



# Interactions between anchovy fisheries and Peruvian boobies revealed by bird-borne cameras and movement loggers

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**ABSTRACT:** Fisheries threaten marine predator populations through bycatch and competition for the same resources, but may also provide feeding opportunities. Understanding benefits and mitigating impacts, therefore, requires a detailed understanding of fishery interactions. The Humboldt Current system supports the world's largest single-species fishery (Peruvian anchoveta *Engraulis ringens*), along with abundant marine predators dependent on these forage fish, including seabirds. We combined bird-borne video cameras and GPS-acceleration-dive loggers to quantify the foraging behaviour of chick-rearing Peruvian boobies *Sula variegata* around Isla Macabi, Peru, in December 2020 and May 2021. Videos revealed that 18 % of 77 Peruvian booby foraging trips included feeding at actively fishing purse seine vessels, diving in and around the nets. Most vessel interactions were close to the colony, and we found no difference in foraging effort (e.g. trip duration) between trips with and without vessel interactions. We recorded fishing effort in the foraging range of the colony using remotely sensed data from the vessel monitoring system accessed via Global Fishing Watch, finding more frequent interactions and catch depredation when fishing effort was high near the colony. We found no evidence that birds expended additional energy (e.g. dynamic body acceleration) or travelled to different locations to reach vessels. We emphasise the value of combining high-resolution movement and video loggers with remotely sensed fisheries data to monitor seabird–fishery interactions in detail, rather than just spatio-temporal overlap, and assess the potential for competition and bycatch. Threatened seabird populations may benefit from no-take zones or reduced fishing effort in core foraging areas of colonies.

**KEY WORDS:** Seabird–fishery interactions · Fishing impact · Seabirds · Humboldt Current · Anchoveta · *Sula variegata* · Bio-logging · Vessel monitoring system

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## 1. INTRODUCTION

Fisheries are an important source of food and livelihoods, but can have major impacts on marine ecosystems (Halpern et al. 2008). Fishing affects marine predators, principally through bycatch mortality (Lewison et al. 2004) and reducing prey availability

(Cury et al. 2011, Grémillet et al. 2018). Seabirds are sentinels of ocean health and are especially impacted by bycatch and competition with fisheries that target low trophic level 'forage fish' (Sydeman et al. 2017, Dias et al. 2019). Competition can be intense during the breeding season, when adults must find sufficient food for themselves and for their offspring close

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to breeding colonies (Ashmole 1963, Birt et al. 1987, Weber et al. 2021). However, fisheries can provide food for seabirds (Furness 2003). Previous research has focused on the use of discards (e.g. Votier et al. 2004, Michel et al. 2022) and bait (e.g. Orben et al. 2021), but seabirds also depredate catch and target spilt, dead or injured fish around fishing gear (Clark, 2020).

A detailed understanding of seabird–fishery interactions is key to management and conservation, but quantifying them is challenging. Tracking the movements of individual birds in relation to remotely sensed vessel information has become a key tool (Votier et al. 2010, Orben et al. 2021). Identifying the spatio-temporal overlap between boats and birds provides the priority sites and times for advocacy and potential protection, for which animal tracking data can be a key input (Maxwell et al. 2015, Davies et al. 2021). However, these methods cannot necessarily differentiate between spatio-temporal overlap and interactions. In contrast, bird-borne video cameras allow us to identify not only interactions, but also fine-scale behaviours related to prey intake and bycatch risk (Grémillet et al. 2010, Votier et al. 2013, Michel et al. 2022). This detailed information on seabird–fishery interactions is vital for prioritising and implementing conservation measures and ecosystem-based management, such as reducing fishing effort or creating ‘no-take’ zones (Okes et al. 2009, Ainley et al. 2018, Sydeman et al. 2021).

The Humboldt Current system is a highly but variably productive upwelling region along the Pacific coast of South America (Gutiérrez et al. 2016). It supports the Peruvian anchoveta *Engraulis ringens* purse seine fishery (Chavez et al. 2008), which has the largest recorded landing for any species worldwide, with over 7 million tonnes in 2018, 10 % of the global marine catch (FAO 2020). The annual anchovy catch is attained in 2 fishing seasons, austral autumn (April–June) and spring–summer (October–December; Oliveros-Ramos et al. 2021), and is influenced by El Niño events, with warmer waters being unfavourable for anchovy recruitment (Cahuin et al. 2009). The Humboldt Current system also sustains a globally important marine predator assemblage, including pinnipeds and cetaceans, and seabirds that provide commercially important guano (Duffy 1983b, Tam et al. 2008, Espinoza et al. 2017).

In the northern Humboldt Current, in Peru, the purse seine fishery operates mostly within 90 km from the shore (Bertrand et al. 2008), which is in the foraging ranges of breeding seabirds (Weimerskirch et al. 2012, Boyd et al. 2014, Zavalaga et al. 2010a). Increased

foraging effort and population declines of guano birds (i.e. Near Threatened guanay cormorant *Leucocarbo bougainvillii* and Peruvian pelican *Pelecanus thagus*, and Peruvian booby *Sula variegata*) have been linked to anchovy harvest by fisheries (Duffy 1983a, Bertrand et al. 2012, Barbraud et al. 2018). Moreover, bycatch may be a threat to seabirds here; it is not well studied for the purse seine fleet in Peru, but 54 % of 59 interviewed fishers mentioned seabird bycatch in a 2009 study (Ayala 2012). Elsewhere, many seabird species are bycaught in purse seines targeting forage fish (Oliveira et al. 2015), including sulids in the southern Humboldt Current (Suazo et al. 2014). Purse seine bycatch can be difficult to record as it can be rare but involve high numbers of birds killed in a single event (Norris et al. 2020, Christensen-Dalsgaard et al. 2022). Discards and bait are not available from purse seiners in Peru, but they may provide access to food trapped inside nets, which may buffer against the effects of competing with fishing vessels. Depredation is common among marine predators (Tixier et al. 2021), but not well understood for seabirds.

Here, we studied interactions between the Peruvian anchoveta purse seine fishery and Peruvian boobies in northern Peru. We used bird-borne video cameras and high-resolution GPS, tri-axial acceleration and dive depth loggers to describe and map individual interactions with fishing vessels, and identify the type of vessel. We tested for differences in effort between foraging trips with and without vessel interactions, while controlling for season, sex and brood size. If purse seines are more easily available food than natural prey schools, we would expect lower energetic expenditure for birds feeding at vessels in comparison to natural prey. We assessed the effect on the proportion of trips containing vessel interactions per day of active fishing hours for all vessels in each grid cell in the foraging range of the colony using remotely sensed data (Kroodsma et al. 2018). In doing so, we evaluated the potential impact of anchoveta fisheries on seabirds and the utility of using bird-borne bio-logging to study this association.

## 2. MATERIALS AND METHODS

### 2.1. Study site and sampling

Fieldwork was carried out on Isla Macabi (7.81° S, 79.50° W) during 2 seasons (2–11 December 2020 and 8–21 May 2021), during which no El Niño conditions were reported. Macabi is in northern Peru, near

the core of Peruvian anchoveta fishing activity, and the proportion of anchoveta in the Peruvian booby diet is particularly high in this region (Jahncke & Goya 1988). There were ~71 000 boobies at the colony in December 2020 (Burga & Valencia 2021a) and ~66 000 in May 2021 (Burga & Valencia 2021b). We captured 117 chick-rearing adults (39 in December 2020 and 78 in May 2021) at the nest soon after dawn (06:00–08:00 h) using a monofilament lasso attached to a 5 m telescopic pole. We selected nests containing 1–3 chicks between 3 and 8 wk old (identified from size and the presence of contour, wing and scapular feathers). Both parents were present, ensuring that chicks were not left unattended. Using Tesa® 4651 waterproof tape, we equipped each bird with a miniature video camera (Techcam, 32 g, resolution 720 P, Technosmart Europe). In addition to cameras, birds were equipped with either a 5 or 25 g combined GPS-acceleration-dive logger (Axy-Trek, Technosmart Europe), making the total tag mass 37 or 57 g, respectively. In December 2020, 18 of 39 Axy-Treks were 25 g and all Axy-Treks in May 2021 were 25 g. We did not attach tags with combined masses of over 5% of bird mass (Fair et al. 2010). Birds weighed between 1200 and 1750 g, leading to variation in the proportion of the mass of the tag compared to the bird (2.55 to 4.75%). The procedure usually took <10 min from capture to release. The Axy-trek was attached to the middle back feathers whereas the video camera was attached right behind the Axy-trek and above the uropygial gland, protecting the camera against the impact of the plunge dive. The camera lens faced forwards, with the lens placed at the highest possible point within the camera logger to maximise the view that included the bird's head. The front of the camera logger had a streamlined shape to reduce impact on air and water resistance, particularly during plunge dives, with the lens inset into a ~50° slope, and the front of the camera logger reaching a ~20° slope towards the bird's body. We set the Axy-Trek loggers to record GPS location every 1 or 10 s, dive depth at 1 s intervals and acceleration between -4 and 4 *g* at a frequency of 25 Hz. Video cameras recorded continuously from deployment until the battery was exhausted after ~6 h. Birds were recaptured late afternoon (15:00–18:00 h) on the day of tagging (except one individual that was recaptured within 18 h). If birds spontaneously regurgitated on recapture, the sample was analysed for diet composition. A permit to work on the island was issued by the Servicio Nacional de Areas Naturales Protegidas por el Estado Peruano (Resolución Jefatural no. 01-2020-RNSIIPG-SERNANP). Bird

capture and handling procedures were approved by the Comité Institucional de Etica en Investigación con Animales y Biodiversidad de la Universidad Científica del Sur (Constancia no. 076-CIEI-AB-CIENTIFICA-2020).

## 2.2. Vessel interactions from bird-borne cameras

We coded behaviours from the videos, recording the start and end of the foraging trip, the number of dives with and without vessels, and the start and end time of each interaction with a vessel. We defined interactions as when the bird flew around the vessels and their nets, and performed dives or landed on the water close to the net or vessel. We did not include encounters where vessels were visible at a distance but the bird continued to fly (i.e. in transit). We modelled the occurrence of vessel interactions in foraging trips in relation to the season, sex and brood size using a generalised linear model with a binomial error family and a logit link (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m701p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m701p145_supp.pdf)). We used R version 3.6.0 for all data processing and analysis (R Core Team 2022). For all statistical analysis, we checked model fit by simulating residuals using the 'DHARMA' R package (Hartig 2020), and conducted backwards stepwise selection retaining variables for which  $p < 0.05$ .

## 2.3. Foraging effort

We identified foraging trips from the GPS data. To do this, we calculated the distance between each GPS location and the colony location using the 'geosphere' package in R (Hijmans 2017). We then identified the nest location for each bird as the modal latitude and longitude rounded to 3 decimal places within 1 km of the colony. We defined the start and end of a foraging trip as when the birds crossed a radius of 100 m around the nest. We removed all tracks during which the bird did not travel over 1 km from the colony and visually checked all tracks to remove those where the bird did not dive or land on the water (e.g. preening). We matched the recorded foraging trips in the video and movement data. Data from both devices covered more than one foraging trip for 2 individuals, so we took the first trip for our analysis to avoid pseudoreplication because this provided too few repeat trips to use a mixed effect modelling framework. We categorised foraging trips into those that contained an interaction with a fishing

vessel and those that did not. We calculated 3 measures of foraging effort from the GPS data: the duration of each foraging trip, the maximum distance reached from the colony, and the total distance travelled. Using the acceleration data, we calculated overall dynamic body acceleration (ODBA) for each position as a measure of relative energetic expenditure (Wilson et al. 2006, Halsey et al. 2011). Dynamic body acceleration is correlated with energetic expenditure measured using the doubly labelled water method for chemically estimating field metabolic rates in seabirds (Elliott et al. 2013), including another sulid, the Australasian gannet *Morus serrator* (Angel 2015). At the level of the foraging trip, we calculated the mean ODBA (relating to average energetic expenditure per unit time), and the trip ODBA as the mean ODBA multiplied by the trip duration (relating to total energetic expenditure; Clark 2020). Using the dive depth data, we recorded the time spent diving during each foraging trip (at depths greater than 0.5 m to exclude periods of inactivity resting on the water). We modelled mean ODBA using a linear model (Gaussian error family and identity link). We used generalised linear models with Gamma error families and inverse links for duration, distance and trip ODBA, and a generalised linear model with a negative binomial error family and a log link for the number of seconds spent diving below 0.5 m (Table S1). We modelled each foraging trip characteristic in relation to the occurrence of a fishing vessel interaction and also season, sex and brood size, as these variables can affect seabird foraging trip characteristics (Grémillet 1997), including in sulids (Weimerskirch et al. 2006, Zavalaga et al. 2010b, Cleasby et al. 2015, Clark et al. 2021). We also included the proportion of tag mass as a proportion of bird mass to measure any possible effect of instrumentation. We did not have a sufficient sample size to fit interaction terms. The video coverage of the trip was 100% for 47 of the 77 birds (mean = 87%), but this varied (22–100%), so to ensure that the estimates were not being strongly impacted by the foraging trips with low coverage, we also ran the foraging trip models using only trips with video coverage over 80% (n = 56).

#### 2.4. Fishing vessel availability

To assess fishing vessel availability, we used fishing effort data from Global Fishing Watch sourced from vessel monitoring system (VMS) data provided by the Peruvian Government's Ministry of Production, Fisheries Sector, and automatic identification system

data obtained and processed by Global Fishing Watch ([www.globalfishingwatch.org](http://www.globalfishingwatch.org)). Global Fishing Watch estimated apparent fishing hours based on vessel identification and vessel speed and direction (Kroodsma et al. 2018). We uploaded polygons for the mean maximum distance from the colony (33 km) and the maximum distance reached by any bird (120 km inclusive of the 33 km radius), and recorded the daily estimate of total apparent fishing effort within each polygon for all vessels combined for each day that birds were tracked (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m701p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m701p145_supp.pdf)). These 2 measures were not strongly correlated ( $r = -0.133$ ,  $t_{20} = -0.601$ ,  $p = 0.555$ ). We modelled the number of foraging trips with and without vessel interactions in each day in relation to the estimated apparent fishing effort within 120 and 33 km and the season, using a binomial generalised linear model with a logit link (Table S1).

### 3. RESULTS

#### 3.1. Vessel interactions from bird-borne cameras

Video data revealed booby foraging behaviour under natural conditions and close to purse seiners fishing for anchoveta where birds dived inside and near to the nets (Fig. 1). No other vessel types were recorded. We had adequate video and movement logger coverage for 77 foraging trips, of which 14 (18%) contained vessel interactions (Fig. 2). There was no relationship between vessel interaction occurrence and sex, season or tag mass, but a slight increase with brood size (Table 1). These interactions occurred at a mean of 19.4 km from the colony (range: 6.3–55.4 km), which is within the maximum distance reached during a foraging trip for 77% of recorded trips. Many foraging events occurred alongside other seabirds including Peruvian boobies, Peruvian pelicans, guanay cormorants and Franklin gulls *Leucophaeus pipixcan* (Fig. 1d).

#### 3.2. Foraging effort

We calculated 6 mean foraging trip characteristics as measures of effort (Table 2). Foraging effort was similar for birds that we did or did not record attending fishing vessels, apart from a higher total trip ODBA when vessels were present (Table 1, Fig. 3). We found some seasonal differences, with greater maximum and total distance, and mean and trip



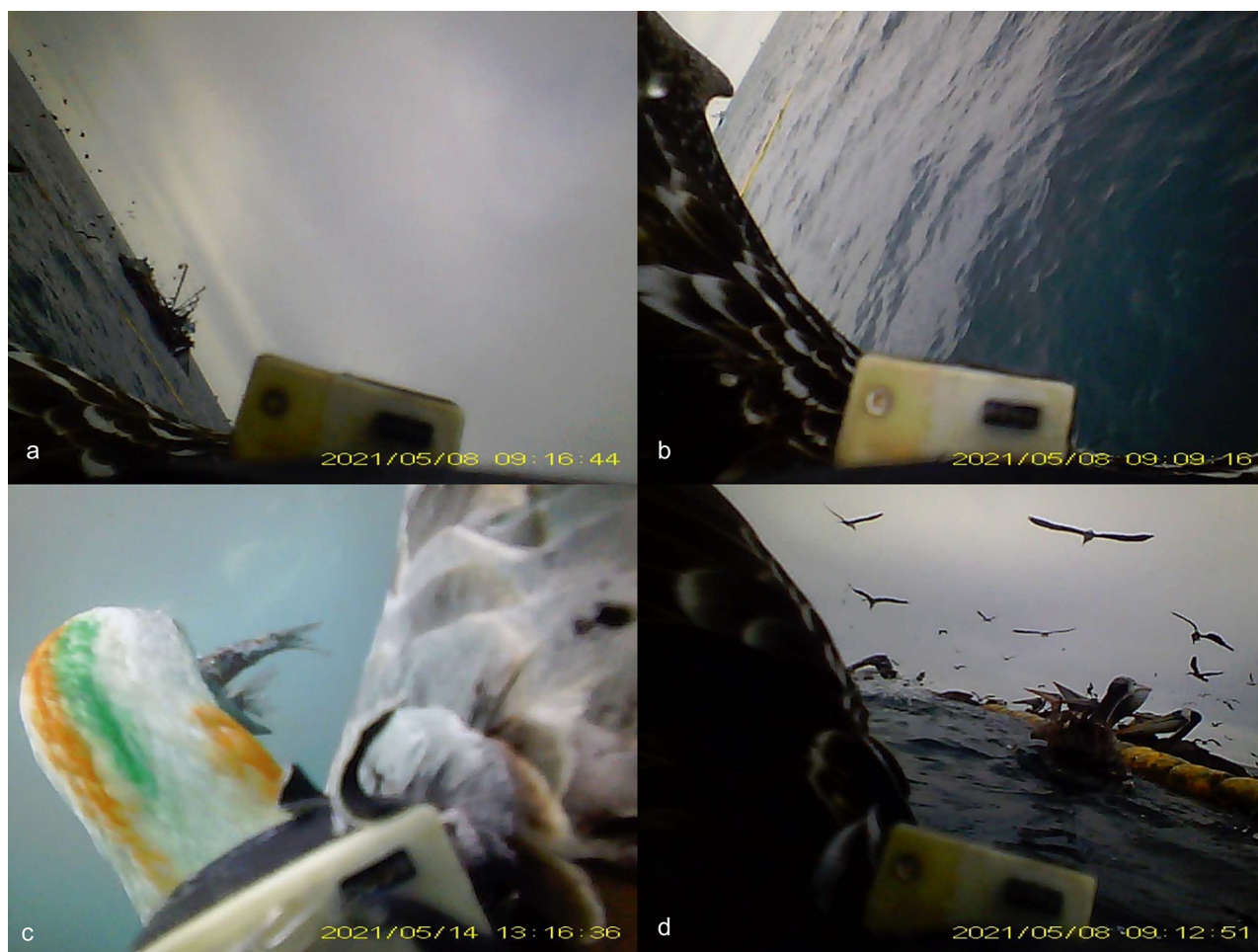


Fig. 1. Images from video camera deployed on foraging Peruvian boobies *Sula variegata* (a) approaching a purse seine fishing vessel, (b) prior to a dive inside the purse-seine net (yellow) of an anchoveta fishing vessel and (c) collecting a dead fish under the water near a net, and (d) after a dive alongside Peruvian pelicans *Pelecanus thagus*

ODBA (Table 1, Fig. 3). The only difference detected between the sexes was that females spent more time diving below 0.5 m (Table 1, Fig. 3). We found no relationship between the proportional of the tag mass to the bird mass in trip duration, distance travelled or ODBA, but we found that birds spent more time diving below 0.5 m with heavier proportional tag mass (Table 1, Fig. 3).

### 3.3. Fishing vessel availability

Remote sensing data showed fishing vessel activity within the 120 km booby maximum foraging radius from the colony during all 22 tracking days (Fig. S1, Table S2). The Global Fishing Watch algorithm for determining whether vessels are actively fishing (Kroodsmma et al. 2018) estimated high fishing effort for vessels classified as ‘purse seines’

within the 33 km radius, and estimated high fishing effort for ‘purse seines’ and ‘drifting longlines and squid jiggers’ between 33 and 120 km (Fig. 4). The number of estimated fishing hours per day for all vessels combined varied greatly from 0 to 626 h within 33 km (mean = 99 h) and from 186 to 5048 h within 120 km (mean = 1782 h; Fig. S1, Table S2). The closest port to the colony (Malabrigo) was closed due to bad weather from 16 to 19 May 2021. The proportion of foraging trips per day that contained vessel interactions was higher when there was more estimated fishing effort within the 33 km radius ( $\chi^2_1 = 38.241$ ,  $p < 0.001$ ; estimate =  $0.018 \pm 0.006$ ; Fig. 5), but not within 120 km ( $\chi^2_1 = 0.956$ ,  $p = 0.328$ ; estimate =  $0.0005 \pm 0.0004$ ). The proportion of foraging trips per day that contained interactions with vessels was not related to whether days occurred in the December 2020 season or May 2021 ( $\chi^2_2 = 0.067$ ,  $p = 0.796$ ; estimate =  $0.442 \pm 1.735$ ).

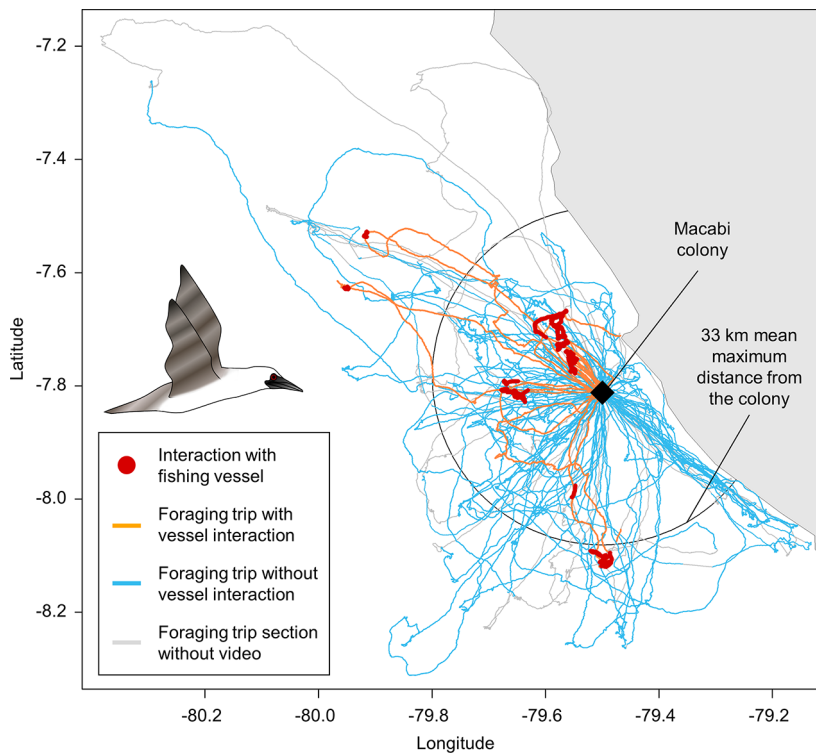


Fig. 2. Peruvian booby *Sula variegata* foraging trips with (orange) and without (blue) interactions with fishing vessels. Grey shows the part of each track that did not have video coverage. Red points show the location of the interactions with vessels within the foraging trip. The black circle around the colony indicates the 33 km mean maximum distance from the colony across all foraging trips

### 3.4. Diet

The vast majority of Peruvian booby diet was anchoveta in both seasons, with 95% (36 of 38 samples) in December 2020 and 98% (62 of 63) in May 2021. The remainder in December 2020 was South Pacific sauri *Scomberesox sauri scombroides* in 1 sample (2.6%) and unidentified fish in 2 samples (5.3%). The remainder in May 2021 was silverside *Odonthestes regia regia* in 3 samples (4.8%) and horse mackerel *Scomber japonicus* in 2 samples (3.2%).

## 4. DISCUSSION

Our bird-borne video cameras showed chick-rearing Peruvian boobies foraging for anchoveta around actively fishing purse seiners, sometimes diving in and around hauling nets indicating catch depredation. However, we found no differences in foraging effort between birds that attended vessels and those that did not. Moreover, the proportion of foraging

trips per day containing fishing vessel associations was positively correlated with estimated fishing effort. We discuss these findings and the implications for using bird-borne loggers to inform fisheries management.

### 4.1. Vessel interactions, foraging effort in relation to vessel interactions, and vessel availability

Overall, 18% of 77 booby foraging trips included interactions with purse-seiners characterised by plunge dives for caught, spilt, dead or injured anchovies inside and around the edge of hauling seine nets. This is important because research has generally focused on bait or discard (unwanted or undersize fish and offal) consumption (Votier et al. 2004, Orben et al. 2021). Seabird depredation is not well understood but is likely to be a growing issue as it is for other taxa, due to stock depletion (Tixier et al. 2021), and because fishers may not be incentivised to avoid depredation (Janc et al. 2021). We did not detect any differences in trip length or ODBA depending on whether birds attended vessels, controlling for season,

sex, brood size and tag mass (Fig. 3, Table 1). A similar comparison of northern gannets foraging naturally and at vessels in the northeast Atlantic also found no differences in energy expenditure (Clark 2020). Most vessel interactions occurred near the colony, and more foraging trips contained interactions when there was a high level of estimated fishing effort close to the colony, but not when vessels were only available within the maximum foraging range from the colony. As birds did not expend additional energy or travel to different locations to reach vessels, our results are consistent with the evidence from concurrent GPS and VMS tracking (Bertrand et al. 2012), and demographic modelling (Barbraud et al. 2018) that fisheries compete with seabirds in this region. However, it is unclear whether prey intake varied between vessel-related or natural foraging. Furthermore, diving close to nets and other fishing gear represents an entanglement risk, supported by an observation of a camera-tagged Peruvian booby at another site (Guañape Norte) becoming trapped in the net for 2.75 min before escaping (C. B. Zavalaga unpubl. data). However, we do not know how this

Table 1. Effect sizes and statistical tests for the relationship between foraging trip characteristics and the occurrence of interactions with vessels, season, sex and tag mass (units or categories compared to the reference categories are given in parentheses). Numbers in square brackets indicate the order of removal during backwards stepwise selection (1 = variable removed first). ODBA: overall dynamic body acceleration. **Bold** indicates  $p < 0.05$

Response variable	Explanatory variable		
	Vessel (Present)	Season (May 2021)	Sex (Male)
Vessel interaction	NA		
Trip duration (h)	[4] Est. 0.114 ± 0.091; $\chi^2_1 = 1.792$ , $p = 0.181$	[3] Est. 0.691 ± 0.727; $\chi^2_1 = 0.980$ , $p = 0.322$	[2] Est. -0.259 ± 0.634; $\chi^2_1 = 0.169$ , $p = 0.681$
Maximum distance (km)	[3] Est. 0.010 ± 0.006; $\chi^2_1 = 2.883$ , $p = 0.090$	[5] Est. 0.095 ± 0.057; $\chi^2_1 = 2.637$ , $p = 0.101$	<b>Est. 0.812 ± 0.404;</b> <b><math>\chi^2_1 = 4.291</math>, <math>p = 0.038</math></b>
Total distance (km)	[4] Est. 0.003 ± 0.002; $\chi^2_1 = 2.338$ , $p = 0.126$	<b>Est. 0.011 ± 0.004;</b> <b><math>\chi^2_1 = 8.202</math>, <math>p = 0.004</math></b>	[1] Est. -0.001 ± 0.038; $\chi^2_1 < 0.001$ , $p = 0.956$
Mean ODBA (g)	[4] Est. -0.072 ± 0.050; $F_1 = 2.043$ , $p = 0.157$	<b>Est. 0.008 ± 0.003;</b> <b><math>\chi^2_1 = 3.886</math>, <math>p = 0.048</math></b>	[1] Est. -0.0004 ± 0.003; $\chi^2_1 = 0.024$ , $p = 0.877$
Trip ODBA (g h)	<b>Est. 0.248 ± 0.139;</b> <b><math>\chi^2_1 = 3.919</math>, <math>p = 0.048</math></b>	<b>Est. -0.184 ± 0.042;</b> <b><math>F_1 = 19.543</math>, <math>p &lt; 0.001</math></b>	[1] Est. 0.0001 ± 0.0009; $\chi^2_1 = 0.017$ , $p = 0.897$
Dive time (s)	[3] Est. -0.394 ± 0.240; $F_1 = 3.011$ , $p = 0.087$	<b>Est. 0.221 ± 0.074;</b> <b><math>\chi^2_1 = 8.643</math>, <math>p = 0.003</math></b>	[2] Est. 0.017 ± 0.027; $F_1 = 0.412$ , $p = 0.523$
		[2] Est. 0.377 ± 0.227; $F_1 = 2.916$ , $p = 0.092$	[1] Est. 0.001 ± 0.078; $\chi^2_1 < 0.001$ , $p = 0.988$
			<b>Est. -0.777 ± 0.215;</b> <b><math>F_1 = 14.949</math>, <math>p &lt; 0.001</math></b>
			[1] Est. 0.142 ± 0.109; $F_1 = 1.692$ , $p = 0.198$
			[3] Est. -11.730 ± 8.814; $\chi^2_1 = 1.780$ , $p = 0.182$
			<b>Est. 105.481 ± 22.847;</b> <b><math>F_1 = 26.050</math>, <math>p &lt; 0.001</math></b>

translates into bycatch mortality numbers, so more work is required to quantify seabird bycatch by purse-seine fisheries in Peru, such as boat-based observations, interviews or necropsies of beach-cast birds, especially because bycatch in purse seines can be highly episodic (Ayala 2012, Suazo et al. 2014, Oliveira et al. 2015, Norriss et al. 2020, Christensen-Dalsgaard et al. 2022).

#### 4.2. Foraging effort in relation to season, sex, brood size and tag mass

Foraging trips were similar in length to those recorded from tracking at other 4 colonies (Zavalaga et al. 2010b, Boyd et al. 2014). In December 2020, birds travelled further from the colony, expended more energy during foraging trips compared to the breeding season in May 2021, indicating behavioural variation or flexibility, potentially in response to food availability. We could not find time-matched data on prey as the hydro-acoustic surveys take place in February–April and September–November (Castillo et al. 2020), but broad-scale data suggest generally similar prey availability in May and December (Passuni et al. 2016), with potentially large inter-annual variation (Swartzman et al. 2008). We did not detect sex differences in any metrics except for females spending more time diving below 0.5 m. This is consistent with previous work showing deeper dives for females, which are larger than males, and no difference in GPS-derived metrics (Zavalaga et al. 2010b, Bertrand et al. 2012), although longer trips for males have been detected (Weimerskirch et al. 2012). Sex differences may vary inter-annually, as shown for other sulids (Castillo-Guerrero & Mellink 2011, Clark et al. 2021). Some *Sula* species raise more chicks when conditions are favourable, and Peruvian boobies have large broods that require more food provisioning (e.g. Anderson & Ricklefs

Table 2. Means ± SE for the foraging effort variables measures per foraging trip for tracked Peruvian boobies. ODBA: overall dynamic body acceleration

Measure of foraging effort	Mean	SE
Trip duration (h)	2.7	0.2
Maximum distance (km)	32.7	2.3
Total distance (km)	102.8	7.8
Mean ODBA (g)	0.73	0.02
Trip ODBA (g h)	1.95	0.16
Dive time below 0.5 m (s)	61.1	6.1

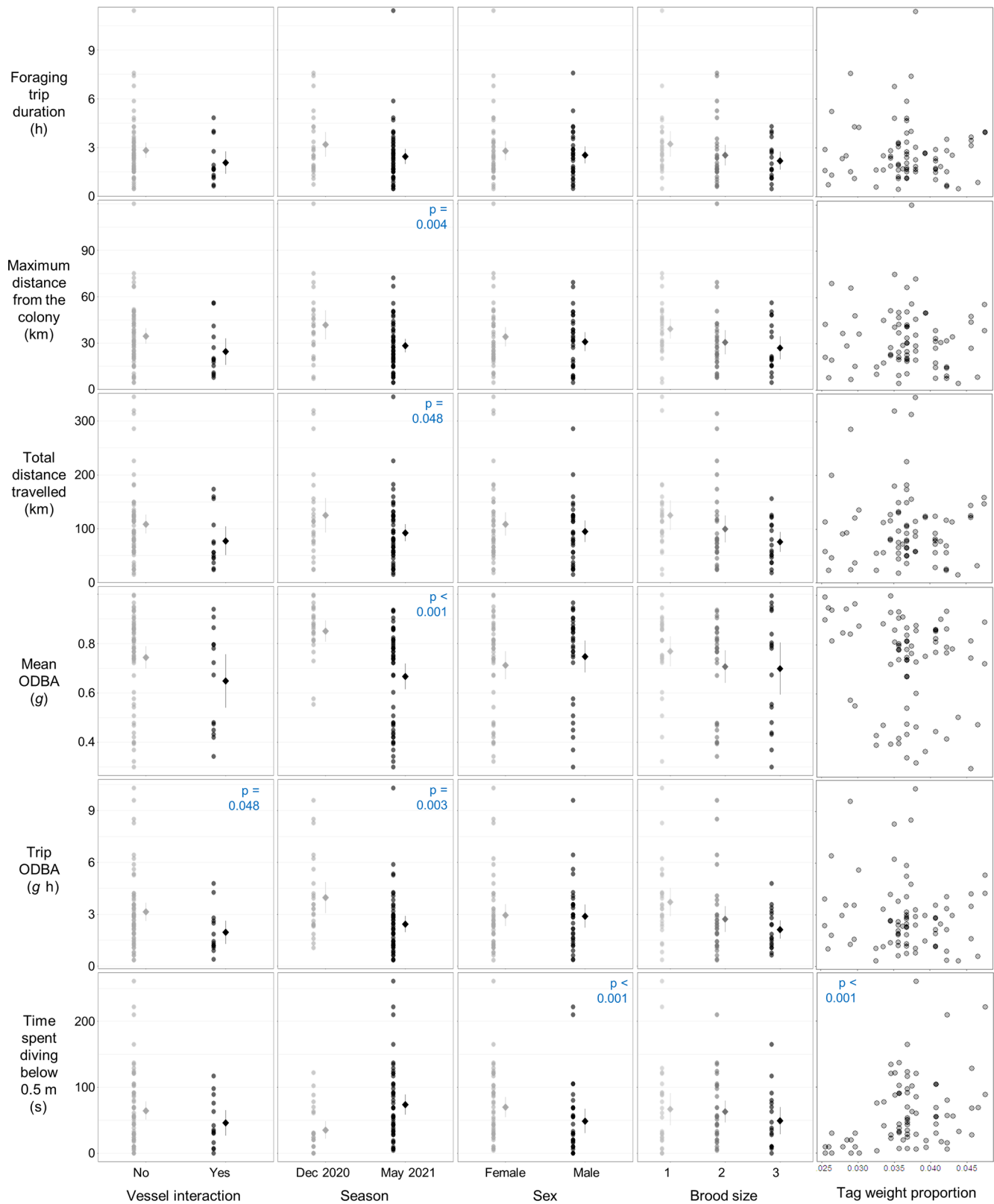


Fig. 3. Peruvian booby *Sula variegata* foraging trip characteristics for trips in relation to vessel interaction occurrence, season, sex, sex, brood size and tag mass as a proportion of body mass. Points are transparent so that darker greys indicate multiple overlapping points. Diamonds show the means  $\pm$  95% confidence intervals. ODBA: overall dynamic body acceleration. P-values are given when  $p < 0.05$  (see Table 1)



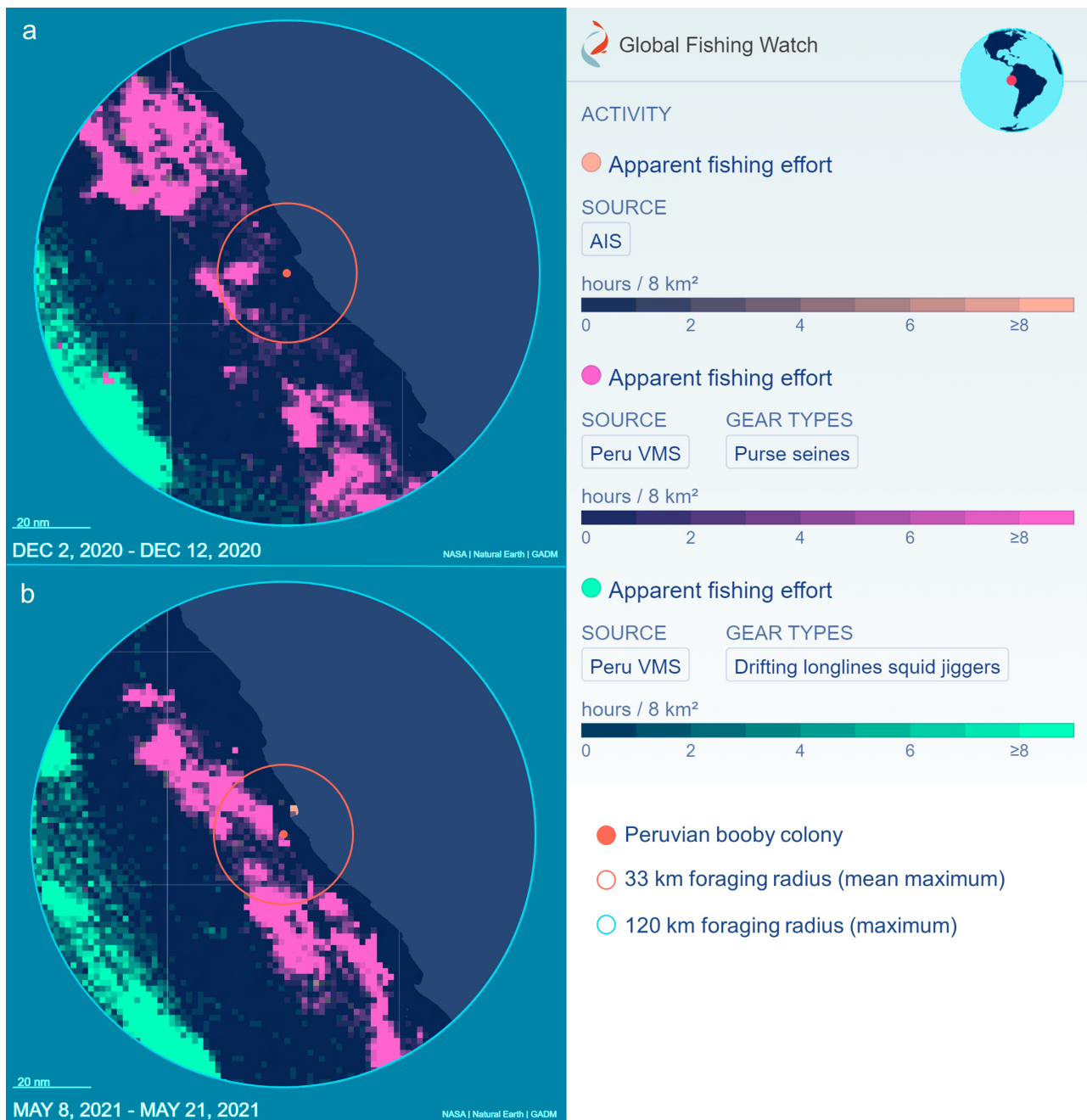


Fig. 4. Apparent fishing effort for the days during which Peruvian boobies were tracked in (a) December 2020 and (b) May 2021 within the mean maximum distance from the colony (33 km) and the maximum distance reached by any bird (120 km inclusive of the 33 km radius; Copyright 2022 Global Fishing Watch, Inc., [www.globalfishingwatch.org](http://www.globalfishingwatch.org)). Data are sourced from vessel monitoring system (VMS) data provided by the Peruvian Government's Ministry of Production, Fisheries Sector, and automatic identification system (AIS) data. Gear type was estimated by the algorithm developed by Global Fishing Watch (Kroodsma et al. 2018). Screenshots have been adapted in accordance with the Commons Attribution Non-Commercial 4.0 license (CC BY-NC): <https://creativecommons.org/licenses/by-nc/4.0/> (adaptation not specifically endorsed by Global Fishing Watch). Disclaimer: Global Fishing Watch has made every attempt to ensure the completeness, accuracy and reliability of the information provided on [www.globalfishingwatch.org](http://www.globalfishingwatch.org). However, due to the nature and inherent limitations in source materials for information provided, Global Fishing Watch qualifies all designations of vessel fishing activity, including synonyms of the term 'fishing activity,' such as 'fishing' or 'fishing effort,' as 'apparent,' rather than certain. And accordingly, the information is provided 'as is' without warranty of any kind.

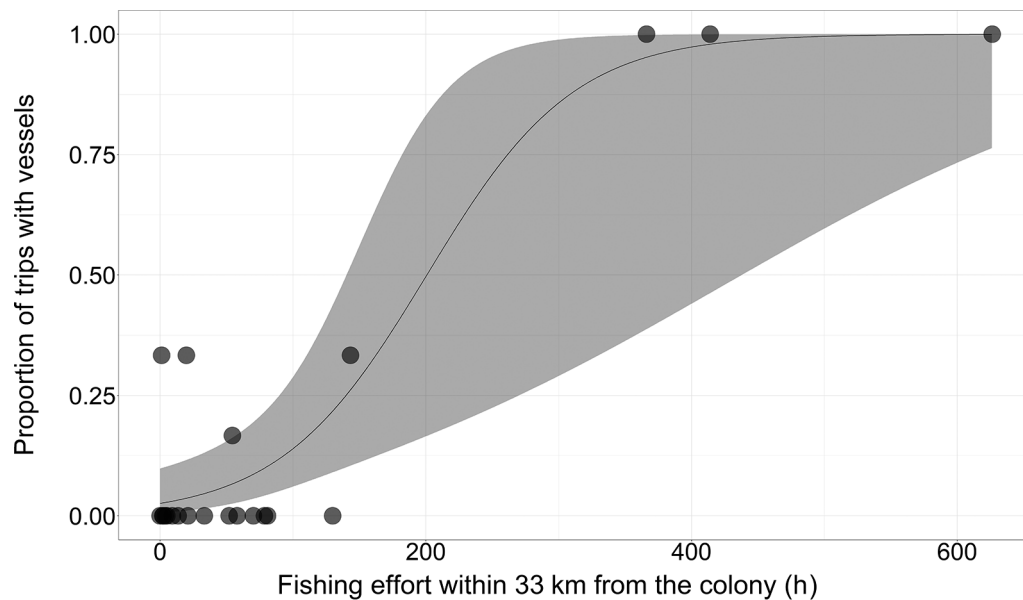


Fig. 5. Proportion of Peruvian booby foraging trips tracked within each day ( $n = 22$ ) in relation to the total daily fishing effort for all vessels as classified by the Global Fishing Watch algorithm (see Fig. S1), sourced from VMS data provided by the Peruvian Government's Ministry of Production, Fisheries Sector, and AIS data. Black line and grey shading indicate model prediction  $\pm 95\%$  confidence interval

1992, Clifford & Anderson 2001), highlighting the Humboldt Current's productivity. We did not detect a difference in foraging effort relating to brood size. We might expect parents that have to complete more foraging trips per day to have shorter trips (Grémillet 1997) because they return to the colony before dusk (Zavalaga et al. 2010b). If the battery life of bird-borne cameras can be increased to cover an entire day, investigating foraging effort at the daily scale would be very informative. We did not detect a relationship between the proportional tag mass compared to bird mass in foraging trip duration, distance travelled or ODBA, but birds with relatively heavier tags spent more time diving below 0.5 m. We recommend checking and statistically controlling for tag effects and working to reduce them where possible (Bodey et al. 2018).

#### 4.3. Conservation and management implications

Combining GPS and video loggers provides a useful tool to monitor seabird–fishery interactions (Grémillet et al. 2010, Votier et al. 2013). Not only does it enable us to identify the location of potential overlap, but it can also provide important fine-scale behavioural information to improve our understanding of competition, depredation and potential bycatch risk. We show that Peruvian boobies regularly encounter purse seiners at a distance of over 5 nauti-

cal miles (9.26 km) from shore, where the industrial fleet are permitted to harvest anchoveta for fish meal and oil (Oliveros-Ramos et al. 2021). Boobies travelled to but did not encounter vessels in areas within 5 nautical miles from shore, where the artisanal fleet harvests anchoveta for direct consumption (Oliveros-Ramos et al. 2021). Within our dataset, individuals were unlikely to encounter longliners, but seabird foraging trips are short during chick-rearing, and so longline bycatch is still a potential issue for other breeding stages or age classes (Jahncke et al. 2001). Our results are consistent with previous work showing negative effects of competition with anchoveta fishing on Peruvian seabird populations (Duffy 1983a, Bertrand et al. 2012, Barbraud et al. 2018), because we observed purse seiners fishing in core seabird foraging areas during chick-rearing. The chick-rearing period restricts adults to using a smaller area around the colony, so a reduction in local prey availability caused by fishing beyond a certain threshold is expected to lower productivity (Cury et al. 2011).

Our study suggests that Peruvian boobies and other piscivorous seabirds (including the Guanay cormorant and Near Threatened Peruvian pelican) may benefit from no-take zones or reduced fishing effort, reducing competition for foraging fish (Ainley et al. 2018, Sydeman et al. 2021) and bycatch risk (Ayala 2012). The industrial Peruvian anchoveta fishery already operates within temporal restrictions (no fishing during spawning) and spatial restrictions (no

industrial fishing within 5 nautical miles from the coast), and uses a VMS, so dynamic approaches are likely to be feasible (Maxwell et al. 2015, Oliveros-Ramos et al. 2021). Our methods indicate priority areas and times where these could be best implemented (i.e. in the core foraging areas of colonies during breeding, particularly when broods are large). This could be particularly important during El Niño events, which can affect booby foraging effort (Howard et al. 2021) and reduce the proportion of anchoveta in seabird diets (Saraux et al. 2021). This could be caused by reduced anchoveta abundance (Chavez et al. 2008, Cahuin et al. 2009, Oliveros-Ramos et al. 2021) and/or anchoveta spending more time at deeper depths that are less accessible to seabirds (Ñiquen & Bouchon 2004). However, the relationships between El Niño and La Niña conditions on anchoveta abundance and accessibility, and seabird populations, are complex and depend on event intensity, timing and length (Jahncke 1998, Swartzman et al. 2008). El Niño events are predicted to increase in strength and frequency as climate change continues (Gutiérrez et al. 2016). Further research into the interactions between Peruvian seabirds and anchoveta fisheries during El Niño and La Niña conditions would shed light on this issue.

#### 4.4. Conclusions

We highlight the value of animal-borne cameras to understand and monitor the responses of wild animals to human activity in their environment. We show that chick-rearing Peruvian boobies dive in and around purse seiners from the Peruvian anchoveta fishery. This only occurred when fishing activity was very close to the colonies; the birds did not save energy on the foraging trips during which they encountered vessels. As such, our results indicate possible bycatch risk, and are consistent with previous work suggesting that competition with vessels for forage fish influences marine predators in the northern Humboldt Current system, but vessels do not prevent boobies foraging concurrently, as the purse-seine nets force anchoveta to the surface at high densities, where they are accessible. Mapping these interactions revealed that they occur more frequently during periods of high fishing effort, so dynamic measures could be suitable in this case.

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