Marine Biology (2026) 173:98
https://doi.org/10.1007/s00227-026-04858-x

ORIGINAL PAPER

Peruvian boobies: unbiased samplers of prey availability and complementary indicators of population size structure of Peruvian anchoveta to fishery landings data

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Received: 26 August 2025 / Accepted: 28 April 2026

Abstract

Seabird diets serve as valuable tools for monitoring forage fish populations, particularly when fishery-dependent data overlook key segments such as juvenile cohorts. In this study, we evaluated whether Peruvian booby (*Sula variegata*), a predator of anchoveta (*Engraulis ringens*), could be used as an ecological indicator of anchoveta size structures during the early industrial fishing season in northern Peru. We analysed regurgitated prey samples derived from tagged birds in combination with GPS tracking, bird-borne video footage, and official fishery landing and effort data. Anchoveta length distributions in booby diets revealed a high proportion of juveniles (< 12 cm), which were significantly underrepresented in concurrent fishery landings. Despite occasional interactions with fishing vessels, the size of the prey consumed did not differ significantly with the vessel presence status, suggesting that boobies forage largely independently of the industrial fleet. Our findings are consistent with other studies that have shown that seabirds effectively track fish recruitment dynamics through their diets. Additionally, the spatial segregation of anchoveta, with juveniles being inshore and adults being offshore, may explain the discrepancies between seabird and fishery size data. These results underscore the utility of the Peruvian booby as a sentinel species for detecting early recruitment signals in anchoveta populations. We propose that systematic seabird diet monitoring, particularly at the beginning of the fishing season, can provide complementary insights into fish population structures and strengthen ecosystem-based fishery management, especially in data-limited or logistically constrained settings.

Keywords Biologging · Ecosystem monitoring · Fishery landings · GPS tracking · Seabird diet

Introduction

Seabirds are increasingly being recognized as effective indicators of marine ecosystem health statuses because of their strong reliance on prey availability and their sensitivity to oceanographic variability and anthropogenic pressures (Cairns 1987; Piatt et al. 2007; Einoder 2009). In the face of these stressors, dietary studies offer a valuable approach for inferring information about the abundances and structures of forage fish populations, particularly when direct stock assessments are limited or require complementary data (e.g., Field et al. 2007; Velarde et al. 2015; Thayer et al. 2021). Understanding the size and age structures of forage fish is critical for fishery science and ecosystem-based management in several regions where these species are central to the food web. The recruitment of forage fish species can be highly variable, strongly influencing future abundance

Communicated by T. A. Clay.

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and catch, but is often highly variable, therefore it can be poorly understood and difficult to predict.

Recent research has shown that seabird diets can provide insights into fish population structures and recruitment dynamics. For example, Thayer et al. (2021) demonstrated that northern anchovy (*Engraulis mordax*) length distributions derived from rhinoceros auklet (*Cerorhinca monocerata*) diets closely matched those obtained from trawl surveys, effectively detecting juvenile cohorts that are often missed by traditional sampling. Similarly, Scopel et al. (2018) reported that the proportions of juvenile herring (*Clupea harengus*) in the diets of common terns (*Sterna hirundo*) and Atlantic puffins (*Fratercula arctica*) strongly correlated with recruitment indices, whereas Field et al. (2007) incorporated seabird-derived data into stock assessments of shortbelly rockfish (*Sebastes jordani*), revealing annual variations in juvenile abundance. These studies highlight the potential of seabirds as bioindicators of forage fish size structure, especially in temperate systems. However, while many studies on this topic have been conducted in other regions, particularly in upwelling systems such as the California Current, such approaches remain relatively rare in the Humboldt Current System, despite it supporting the world's largest single-species forage fishery, targeting anchoveta (*Engraulis ringens*).

The Peruvian booby (*Sula variegata*) is an endemic seabird of the Humboldt Current System that feeds almost exclusively on anchoveta (Jahncke and Goya 1998; Jahncke and Zileri 1998; García-Godos and Goya 2000; Clark et al. 2022), a key forage fish that supports the world's largest monospecific fishery (Chávez et al. 2008). Anchoveta reproduces through multiple spawning events throughout the year. In Peruvian waters, reproductive activity is bimodal, with a dominant peak between August and September and a smaller secondary peak between February and March. Commercial fishing typically occurs outside the main spawning periods, generally between May–July and November–January (Oliveros-Ramos et al. 2021). Predicting the strength and timing of anchoveta recruitment remains a key challenge within stock assessments because of the complex and variable environmental conditions in the Humboldt Current system, which highlights the value of developing independent proxies for juvenile abundance to improve the accuracy of assessments (Bertrand et al. 2004). Industrial fishing activities targeting anchoveta in Peru are concentrated in the north-central region; landings are primarily located at ports such as Malabrigo and Chimbote, which together account for over 50% of the annual catches (IMARPE 2022). However, these ports are near important seabird colonies, including Isla Guañape Norte, where Peruvian boobies are particularly abundant (SERNANP 2019; Burga and Valencia 2021).

The abundance and breeding success of guano-producing seabirds in this region exhibit temporal fluctuations that are linked to oceanographic conditions and anchoveta availability. These studies include direct effects of large-scale anchoveta removals and localized prey depletion near breeding colonies, as well as indirect effects on breeding performance and population dynamics mediated by changes in prey availability and spatial distribution (Jordán and Fuentes 1966; Duffy 1983; Bertrand et al. 2012; Barbraud et al. 2018; Clark et al. 2022). Given Peruvian boobies' dietary specialization and spatial overlap with anchoveta fishing areas, evaluating their diet offers a promising approach for indirectly monitoring anchoveta population structure. In the Peruvian industrial anchoveta fishery, regulations limit the proportion of juveniles (< 12 cm) allowed in each haul, resulting in landings data that are inherently biased toward larger individuals. If Peruvian boobies consume smaller size classes than those represented in fishery landings, their diet may provide complementary information on juvenile cohorts that are underrepresented in catch data. In this way, seabird-derived size information could serve as an early indicator of age-0 abundance, offering additional insight for forecasting future stock dynamics.

Peruvian boobies typically forage solitarily or in small groups, and they do not rely on the formation of columns or seabird rafts to coordinate their movements or locate prey (Weimerskirch et al. 2012). Their foraging behaviours may shift in response to the presence of fishing vessels. Bertrand et al. (2012) reported spatial segregation between boobies and vessels, whereas Clark et al. (2022) reported no significant behavioural changes or energetic costs associated with vessel interactions. Because boobies capture multiple prey items in proximity to their colonies and store them largely undigested in the stomach prior to returning to their nests, their diet can reflect the size and age composition of prey populations, reinforcing their value as ecological indicators of prey population structure (Duffy and Schneider 1994; Scopel et al. 2018; Thayer et al. 2021).

In this study, we evaluate whether Peruvian boobies can serve as biological indicators of anchoveta size structures during the early periods of the fishing season. Specifically, we (a) compare the size structure (juvenile vs. adult) of anchoveta consumed by boobies with that of anchoveta in industrial fishery landings, and (b) evaluate whether foraging in association with fishing vessels affects the prey size composition in booby diets. By integrating seabird diet data, behavioural data, and fishery information, we test the hypothesis that booby diets reflect population-level variations in anchoveta size structures within a single fishing and breeding season, thereby supporting their use as ecological indicators in fishery-independent monitoring systems.

Materials and methods

Study area

Isla (Island) Guañape Norte (08°32'S; 78°59'W) lies within the *Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras* (RNSIIPG) in Peru. Located 9.15 km offshore, the island covers a total area of 0.34 km^2 (Agro Rural 2015). Up to 40 seabird species, seven marine mammals and three sea turtle species have been reported on the island or its nearby waters (SERNANP 2019). Furthermore, Isla Guañape Norte has supported the largest population of Peruvian boobies within the RNSIIPG in the past decade, with its maximum population estimates ranging from approximately 396,300 individuals in June 2016 to ~256,500 in October 2021 (SERNANP 2019; Burga and Valencia 2021). The island lies at the core of the anchoveta purse seine fishing operations conducted on the northern Peruvian coast and is situated between two major anchoveta landing ports: Malabrigo in the north and Chimbote in the south (Fig. 1). Although Morín Port is geographically closest to the booby colony (Fig. 1a), it is a small-scale artisanal port and was therefore not included in this study.

Study period and environmental context

Fieldwork was conducted during the Peruvian booby's chick-rearing season, between 20 November and 08 December 2021. This period coincided with the beginning of the second anchoveta fishing season in November of 2021. According to PRODUCE (2021), an exploratory fishing phase was authorized from 15 to 22 November 2021 to evaluate the availability and distribution of anchoveta. The regular fishing season officially opened on 23 November and continued until the total allowable catch of 2,047,000 metric tons was reached (January 2022). On the basis of the coastal El Niño index (ICEN), the year was classified as a weak La Niña year (IMARPE 2023). Reproductive activity of the Peruvian booby population continued throughout the study period (SERNANP 2019).

Devices used

Two types of dataloggers (TechnoSmart Europe www.technosmart.eu) with GPS, a time-depth recorder (TDR), a tri-axial accelerometer and temperature sensors were used to analyse the movement trajectories and behaviour of each equipped individual. The two models included 1) Axy-Trek Marine (25 g; 24 × 24 × 17 mm, with a ceramic GPS antenna) and (2) Axy-Trek (5 g; 28 × 15 × 9 mm, with a GPS wire antenna). Additionally, a miniature video camera (Techcam; 720p resolution; 32 g; 70 × 27 × 24 mm; TechnoSmart Europe) was deployed in tandem with Axy-Trek. The Axy-Trek Marine devices recorded GPS positions every second in the continuous mode, whereas the Axy-Trek devices with wire antennas recorded at 10- or 20-second intervals due to battery limitations. Depth data were recorded at one-second intervals in all devices. Accelerometer and temperature data

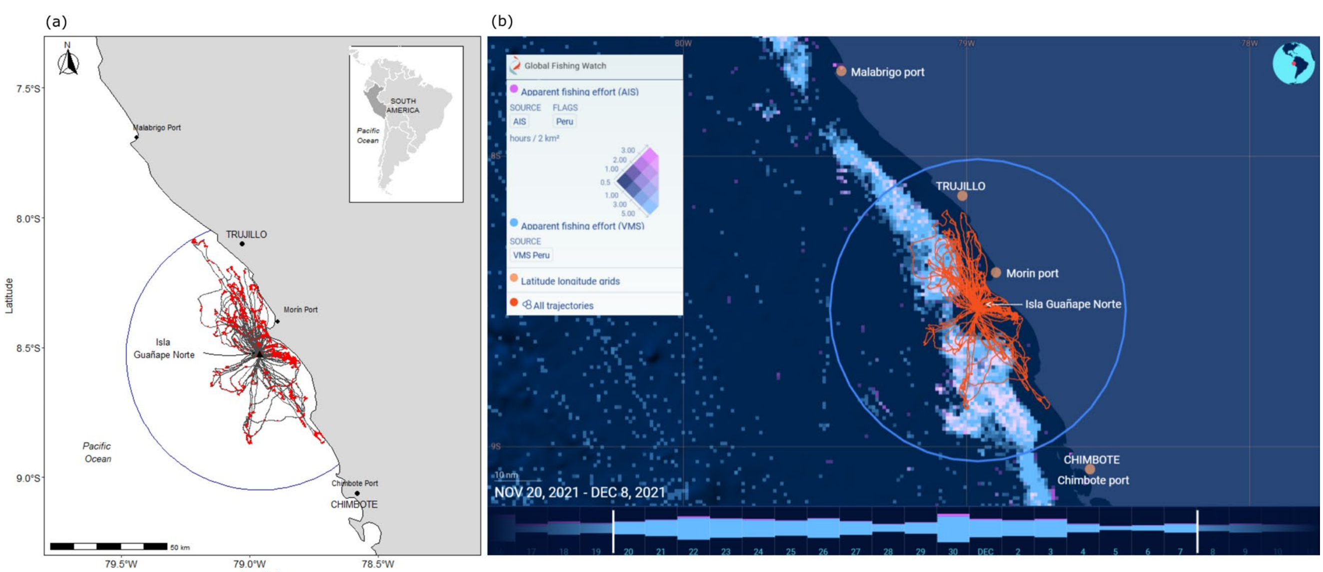

Fig. 1 Locations of the ports of Malabrigo, Morín and Chimbote and the cities of Trujillo and Chimbote near Isla Guañape Norte. (**a**) Trajectories (grey) and dives (red points) of Peruvian boobies (*Sula variegata*) are shown on a map. (**b**) Apparent fishing effort (h) for Peruvian vessels (blue scale) during the field season, i.e., 20 November to 08 December 2021, and all tracks (orange lines) of the Peruvian booby (Global Fishing Watch, Inc., http://www.globalfishingwatch.org.*).* In both images, the maximum distance from the colony (km) of all individuals (57.5 km) is represented by a blue circle

were not used in the present study. The video cameras were mounted with the lens oriented forwards and positioned at the top of the logger to maximize the field of view and include the bird's head in the frame. The lens was set to an angle of approximately 50°, whereas the front of the logger inclined towards the bird's body at approximately 20°. The cameras recorded continuously for 5–6 h. The video cameras were time-synchronized with Axy-Trek using a precision clock set to the local time.

Procedures in the field: capture, handling and instrumentation of birds

Tagging was conducted on adult Peruvian boobies attending nests with 1 to 3 chicks between 2 and 5 weeks of age. The selected nests were always left under the care of one adult. Capture and recapture were conducted with a telescopic pole (5–6 m) featuring a nylon loop at one end. Captures occurred early in the morning (05:30–08:30 h), targeting individuals with visibly dirty plumage, which was indicative of birds that had not yet departed for their first foraging trip of the day. Once captured, the birds were equipped with Axy-Trek devices and video cameras, which were attached to their back and tail feathers, respectively, using Tesa tape (No. 4651, Tesa, Germany). The combined mass of the devices was kept below 3% of the bird's body mass, in accordance with ethical guidelines (Fair et al. 2010). To facilitate post-trip identification, birds were marked with nontoxic crayon (Raidex GmbH, Germany) on their chests and heads and were released near their original nesting site. After completing at least one foraging trip within the day, the individuals were recaptured at their nests between 11:30 and 18:40 h to retrieve the devices. None of the instrumented birds abandoned their nests following either the deployment or removal of equipment.

Diet analysis

A total of 46 spontaneous regurgitates from tagged Peruvian boobies were collected upon their recapture during the fieldwork period described in the previous section. Regurgitate samples were collected at the nest upon birds' return from foraging trips. As these samples represent prey consumed over the duration of the trip, individual prey items cannot be assigned to specific capture locations along the GPS track. Each regurgitate was examined to identify and measure prey items in situ using an ichthyometer (Krausshenke®, KH-Anchoveta-22, accuracy of 0.25 cm), which was specific for anchoveta, to obtain their total length. Anchoveta were categorized as juveniles when their total length was < 12 cm (Ñiquen et al. 2000).

These data allowed us to assess the size structures (juvenile or adult) of the anchoveta consumed by Peruvian boobies during the fishing season. To evaluate the potential spatiotemporal overlap between seabird foraging and fishing activities, we integrated dietary information with industrial fishing effort and anchoveta landing data, as described in the following sections.

Sampling efforts, including bird capture and diet analyses, were conducted with minimal disturbance to the Peruvian boobies. Importantly, the geographical isolation of the islands and the large sizes of the colonies helped ensure that the sampling process had a minimal impact on the broader population. This characteristic is particularly crucial in the context of long-term seabird monitoring programs, as it enhances both the feasibility and ethical soundness of a study, ensuring that the populations of interest remain unaffected by the research process.

Fishery vessel data

To investigate whether booby foraging behaviours coincided with industrial fishing activities, we analysed the vessel movement patterns and apparent fishing effort data obtained from the Global Fishing Watch platform (Global Fishing Watch - GFW, Inc., https://globalfishingwatch.org/), which monitors global fishing activity. This platform uses the Automatic Identification System (AIS) and Vessel Monitoring System (VMS) data, capturing information such as vessel types, identities, locations, speeds, and directions. The Peruvian Government's Ministry of Production (PRODUCE) provided VMS data to the GFW, allowing us to assess the apparent fishing effort (in hours) and the behaviours of the vessels involved in the industrial anchoveta fishery. We defined a circular area representing the maximum foraging distance of the boobies (57.5 km from the colony) to overlay the fishing effort data. Additionally, we recorded the estimated total apparent fishing effort for all vessels during the period in which the birds were tracked, using GFW data at a spatial resolution of 2 km^2, expressed as hours of fishing activity per grid cell accumulated within each day.

Daily landing and size distribution of the landed anchovies

To contextualize the availability of prey during the tracking period, we analysed the daily landings and size distributions of anchoveta at the ports of Chimbote and Malabrigo by accessing public information from PRODUCE. These datasets included landing date, port of origin, total landed biomass (in metric tons, MT), and biometric samples consisting of individual size measurements of anchoveta.

Biometric assessments were carried out on more than 70% of the fishing vessels by fishmeal processing companies as part of the *Programa de Vigilancia y Control de las Actividades Pesqueras y Acuícolas en el Ámbito Profesional* of PRODUCE. During the study period, the data collection process at Chimbote spanned from 15 November 2021 to 15 January 2022, and the data collection process at Malabrigo spanned from 15 November 2021 to 7 January 2022, which corresponded with the booby tracking and diet sampling periods.

On the basis of data acquired from PRODUCE, landings used for biometric assessments were contributed throughout the fishing season by 3,702 vessel-trips at Chimbote and 2,342 vessel-trips at Malabrigo. In total, 722,942.36 MT of anchoveta from Chimbote and 725,124.16 MT from Malabrigo were biometrically sampled. During the fieldwork period (20 November to 08 December 2021), 554,183.66 MT from 2,095 vessel-trips in Chimbote and 378,158.58 MT from 1,194 vessel-trips in Malabrigo were sampled.

Data analysis

Data preprocessing

Date, time, longitude, latitude, and diving depth information was obtained from Axy-Treks for each tracked Peruvian booby. A cleaning process was applied to remove outlier points and locations outside the study area. Since individuals performed multiple trips in a day while equipped with the tracking devices, we identified distinct foraging trips by applying a 1.5-km buffer around the colony. Each trip was defined as the bird departing from and returning across this buffer, marking the start and end of a foraging trip, respectively. Depth data from the TDR were used to identify foraging dives, which were defined as dives reaching depths > 0.5 m (following Zavalaga et al. 2010). The foraging area of the birds was determined by the maximum distance travelled, which was then used to overlay the fishing effort data acquired from the Peruvian vessels tracked via the VMS on the Global Fishing Watch platform.

Videos obtained from bird-borne cameras were reviewed using VLC player software (speed: 0.5× to 1×) to examine potential interactions with fisheries. From video frames, we recorded the date and the start and end times of each recording. We classified bird-fishery interactions based on direct foraging behaviour associated with purse seine operations. Specifically, interactions corresponded to birds actively feeding on prey aggregated by fishing nets, either inside or immediately outside the purse seine net. Interactions were coded as (0) no feeding interaction with fishing gear, including cases where no vessel was observed or vessels were present but birds were not feeding (Fig. 2a, b), and (1) active feeding associated with purse seine nets, defined as birds feeding inside or immediately outside the net (Fig. 2c, d, e). This classification focused specifically on trophic interactions with fishing operations, as these represent direct ecological interactions relevant to prey acquisition. Due to variability in visibility and camera field of view, the precise start and end times of bird-vessel interactions could not be reliably determined. Consequently, interaction duration was not quantified, and interactions were instead recorded as presence/absence events, which provided a more consistent and reliable measure across videos. Representative examples of non-interaction (Fig. 2a, b) and interaction events (Fig. 2c–e) are shown in Fig. 2 to illustrate the behavioural criteria used for classification.

For individuals whose cameras did not capture entire trips, GPS data from Axy-Trek loggers were used to identify potential fishery interactions using vessel locations obtained from the Global Fishing Watch (GFW) platform (Fig. 1b). Bird GPS positions were visually compared with the spatial distribution of fishing vessels to identify spatiotemporal overlap. Camera data allowed direct confirmation of behavioural interactions and were considered the primary evidence of interaction, whereas GPS-GFW overlap was used as a complementary method to identify potential encounters when video footage was incomplete.

Tracking data were used to identify foraging trips and diving events, and to determine whether foraging activity occurred in association with fishing vessels. Trips and dives were therefore classified according to vessel presence within the foraging area. This classification scheme was used to enable comparison of anchoveta size composition in booby diets between trips with and without vessel presence. Vessel presence was determined for 55 individuals during foraging trips and for 51 individuals during dives.

Statistical analysis

All the statistical analyses were conducted using R version 4.0.4 (R Core Team 2021). The *geobuffer* package (Valentin 2019) was used to delineate the foraging area of Peruvian boobies and to evaluate the apparent fishing effort of the vessels tracked on the GFW platform. A Kolmogorov-Smirnov test was applied to determine whether Peruvian boobies were reliable indicators of the size distribution of the anchovies caught by the industrial anchoveta fishery. We used chi-square tests to examine the relationship between the total anchoveta length distributions in diets and landings, including the juvenile-to-adult ratio, and the relationships between these parameters and the presence or absence

Fig. 2 (**a**, **b**) Frames taken from videos of different individuals of Peruvian boobies (*Sula variegata*), showing direct interactions with anchoveta (*Engraulis ringens*) fishing. In both images, the fishing net and conspecifics are visible; in (**a**), an industrial purse seine vessel is present. (**c**, **d**, **e**) Snapshots derived from videos of other individuals with direct interactions with anchoveta fishing activities. In (**c**) and (**d**), the Peruvian booby captures anchoveta outside the fishing net, whereas in (**e**), the bird is inside the net

of fishing vessels. The results were considered statistically significant when $p < 0.05$.

Results

Diet composition and size structure of the anchoveta consumed by Peruvian boobies

A total of 46 regurgitates were collected and analysed from the tagged individuals. All samples contained exclusively Peruvian anchoveta, resulting in $n = 402$ fish (total length $= 12.69 \pm 1.36$ cm, min $= 8.95$ cm, max $= 16.25$ cm). Juvenile anchovies (< 12 cm) represented 30.6% of the diet.

Peruvian booby foraging effort and interactions with fishing vessels

A total of 79 boobies were tracked in this study, with 69 individuals providing usable video footage (~453 h) and 73 individuals contributing GPS and depth data. Among the 69 individuals with video footage, 55 undertook foraging trips, for a total of 84 trips (Figs. 1a and 3). Among these trips, 11.9% ($n = 10$) involved interactions with the industrial anchoveta fishery.

Apparent fishing effort (h) data for the Peruvian vessels (Peru VMS) in the foraging area during the study period, obtained from the GFW platform, revealed a total of 17,042 h of fishing effort by 569 vessel-trips (max: 2,104.79 h, min: 1.95 h) (Fig. 1b). The presence or absence of vessels was determined for 55 individuals during foraging trips and for 51 individuals during dives. In total, 84 trips and 2,292

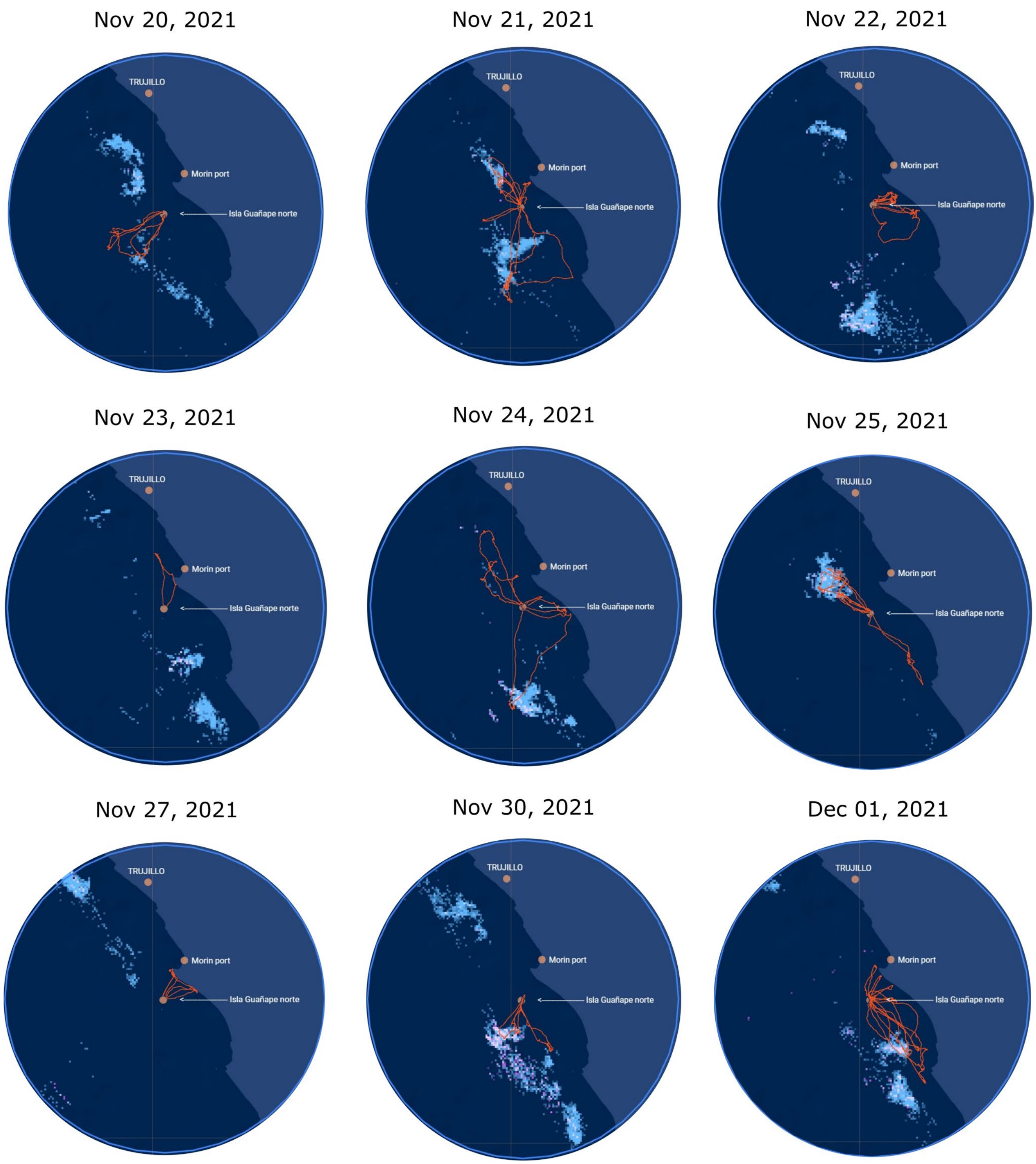

Fig. 3 Daily trajectories of Peruvian boobies (*Sula variegata*) (orange) and the daily apparent fishing effort (blue scale) derived from Global Fishing Watch AIS / VMS data. The blue circle represents the 57.5-km foraging radius, overlaid on data from the Global Fishing Watch (GFW) platform. Data correspond to the tracking period from 20 November to 7 December 2021

dives were analysed, with vessels being present during 10 trips and 210 dives (Table 1).

Booby diet in the presence or absence of fishing vessels

Interactions with fishing vessels were recorded on just five

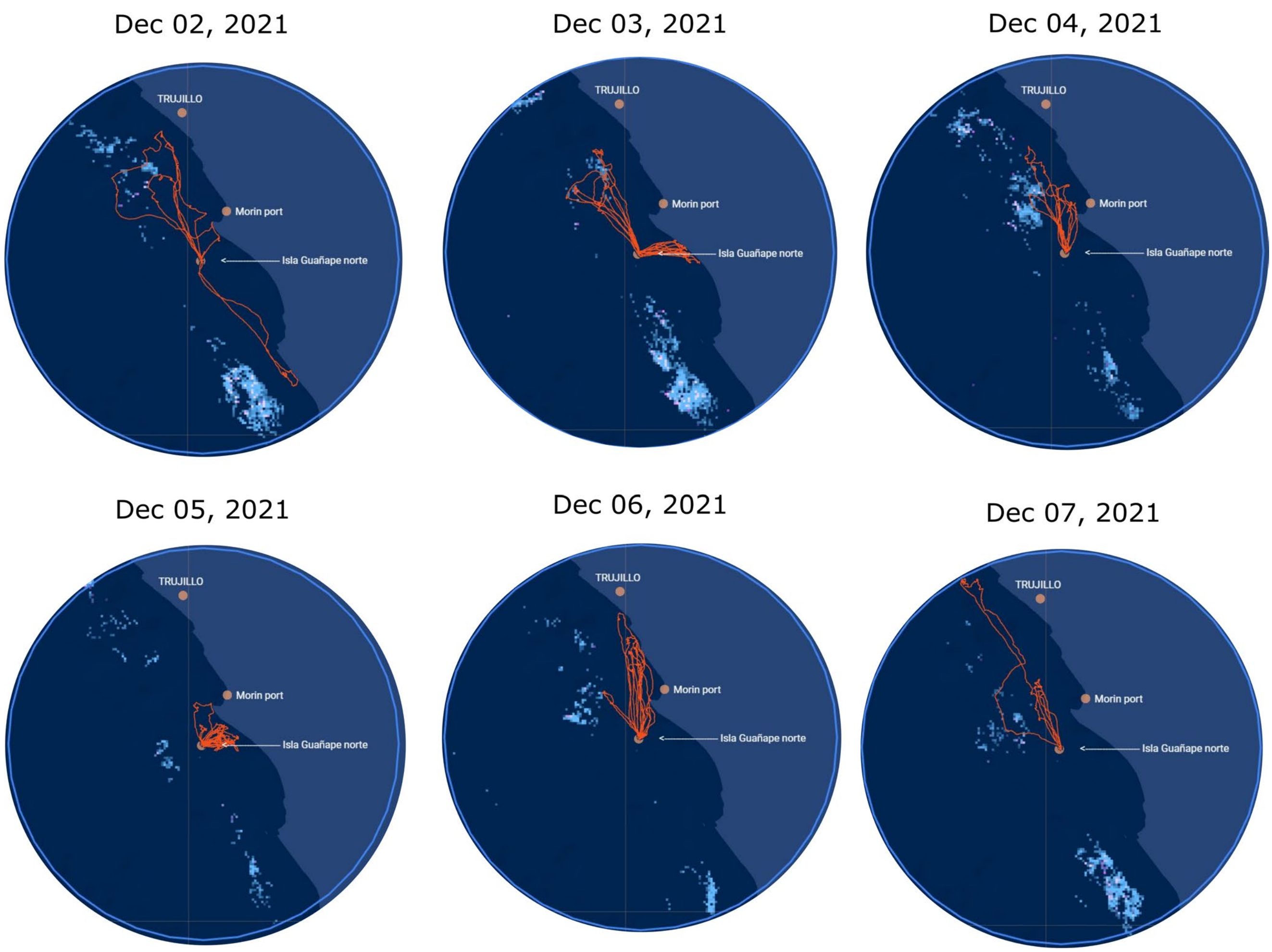

Fig. 3 (continued)

Table 1 Trip and dive parameters of Peruvian boobies (*Sula variegata*) nesting on the Isla Guañape Norte, Peru, in 2021 in the presence and absence of interactions with purse seine fishing vessels that target anchoveta (*Engraulis ringens*). The absence/presence of vessels was detected with bird-borne video cameras or inferred via the Global Fishing Watch platform. The values are means ± 1 standard deviation

	Absence	Presence
Trip parameters		
Total number of individuals (*n*)	47	8
Total number of trips (*n*)	74	10
Trip duration (h)	1.76 ± 1.10	1.57 ± 0.98
Total distance travelled (km)	51.57 ± 34.89	56.15 ± 32.77
Max. distance travelled from colony (km)	17.48 ± 12.01	20.23 ± 11.59
Dive parameters		
Total number of individuals (*n*)	44	7
Total number of dives (*n*)	2,082	210
Mean number of dives per trip	31.55 ± 14.78	23.33 ± 16.59
Mean maximum duration of dives (s)	5.29 ± 2.85	11.22 ± 7.26
Mean maximum depth of dives (m)	4.82 ± 1.59	4.51 ± 2.31

days during the study period (21, 25 and 30 November; 1 and 4 December). An analysis of the size structure of the anchoveta in the diet of the Peruvian boobies revealed similar prey sizes regardless of the absence (n = 36 Peruvian boobies; n = 319 anchovies; total length = 12.68 ± 1.36 cm; min = 8.95 cm; max = 16.25 cm; 32.3% juveniles) (Figs. 4a, c) or presence (n = 8 Peruvian boobies; n = 74 anchovies; total length = 12.7 ± 1.38 cm; min = 9.75 cm; max = 15.75 cm; 24.3% juveniles) (Figs. 4b, d) of fishing vessels in the boobies' foraging areas. The difference was not statistically significant (χ^2 = 1.434, df = 1, p = 0.231). These results suggested that, at least during the study period, direct interactions with fishing vessels did not significantly influence the size of the prey targeted by Peruvian boobies.

Anchoveta landings and size structure during the study period

We obtained daily anchoveta landing data for the second fishing season (15 November 2021 to 15 January 2022),

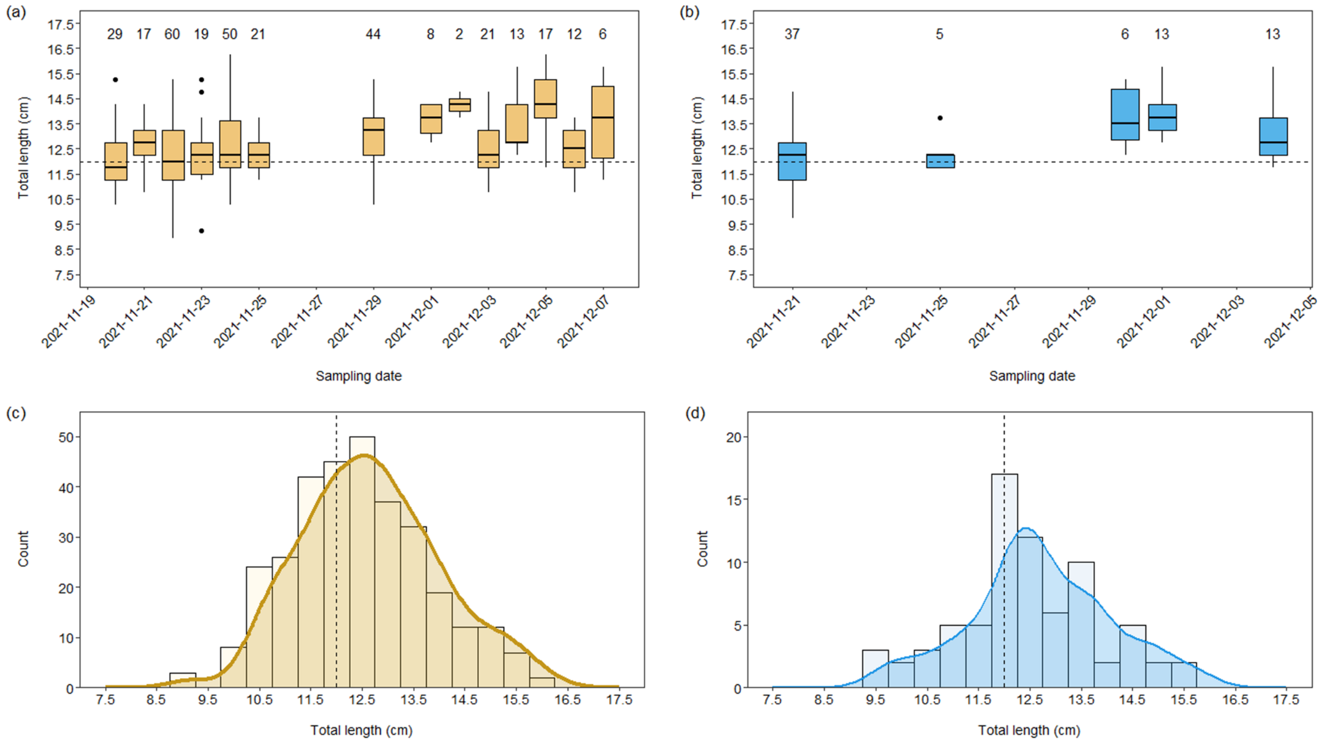

Fig. 4 Size structure of anchoveta (*Engraulis ringens*) from Peruvian booby (*Sula variegata*) regurgitates at Isla Guañape Norte, Peru (20 Nov–08 Dec 2021). A total of 36 regurgitates were sampled without fishery interactions and 8 with fishery interactions. Panels: (**a**, **b**) box-plots of daily size distributions; (**c**, **d**) histograms with density lines (yellow: without fishery interactions; blue: with fishery interactions); dashed lines indicate juveniles (< 12 cm)

which overlapped with our tracking period, from the two main ports in the north-central region of Peru: (a) Malabrigo, which accounted for 18.2% of the total national anchoveta landings during that fishing season (9,757 ± 4,879.78 MT), and (b) Chimbote, which accounted for 32.4% of the total national anchoveta landings (12,447 ± 3,553.78 MT). These two ports recorded the highest landing volumes in the north-central fishing zone during this period (IMARPE 2022). According to PRODUCE data, anchoveta landings at both ports exhibited two peaks, the first coinciding with our fieldwork (Fig. 5).

The anchoveta size data collected from landings during the fieldwork period were as follows: (a) Malabrigo ($n = 229{,}024$; total length = 13.15 ± 0.86 cm; 4.1% juveniles) (Figs. 6 and 7) and (b) Chimbote ($n = 390{,}986$; total length = 13.19 ± 0.94 cm; 2.2% juveniles) (Figs. 6 and 7). Significant differences were observed between the size structures of the anchoveta in the Peruvian booby diets and in the fishery landings from the north-central region, with juveniles being substantially more prevalent in the diet samples ($D = 0.789$, $p < 0.001$). The juvenile-to-adult ratio differed significantly between the landings and diet samples ($\chi^2 = 294.54$, $df = 1$, $p < 0.001$), with a greater proportion of juvenile fish being recorded in the booby diet than in the landings.

Discussion

To our knowledge, this is the first study in the Humboldt Current System to integrate bird-borne GPS tracking, a direct diet analysis, video recordings from bird-mounted cameras, fishery landings data, and fishing effort information from the Global Fishing Watch to assess foraging interactions of seabirds with industrial fishing vessels. While previous studies have examined seabird diets or spatial overlap with fisheries separately (e.g. Jahncke and Zileri 1998; Bertrand et al. 2012; Clark et al. 2022), our approach provides a uniquely comprehensive and fine-scale perspective regarding predator-fishery dynamics.

The study period occurred during a weak La Niña year, a condition known to influence anchoveta distribution and availability in the Humboldt Current System. Such environmental variability can affect seabird foraging behaviour as well as fishing activity. Nevertheless, Peruvian booby reproductive activity continued during the study period, suggesting that breeding was not visibly disrupted. This environmental context provides important background for interpreting the observed relationships between seabird foraging, anchoveta size structure, and fishing activity.

By using miniaturized video cameras and GFW data, we documented that 11.9% of foraging trips and 9.2% of dives

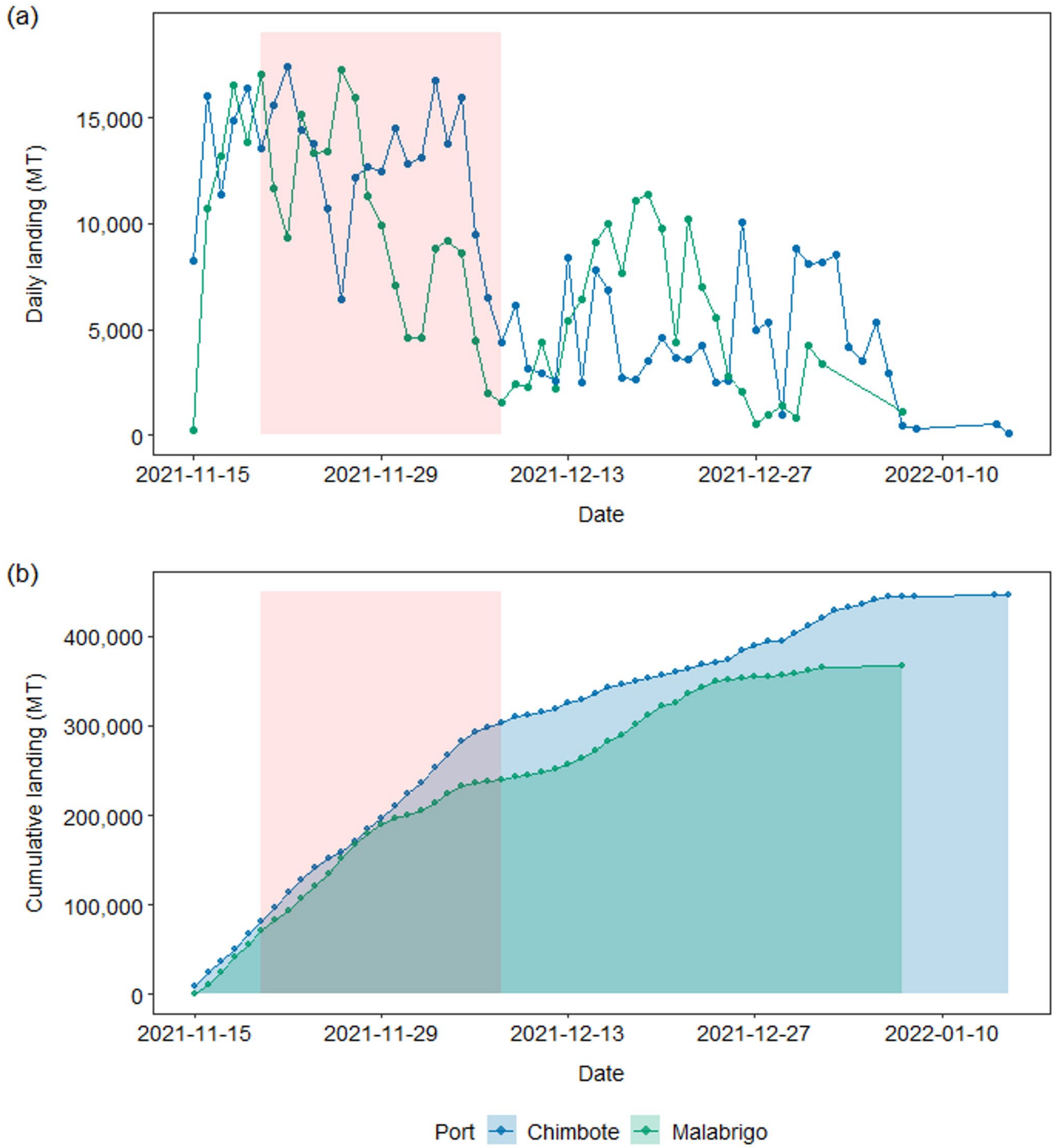

Fig. 5 Total cumulative anchoveta (*Engraulis ringens*) landings (MTs) at the Malabrigo and Chimbote ports (blue areas) and total anchoveta landings per day (MTs) at the Malabrigo (red) and Chimbote (blue) ports during the second fishing season of 2021. The fieldwork was carried out between 20 November and 08 December (red area), which corresponded to days 6 and 24 of the anchoveta fishing season and coincided with the first peak of the highest resource landings (red area)

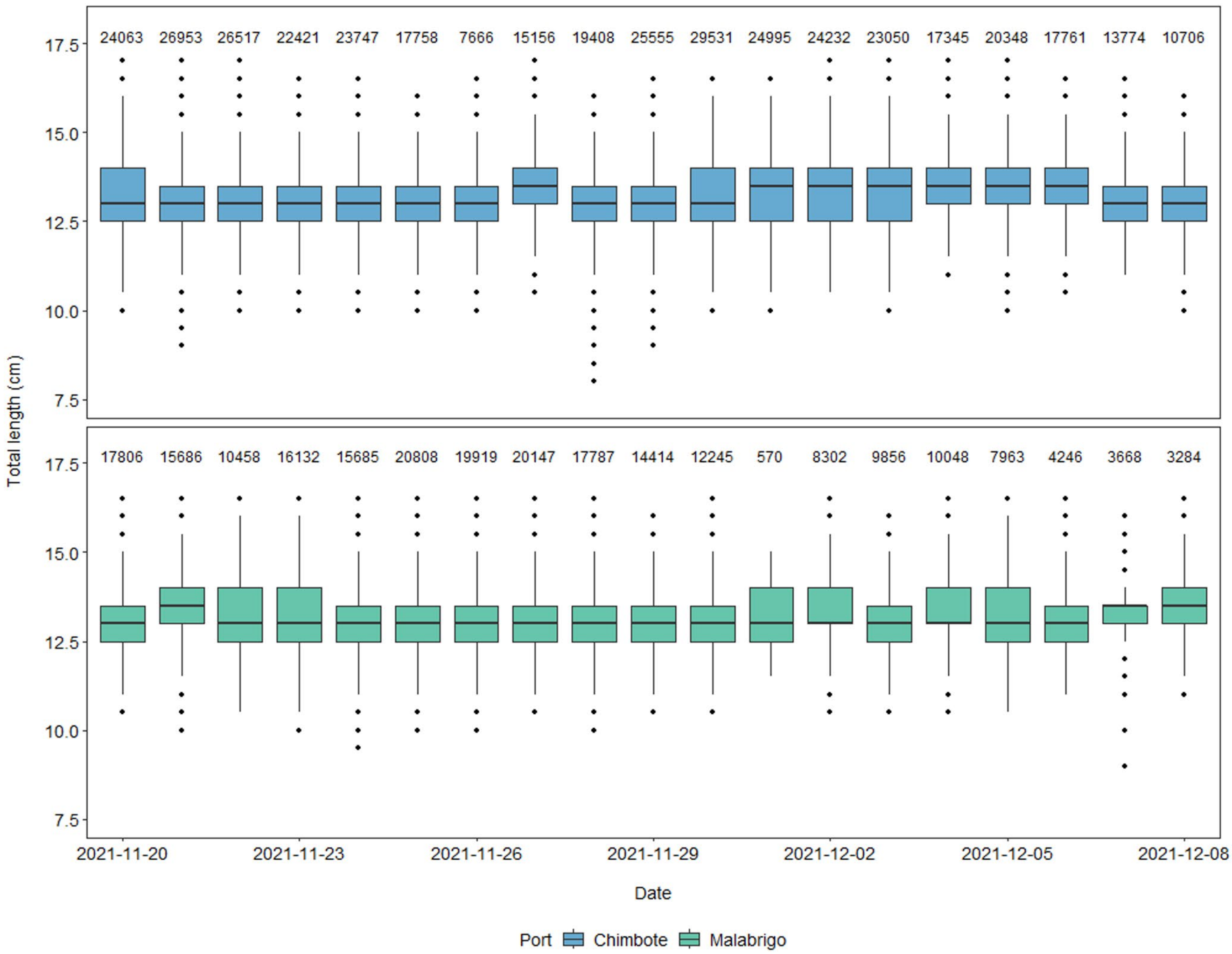

Fig. 6 Characterization of the size structure of anchoveta (*Engraulis ringens*) during fieldwork conducted between 20 November and 08 December 2021 at the Chimbote (blue, above) and Malabrigo (green, below) ports. Numbers above indicate number of fish measured.

by Peruvian boobies involved interactions with industrial fishing vessels, including foraging events near or inside purse seine nets. Interestingly, our results revealed differing proportions of juvenile and adult anchoveta between the booby diets and fishery landings. Despite the presence of vessels, the anchoveta size distributions in the booby diet remained similar, with only a slight increase in adult prey, suggesting that the presence of vessels did not strongly influence the size of prey taken.

Although other researchers have used seabird diets as indicators of prey availability or size structures (e.g., Jahncke and Zileri 1998; Mills et al. 2007; Lorentsen et al. 2018), our results demonstrate the value of integrating behavioural and fisheries data to interpret predator-fishery interactions at finer spatial and temporal scales. This approach highlights the potential of Peruvian boobies as sensitive bioindicators of fishery-relevant dynamics.

Peruvian boobies as bioindicators of the anchoveta size structure

The diet of Peruvian boobies reflects the size structure of anchoveta present in the environment, with juveniles recorded in 31.1% of individuals, compared to 4.1% and 2.2% in fishery landings from Malabrigo and Chimbote, respectively. This finding suggests that while boobies can serve as indicators of anchoveta availability, their diet predominantly reflects size classes that are more accessible within their coastal foraging habitats, which are often smaller than those most represented in industrial fishery landings. Previous studies have shown that seabirds frequently consume smaller and more vulnerable individuals due to their greater accessibility and spatial overlap with predator foraging areas (Mills et al. 2007; Lorentsen et al. 2018). Long-term observations of Peruvian booby foraging indicate no intrinsic preference for a specific prey size, but rather a tendency

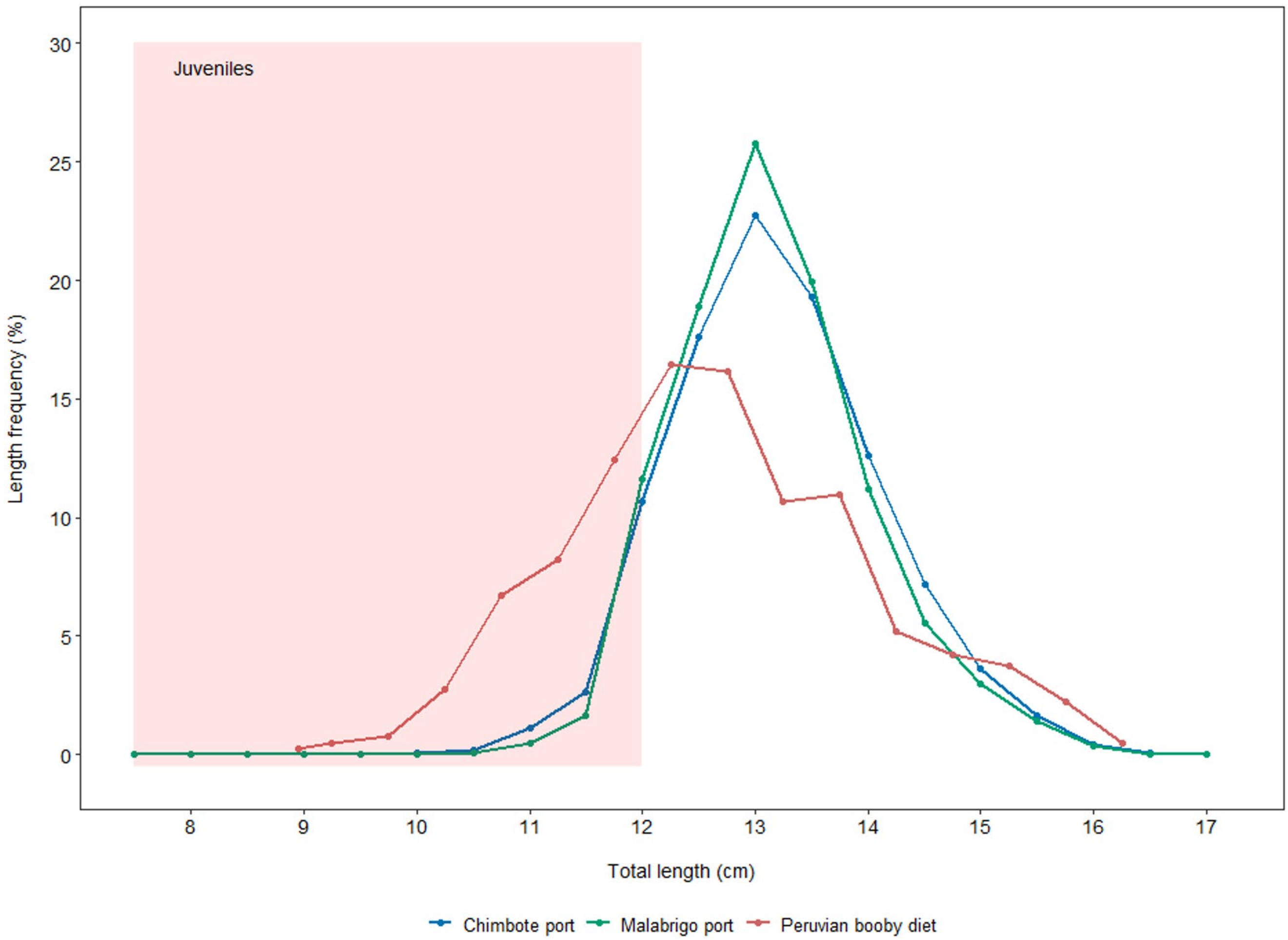

Fig. 7 Sizes (in cm) of anchoveta (*Engraulis ringens*) landings during the second fishing season at the Malabrigo (*n* = 229,024) and Chimbote ports (*n* = 390,986) compared with the anchoveta sizes in the diets of Peruvian boobies from Isla Guañape Norte (*n* = 409) during the fieldwork conducted between 20 November and 08 December 2021. Red area: anchoveta juveniles (< 12 cm)

to consume prey according to local availability (Jahncke and Zileri 1998). Accordingly, the high proportion of juveniles in their diet likely reflects the greater availability of smaller anchoveta in coastal waters during the study period rather than active selection for juvenile prey. In contrast, the industrial anchoveta fishery operates under regulatory constraints that limit the proportion of juveniles (< 12 cm) in catches and primarily targets offshore aggregations suitable for exploitation. These ecological and regulatory differences explain the higher representation of juveniles in booby diets compared to industrial fishery landings. IMARPE (2021) reported spatial segregation of anchoveta along the north-central Peruvian coast, with juveniles distributed closer to the shore and adults occurring farther offshore. This spatial structuring influences prey accessibility for seabirds and industrial vessels and contributes to the observed differences in size composition between seabird diets and fishery landings. In addition, IMARPE (2026) reports substantial interannual variability in anchoveta size composition over a long-term time series (1996–2025), with several years showing relatively high proportions of juveniles in catches. Together, these spatial and temporal patterns suggest that the availability of juvenile anchoveta to coastal predators may vary markedly among years. However, because regurgitate samples represent prey accumulated over entire foraging trips and were collected at the colony upon return, the precise capture location of individual prey items cannot be determined. Therefore, while spatial segregation of anchovy size classes provides a plausible ecological explanation, our data do not allow direct attribution of prey size to specific foraging locations. It is also important to note that fishery landings are biased toward larger individuals, as regulations likely limit the capture of juveniles, which further contributes to the observed differences between seabird diets and catch data.

While previous studies have demonstrated the utility of seabird diets in other systems, our work introduces a novel methodological approach for the Humboldt ecosystem. Our results are consistent with the broader patterns observed in other ecosystems, where seabird diet data have been used to infer the availability of small pelagic fish. For example, Thayer et al. (2021) reported a close match between rhinoceros auklet diet-derived anchovy lengths and fishery-independent trawl survey data, whereas Scopel et al. (2018) reported that the chick diets of common terns tracked juvenile herring abundance and predicted recruitment strength. Similarly, Field et al. (2007) incorporated seabird diet data into stock assessments of shortbelly rockfish and reported strong agreement with trawl survey results. However, our study provides a novel contribution by combining diet analysis with bird-borne video technology, enabling the direct observation of fine-scale foraging interactions, including those involving fishing vessels. This approach offers ecological insights that are not accessible through diet or tracking data alone, particularly regarding the spatial overlap between seabirds and industrial fisheries. Together with these previous findings, our results reinforce the value of seabirds as independent samples of juvenile fish cohorts. In particular, the Peruvian booby—an obligate anchoveta feeder with high foraging site fidelity—emerges not only as a bioindicator of anchoveta availability but also as a model for studying the real-time interactions between predators and fisheries in the Humboldt ecosystem. Although individuals may travel considerable distances while foraging, their close association with breeding sites and reliance on anchoveta ensure that their diet reliably reflects local prey availability in the surrounding waters.

Importantly, these differences highlight the complementary role of seabird-derived data in ecosystem monitoring. The size structure observed in booby diets differs from that reported in fishery landings, as seabirds tend to capture smaller individuals. Consequently, seabirds can provide early and sensitive indicators of juvenile anchoveta that may be underrepresented or missed in fishery-dependent data. This is particularly relevant early in the fishing season, when industrial landings may not yet reflect the full range of anchoveta size classes occurring in the system.

Limited direct interactions with fishing vessels

Despite integrating high-resolution GPS and video data, only 11.9% of trips involved direct interactions with fishing vessels. This value is slightly lower but comparable to the 18% reported by Clark et al. (2021) for the same species in a nearby region. Moreover, the sizes of the anchoveta consumed did not differ significantly between trips with and without the presence of vessels. These results indicate that Peruvian boobies primarily forage independently of the industrial fleet, likely due to spatial or temporal segregation, prey patch structure differences, or the high mobility and foraging adaptability of boobies.

This finding contrasts with the expectations derived from other seabird-fishery systems, where intense interactions are common (e.g., Thiebault et al. 2016; Grémillet et al. 2019). However, prior research conducted in Peru similarly reported limited overlap, with some seabird species opportunistically using fishery discards but not relying on them (Zavalaga et al. 2011). Our data reinforce this pattern for Peruvian boobies breeding on the Isla Guañape Norte. The primary result of our study is that their foraging activity appears largely independent of fishing operations, which enhances their value as unbiased samplers of prey availability, particularly in regions or periods that are not actively exploited by the fishery.

Nevertheless, bird-borne video successfully captured fine-scale foraging interactions with fishing vessels, offering novel insights into the ecological context of anchoveta predation and underscoring the utility of this approach. As shown in other systems (Tremblay et al. 2014; Votier et al. 2013; Garrod et al. 2021; Michel et al. 2022), animal-mounted video provides access to fine-scale behaviours and interactions that GPS tracking alone cannot reveal. In several instances, Peruvian boobies were observed feeding near or even inside purse seine nets, directly engaging with fishing activity. These interactions were recorded on five days during the study period and involved eight tagged individuals. Although such events were infrequent, they demonstrate the ability of the species to exploit these situations opportunistically. Such opportunistic behaviour reveals the nuanced and adaptable foraging strategies of seabirds, which are insights that are accessible only through video technology.

Implications for fishery monitoring and ecosystem-based management

By comparing the diet of a top marine predator in the Humboldt Current system with fishery landing records, this study provides a proof of concept for the use of seabird-derived data in fishery monitoring scenarios. The predominance of juveniles in the booby diet suggests that these birds may serve as early indicators of the presence of new cohorts and shifts in population size structure, providing valuable complementary ecological information. This is particularly important because industrial landings do not reflect the full range of anchoveta size classes that are present in the environment.

Seabirds often access prey patches or size classes that are either underrepresented or entirely absent in fishery-dependent datasets, thereby expanding the ecological lens through which anchoveta population structures can be assessed. Booby-derived data may act as early signals of age-0 cohorts, supplying fisheries management with timely ecological information. Together with the independence from fishing activity demonstrated above, this finding underscores the value of seabirds as ecological indicators of anchoveta population structure. In the Peruvian industrial anchoveta fishery, current regulations limit the proportion of juveniles (< 12 cm) in each haul to 10% before temporal or permanent fishing closure (PRODUCE 2021). Consequently, juveniles are systematically underrepresented in landing data, either due to real avoidance or discards at sea. While this regulation plays a key role in protecting recruitment, it limits the ability of fishery-dependent monitoring to capture the full-size spectrum of anchoveta in the environment. In contrast, predators such as the Peruvian booby are not constrained by these regulations, making their diet a valuable and unbiased indicator of juvenile abundance.

This approach aligns with findings derived from other upwelling systems, where early-season seabird diet data have revealed the presence of newly recruited cohorts before they become evident in fishery catches (e.g., Velarde et al. 2015). The limited overlap between the size distributions of the seabird diets and fishery landings does not diminish the utility of seabird-based monitoring; in contrast, it enhances it by capturing segments of an otherwise missed population. These results emphasize the role of top predators as independent samplers of ecosystem variability and highlight the potential for integrating seabird-derived metrics into ecosystem-based fishery management methods. The implementation of systematic seabird diet monitoring, particularly at the onset of the fishing season, may significantly increase the responsiveness and resilience of management strategies, especially under variable oceanographic conditions such as El Niño or La Niña events.

Conclusion and future directions

This study provides empirical evidence that the Peruvian booby is a reliable ecological indicator of anchoveta size structures and early recruitment dynamics in north-central Peru. By integrating a diet analysis, GPS tracking, bird-borne video, and fishery records, we show that seabird-derived data capture juvenile cohorts that are underrepresented in fishery landings. These findings highlight the value of incorporating seabird monitoring into ecosystem-based fishery management, particularly during the early fishing season when recruitment signals are most clearly reflected in predator-derived data. Future research should evaluate long-term changes in anchoveta size structure by combining fishery-independent surveys with predator-based indicators. The observed increase in the proportion of smaller individuals warrants further investigation to disentangle the roles of recruitment variability, environmental forcing, and fishing pressure.

Analysing diet is relatively straightforward and provides a direct measure of prey size structure, whereas video recordings of foraging behaviour require substantial time to review but provide high-resolution, fine-scale information on bird-fishery interactions. GPS tracking of birds and fishing vessels offers a practical and efficient way to identify spatial overlap and potential encounters. Overall, our study demonstrates the feasibility of integrating seabird-derived data into fishery science and highlights the need to monitor programs that balance data resolution with logistical feasibility.

Long-term seabird diet monitoring has already proven valuable in other upwelling systems, such as the Gulf of California, where it provides early insights into anchovy recruitment dynamics and supports adaptive fishery management (Velarde et al. 2015). Developing standardized predator-based monitoring frameworks could improve early detection of recruitment variability, particularly in data-limited systems such as the Humboldt Current. Our findings reinforce the potential of this approach, positioning the Peruvian booby as a sentinel species for tracking early anchoveta population shifts. Moreover, this integrative methodology combining seabird diet, biologging, and fishery data can be readily applied to other forage fish fisheries worldwide, offering a cost-effective, ecologically grounded, and independent complement to traditional stock assessment tools in the face of increasing climate variability and management complexity.

Acknowledgements This study was conducted considering the project "Aves Marinas como Centinelas del Mar: Uso de Videocámaras y GPS en piqueros para monitorear las actividades pesqueras ilícitas en el Perú" (PNIPA-PES-SIADE-PP-000169, CONTRACT 271-2019-PNIPA-SP and Universidad Científica del Sur) and the course "Programación en R para estudios de biologging que midan las interacciones de vertebrados marinos y las pesquerías en el Perú" (271-2019-PNIPA-SP PNIPA-PES-SFOCA-PP-000107) conducted by C.Z. from Universidad Científica del Sur (Peru). The authors thank Ministerio de la Producción - PRODUCE for access to the information concerning the fishing landings of the second fishing season of anchoveta 2021 in the ports of Chimbote and Malabrigo (Letter N° 00001424-2022-PRODUCE/FUN.RES.ACC.INF) and the size structures of the anchoveta stocks at those ports (Letters N° 00001424-2022-PRODUCE/FUN.RES.ACC.INF and 00001040-2023-PRODUCE/FUN.RES.ACC.INF). The authors are grateful to Cinthia Irigoin Lovera and Diego González del Carpio for their fieldwork assistance. We thank Agro Rural Administration personnel for allowing us to use the installations on Isla Guañape Norte during the fieldwork. Additionally, we appreciate the attention and assistance of the guard of Isla Guañape Norte, Alfredo Flores. Thanks are due to Drs. Lauro Madureira, Rocío Joo and Yann Tremblay for suggestions on a previous version of the current manuscript. The authors thank anonymous reviewers and the subject editor Thomas Clay for constructive and insightful comments, which helped improve the manuscript.

Authors' contributions **M. Arangüena-Proaño**: fieldwork, data

analysis, fund acquisition, writing and editing. **C. Zavalaga**: design, fieldwork, fund acquisition, revision, editing and cosupervision. **L. Bugoni**: revision, editing and supervision.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This work was supported by the project "Aves Marinas como Centinelas del Mar: Uso de Videocámaras y GPS en piqueros para monitorear las actividades pesqueras ilícitas en el Perú" (PNIPA-PES-SIADE-PP-000169 and Universidad Científica del Sur, CONTRACT 271-2019-PNIPA-SP, Project Registration Code 032-2020-PRO99). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) awarded the MSc. Scholarship to M.A-P. and supported part of the project (CAPES Finance Code 001). L.B. is a research fellow at Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq Grant N° 310145/2022-8).

Data availability Data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests, financial or nonfinancial, that could have influenced the work reported in this paper.

Ethics approval All the protocols adhered to established ethical guidelines for the use of wildlife in research, and permits were obtained from the appropriate authorities to ensure compliance with conservation regulations. All applicable international, national, and institutional guidelines for the care and use of animals were followed. This study was approved by the Institutional Committee for Ethics in Research on Animals and Biodiversity of the Universidad Científica del Sur (Ethical Certificate No. 076-CIEI-A-CIENTIFICA 2020) and by the Ethics Committee on Animal Use (CEUA) of the Universidade Federal do Rio Grande – FURG (Brazil) under protocol number P009/2022.

References

Agro Rural (Programa de Desarrollo Productivo Agrario Rural) (2015) Plan Anual de Manejo de Recolección de Recursos Guano de la Isla – 2015 - Guañape Sur (Isla e Islote Cantores)

Barbraud C, Bertrand A, Bouchón M, Chaigneau A, Delord K, Demarcq H, Gimenez O, Gutiérrez MT, Gutiérrez D, Oliveros-Ramos R, Passuni G, Tremblay Y, Bertrand S (2018) Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. Ecography 41:1092–1102. https://doi.org/10.1111/ecog.02485

Bertrand A, Segura M, Gutiérrez M, Vasquez L (2004) From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish 5:296–316. https://doi.org/10.1111/j.1467-2679.2004.00165.x

Bertrand S, Joo R, Arbulu Smet CA, Tremblay Y, Barbraud C, Weimerskirch H (2012) Local depletion by a fishery can affect seabird foraging. J Appl Ecol 49:1168–1177. https://doi.org/10.1111/j.1365-2664.2012.02190.x

Burga C, Valencia D (2021) Reporte Mensual de Conservación en Islas y Puntas Guaneras. Programa de Desarrollo Productivo Agrario Rural (Agro Rural) 2:1–15

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271. https://doi.org/10.1080/01965581.1987.10749517

Chávez FP, Bertrand A, Guevara-Carrasco R, Soler P, Csirke J (2008) The Northern Humboldt Current System: brief history, present status and a view towards the future. Prog Oceanogr 79:95–105. https://doi.org/10.1016/j.pocean.2008.10.012

Clark B, Irigoin-Lovera C, Gonzales-DelCarpio D, Diaz-Santibañez I, Votier SC, Zavalaga CB (2022) Interactions between anchoveta fisheries and Peruvian boobies revealed by bird-borne cameras and movement loggers. Mar Ecol Prog Ser 701:145–157. https://doi.org/10.3354/meps14195

Duffy DC (1983) Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. Biol Conserv 26:227–238. https://doi.org/10.1016/0006-3207(83)90075-7

Duffy DC, Schneider DC (1994) Seabird-fishery interactions: a manager's guide. In Nettleship DN, Burger J, Gochfeld M (eds.). Seabirds on Islands: Threats, Case Studies and Action Plans. BirdLife Conservation Series No. 1, Cambridge, pp. 26–38

Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. Fish Res 95:6–13. https://doi.org/10.1016/j.fishres.2008.09.024

Fair J, Paul E, Jones J (2010) Guidelines to the Use of Wild Birds in Research. Washington, D.C., Ornithological Council

Field JC, Ralston S, MacCall AD, Pearson DE (2007) Status of the U.S. Pacific Coast Bocaccio Stock in 2007 (NOAA Technical Memorandum NMFS-SWFSC-404). U.S. Department of Commerce, National Oceanic and Atmospheric Administration

García-Godos A, Goya E (2000) Dieta de las aves guaneras en la costa peruana durante noviembre 1999. Inf Prog Bol Inst Mar Perú 115:3–11

Garrod A, Yamamoto S, Sakamoto KQ, Sato K (2021) Video and acceleration records of streaked shearwaters allows detection of two foraging behaviours associated with large marine predators. PLoS ONE 16:e0254454. https://doi.org/10.1371/journal.pone.0254454

Grémillet D, Collet J, Weimerskirch H, Courbin N, Ryan PG, Pichegru L (2019) Radar detectors carried by Cape gannets reveal surprisingly few fishing vessel encounters. PLoS ONE 14:e0210328. https://doi.org/10.1371/journal.pone.0210328

IMARPE (Instituto del Mar del Perú) (2021) Informe de la Pesca Exploratoria de Anchoveta (*Engraulis ringens*) en la Región Norte-Centro del Mar Peruano (15 al 21 de noviembre del 2021). https://cdn.www.gob.pe/uploads/document/file/2582779/Informe-correspondiente-Oficio-955-2021-IMARPE-PCD.pdf?v=1638905704

IMARPE (Instituto del Mar del Perú) (2022) II Temporada de Pesca de Anchoveta en el NC – 2021 al 15 de ene 2022 (AFIRNP – IMARPE). http://www.imarpe.gob.pe/imarpe/archivos/reportes/Reporte_Anchoveta_II_Temporada_2021.html#desembarques

IMARPE (Instituto del Mar del Perú) (2023) Índice Costero El Niño (ICEN). https://www.imarpe.gob.pe/imarpe/index2.php?id_seccion=I0178090300000000 000000
IMARPE (Instituto del Mar del Perú) (2026) Situación del stock norte-centro de la anchoveta peruana (*Engraulis ringens*) al 23 de marzo y perspectivas de explotación para la primera temporada de pesca de 2026
Jahncke J, Goya E (1998) Las dietas del guanay y del piquero peruano como indicadores de la abundancia y distribución de anchoveta. Bol Inst Mar Perú 17:15–33
Jahncke J, Zileri D (1998) Estudio sobre dieta en piqueros como indicadores de la estructura por tallas de los stocks de anchoveta en el mar peruano. Bol Inst Mar Perú 17:47–54
Jordán R, Fuentes H (1966) Las poblaciones de aves guaneras y su situación actual. Bol Inst Mar Perú 10:1–31
Lorentsen S-H, Anker-Nilssen T, Erikstad KE (2018) Seabirds as guides for fisheries management: European shag *Phalacrocorax aristotelis* diet as indicator of saithe *Pollachius virens* recruitment. Mar Ecol Progr Ser 586:193–201. https://doi.org/10.3354/meps12440
Michel L, Cianchetti-Benedetti M, Catoni C, Dell'Omo G (2022) How shearwaters prey. New insights in foraging behavior and marine foraging associations using bird-borne video cameras. Mar Biol 169:7. https://doi.org/10.1007/s00227-021-03994-w
Mills KL, Laidig T, Ralston S, Sydeman WJ (2007) Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. Fish Oceanogr 16:273–283. https://doi.org/10.1111/j.1365-2419.2007.00429.x
Ñiquen MC, Bouchón MC, Cahuín SV, Díaz EA (2000) Pesquería de anchoveta en el mar peruano 1950–1999. Bol Inst Mar Perú 19:117–123
Oliveros-Ramos R, Niquen M, Csirke J, Guevara-Carrasco R (2021) Management of the Peruvian anchoveta (*Engraulis ringens*) fishery in the context of climate change. In: Bahri T, Vasconcellos M, Welch DJ, Johnson K, Perry RI, Ma X, Sharma R (eds) Adaptative Management of Fisheries in Response to Climate Change, vol 667. FAO Fisheries and Aquaculture Technical Paper No, pp 237–244
Piatt JF, Sydeman WJ, Wiese F (2007) Introduction: a modern role for seabirds as indicators. Mar Ecol Prog Ser 352:199–204. https://doi.org/10.3354/meps07070
PRODUCE (Ministerio de la Producción) (2021) Resolución Ministerial Nº 00380-2021-PRODUCE
R Core Team (2021) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Scopel LC, Diamond AW, Kress SW, Hards AR, Shannon P (2018) Seabird diets as bioindicators of Atlantic herring recruitment and stock size: a new tool for ecosystem-based fisheries management. Can J Fish Aquat Sci 75:1215–1229. https://doi.org/10.1139/cjfas-2017-0140
SERNANP (Servicio Nacional de Áreas Naturales Protegidas por el Estado) (2019) Línea Base Biológica Terrestre y Marina de la Reserva Nacional Sistema de Islas, Islotes y Puntas Guaneras - Islas Guañape (La Libertad)
Thayer JA, Burr Z, Field JC, Carle RD, Warzybok P (2021) Interannual variability in forage fish population size structure: comparison of selectivity of traditional vs. non-traditional sampling devices. Fish Res 234:105801. https://doi.org/10.1016/j.fishres.2020.105801
Thiebault A, Semeria M, Lett C, Tremblay Y (2016) How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. J Anim Ecol 85:157–167. https://doi.org/10.1111/1365-2656.12455
Tremblay Y, Thiebault A, Mullers R, Pistorius P (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. PLoS ONE 9:e88424. https://doi.org/10.1371/journal.pone.0088424
Valentin S (2019) geobuffer: R Package for Constructing Geodesic Buffers Using Metric Radii. https://doi.org/10.5281/zenodo.7127818. Zenodo
Velarde E, Ezcurra E, Anderson DW (2015) Seabird diet predicts following-season commercial catch of Gulf of California Pacific sardine and Northern anchovy. J Mar Syst 146:82–88. https://doi.org/10.1016/j.jmarsys.2014.08.014
Votier SC, Bicknell A, Cox SL, Scales KL, Patrick SC (2013) A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions. PLoS ONE 8:e57376. https://doi.org/10.1371/journal.pone.0057376
Weimerskirch H, Bertrand S, Silva J, Bost C, Peraltilla S (2012) Foraging in Guanay cormorant and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System. Mar Ecol Prog Ser 458:231–245. https://doi.org/10.3354/meps09752
Zavalaga CB, Halls JN, Mori GP, Taylor SA, Dell'Omo G (2010) At-sea movement patterns and diving behavior of Peruvian boobies *Sula variegata* in northern Peru. Mar Ecol Prog Ser 404:259–274. https://doi.org/10.3354/meps08490
Zavalaga CB, Dell'Omo G, Becciu P, Yoda K (2011) Patterns of GPS tracks suggest nocturnal foraging by incubation Peruvian pelicans (*Pelecanus thagus*). PLoS ONE 6:e19966. https://doi.org/10.1371/journal.pone.0019966