increased during the second period (23–27 November). Increased energy requirements because of chick growth cannot be invoked to explain higher needs in prey within such a short period because there was no significant difference in the ages of the chicks from the nests we worked with among days (Kruskal–Wallis chi-squared = 13·42, d.f. = 9, *P*-value = 0·14). A shift in anchovy distribution along the coast does also not provide a satisfying explanation. Despite a high variability
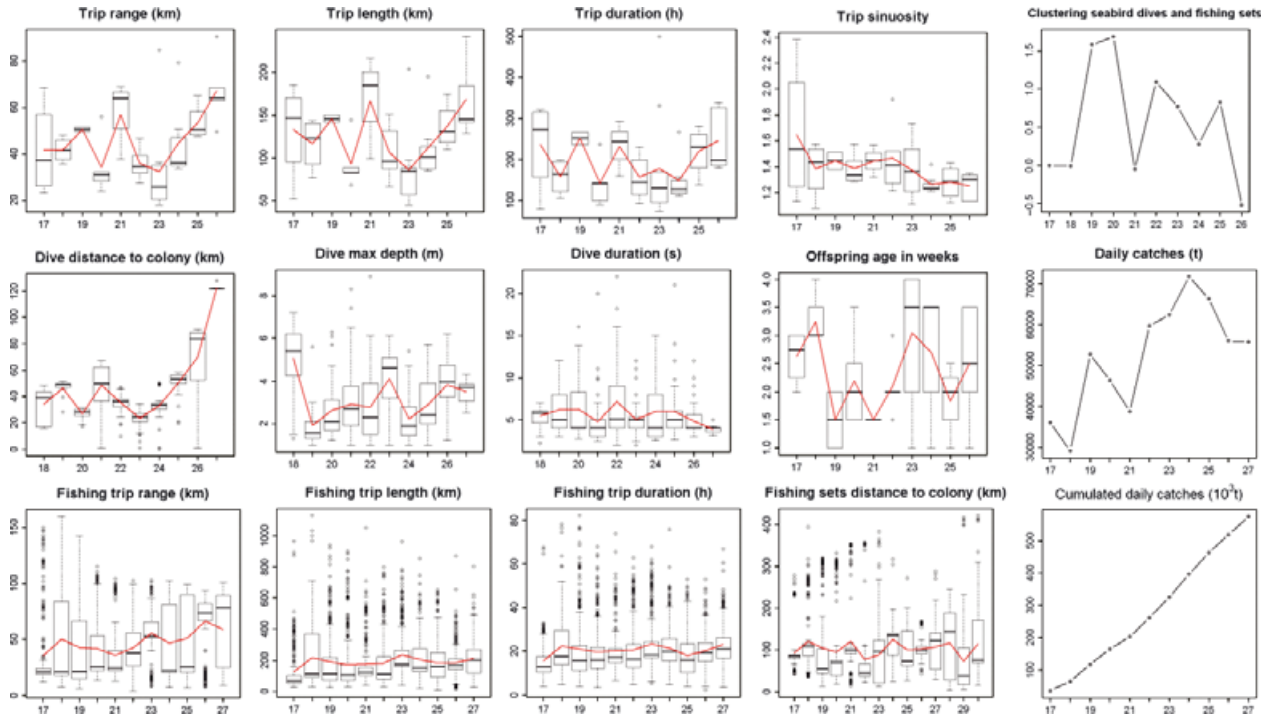
Fig. 3. General daily patterns of the boobies foraging trips and the fishing activity during the study period (17–27 November 2007). The *x*-axis gives the date and the variables considered are: trip range (D_{max}, km), trip length (D, km), trip duration (T, h), trip sinuosity (S), spatial clustering of seabird dives and fishing sets (*clust*), dive distance to colony (D_{dist}, km), maximum depth of the dives (D_{maxd}, m), dive duration (D_d,s), age of the chicks in the working nests, daily catches by the fishery (*catch*, t), fishing trips range (km), fishing trips length (km), fishing trips duration (h), fishing sets distance to colony (FS_{dist}, km), daily cumulated catches by the fishery (*cum.catch*, t).

(e.g. Gutiérrez *et al*. 2007; Bertrand *et al*. 2008), anchovy distribution patterns off the coast of Peru present robust patterns: in austral spring (our study period), anchovy distribution is closer to the coast (Swartzman *et al*. 2008), and aggregations become larger and denser; which should make anchovy more available to seabirds. Moreover, as fishers are able to maintain their activity in the area during the study period, the increased effort from the seabirds cannot thus be linked to a migration of anchovy outside the area.

Conversely, we showed that this increase in the seabird foraging effort was significantly related to the concomitant fishing activity. Results do not support the hypotheses of local enhancement, as seabirds may forage associated with or dissociated from fishing vessels and long trips from the colony were spatially dissociated from fishing vessels. Rather, the increase in the seabird foraging effort was positively and significantly related to the increasing quantity of anchovy removal by the fishery (cumulated catches by the fishery). This result supports the hypothesis that seabirds needed to forage farther to cope with the regional prey depletion created by the fishery. The prey depletion by the fishery is illustrated by the magnitude of the removals (*c.* 30% of the local biomass in 10 days) and by the observed effect of a single purse seine set on an anchovy aggregation (Fig. S1, Supporting Information). From this example from a single vessel, one may speculate that hundreds of such vessels competing for fish may create a true

gap in the anchovy distribution within few days. Therefore, our results provide an illustration of a compensatory strategy developed by breeding seabirds when facing local depletion generated by a specific configuration of the fishing activity (overcapacity, concentration in time of the fishing season, substantial overlap with the seabird breeding season and foraging grounds).

Since this study in 2007, changes have occurred in the Peruvian fishery. First, the fishery is no longer open access. Individual quotas were implemented in April 2009. Each fishing company being provided with its own quota, the competitive race for fish disappeared and the fishing season is now much more extended: for the North-centre fishery, 5.3×10^6 tons of anchovy were fished in 48 days in 2007, while 5.5×10^6 tons were fished in 189 days in 2009. Whereas the total quantity of anchovy removed remains comparable, the daily amount of fishery removals is much lower (*c.* 110 000 tons day^{-1} in 2007 vs. *c.* 29 000 tons day^{-1} in 2009). Owing to the highly mobile behaviour of anchovy, the probability of local intense depletions is probably lower today. Second, in 2010, 22 islands and 11 headlands hosting breeding colonies of guano-producing seabirds were designated as National Reserves by the Ministry of Environment, including a surrounding 3·7-km marine area. Our data indicate that this area is not sufficient to sustain the foraging of seabirds. In addition, control facilities are still weak to efficiently enforce the protection of these protected

areas. However, this is a crucial first step towards seabird conservation as far as the law and the fishery managers are concerned. As suggested by Crawford (2007) and Pichegru

Table 2. GAM and GAMM results for GPS- and TDR-derived seabird foraging variables (D_{max}, maximum distance to the colony; D, total distance travelled; S, sinuosity of the path; D_{dist}, dive distance to colony) as a function of the distance of the fishing sets to the breeding colony (FS_{dist}), the spatial association between seabird dives and fishing sets (*clust*) and the daily cumulated catch by the fishery (*cum.catch*)

Variable	Adjusted R^2	FS_{dist}	*clust*	*cum.catch*
D_{max}	**0·236**	$F = 1.497$	–	**$F = 3.576$**
		$P = 0.221$		**$P = 0.0256$**
D	0·145	$F = 0.657$	–	$F = 3.026$
		$P = 0.3911$		$P = 0.0508$
S	**0·150**	$F = 1.098$	–	**$F = 7.340$**
		$P = 0.281$		**$P = 0.009$**
D_{dist}	**0·615**	$F = 0.729$	**$F = 3.436$**	**$F = 6.568$**
		$P = 0.470$	**$P = 0.022$**	**$P = 3.9e\text{-}5$**

FS, flight speed; TDR, Time Depth Recorders; values in bold correspond to statistically significant results..

et al. (2009) for South African seabirds, establishing areas closed to fishing, at least temporarily during the breeding season, around the main seabird colonies seems a reasonable management option to consider. Although first mentioned a long time ago in Peru (Murphy 1936), this management option was never implemented. It may be that the recent interest of the fishing companies in the certification process (implying good environmental practices) will finally allow this management option to move beyond paper proclamations.

We showed here that not only the global quantity but also the temporal and spatial patterns of fish removals by fisheries have important effects on foraging success in breeding seabirds. An ecosystem-based definition of fishery management (e.g. Furness & Tasker 2000; Murawski 2000) should therefore (i) take into account the needs of the natural predators at the stock scale (e.g. Duffy 1983b), using for instance the 'one-third for the birds' rule (Cury *et al.* 2011) for defining the fishing quota and (ii) limit the risk of local depletion around breeding colonies by limiting fishing effort. The economic rationalization of the fishery, as
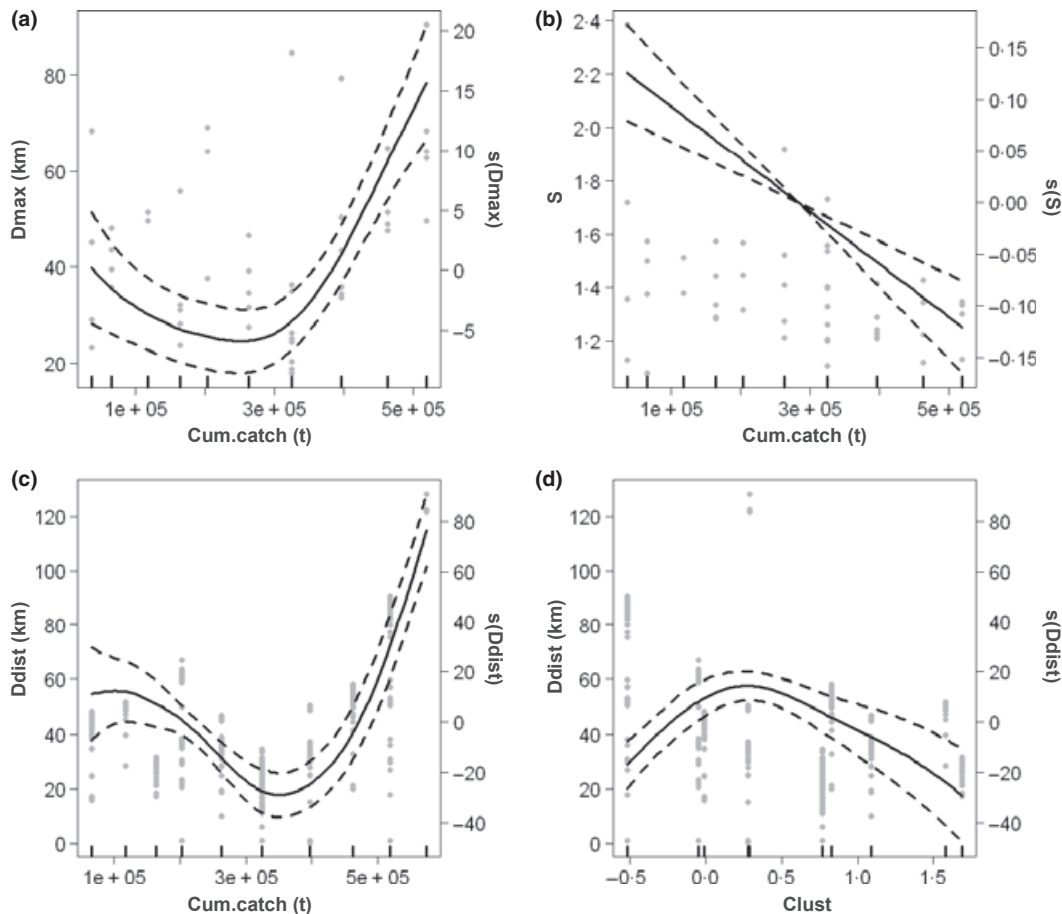

Fig. 4. Fitted GAM and GAMM results showing the relationship between the seabird foraging effort and the fishery activity in the Guañape area: range (a) and sinuosity (b) of the seabird foraging trips as a function of the fishery daily cumulated catch; dive distance to the colony (c) as a function of the fishery daily cumulated catch; dive distance to the colony (d) as a function of the spatial association between seabirds and fishing vessels. Left *y*-axis gives the original variable value; right *y*-axis gives the smooth transformed value; *x*-axis for (a), (b) and (c) gives daily cumulated catches in tons (*cum.catch*); *x*-axis for (d) gives daily index of spatial association between seabirds and fishing vessels (*clust*).

implemented in Peru through individual quotas, reduces the risk of local depletion by spreading the fishery removals over longer periods. Limitations of effort around breeding colonies could also be achieved by the design of specific, possibly temporal, adaptive marine protected areas (MPA). These coastal pelagic MPA would have the particularity to be fixed in space (centred on the breeding colonies), while adaptive in size and duration, according to the given fish prey biomass and the seabird breeding phenology.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Echograms collected onboard an industrial fishing vessel exactly at the same location before a set (a) and just after a set (b).

Table S1. Parameters used to estimate the daily anchovy consumption by individuals of each species of guano-producing seabirds.

Table S2. Estimation of fish removals by seabirds.

Appendix S1. Additional information on statistical analyses performed on seabird and fishery data.

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