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Occurrence, abundance and some ecological aspects of the offshore bottlenose dolphin off Ecuador's central coast

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Abstract

The presence of the offshore bottlenose dolphin (*Tursiops truncatus*) is poorly understood for most of the southeast Pacific Ocean. Its wide distribution, low density, and lack of understanding of its ecology make the species unpredictable to observe and difficult to study compared to the coastal ecotype. We assessed the occurrence of offshore bottlenose dolphins off the central coast of Ecuador (01°36' S, 80°58' W) using information taken from 2001 to 2022. Data were collected by two research groups based 80 km apart, one in Puerto López (north) and the other in Salinas (south). A total of 48 dolphin groups were documented, 22 at Puerto López and 26 at Salinas. In Puerto López, 163 dolphins were individually identified, of which 70 intra-annual sightings and 102 inter-annual sightings were found. Inter-annual resightings at Puerto López corresponded to 55 individuals (33.7%) recorded between two and 17 years (mean = 5.82 years, SD = 5.1). In Salinas, 58 dolphins were identified, without intra-annual resightings and only two inter-annual sightings. Only one individual was recorded in both areas. Two site fidelity indexes were calculated, Occurrence (O_i) and Permanence (P_i), resulting in 11 and 13.7 times higher respectively, in Puerto López. The abundance at Puerto López, 163 animals (95% CI, 120 - 203) in 2021-2022, was estimated with a closed population model. The prevalence of scars associated with previous encounters with fishing gear was 43.6%, commensal barnacle (*Xenobalanus globicipitis*) infestation 42.3%, predation 3.6%, and dermal nodules 0.61%. Our findings suggest both site fidelity and some degree of population structure, but additional monitoring and genetic studies are needed to clarify these aspects. Nevertheless, this study provides information on key aspects necessary for developing conservation strategies for offshore bottlenose dolphins.

Keywords:
bottlenose dolphin, conservation, distribution, ecology, offshore ecotype

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Introduction

The common bottlenose dolphin (*Tursiops truncatus*) is characterized by worldwide distribution and complex residence patterns throughout its range in tropical and temperate waters (Wells & Scott, 2008; Wells et al., 2019). The plasticity of the species to adapt to different environmental conditions has resulted in two genetically differentiated ecotypes commonly referred to as "coastal" (inshore) and "offshore" as well as multiple morphotypes (*e.g.*, Walker, 1981; Hoelzel et al., 1998; Natoli et al., 2004; Bearzi et al., 2009; Tezanos-Pinto et al., 2009; Viloria-Gómora & Medrano-González, 2015; Fruet et al., 2017; Vermeulen et al., 2017). Offshore bottlenose dolphins show higher gene flow with other populations and, therefore, higher genetic diversity than the coastal ecotype (Natoli et al., 2004; Tezanos-Pinto et al., 2009). At the morphological level, the most important differences between ecotypes involve external coloration (Viloria-Gómora & Medrano-González, 2015), dorsal fin shape (Morteo et al., 2017; Félix et al., 2018a; Simões-Lopes et al., 2019), and skull structures (*e.g.*, Mead & Potter, 1990; Van Waerebeek et al., 1990; Perrin et al., 2011; Ott et al., 2016). Differences also extend to their social behavior: coastal bottlenose dolphins are mostly resident and form family groups of two dozen animals or fewer, while offshore bottlenose dolphins have an extensive range and form groups of up to several hundred individuals (*e.g.*, Scott & Chivers, 1990; Viloria-Gómora & Medrano-González, 2015; Wells & Scott, 2018). Despite their morphological differences and ecological specialization, only three subspecies are recognized: the Black Sea bottlenose dolphin (*T. t. ponticus*), the Lahille (*T. t. gephyreus*) in the southwestern Atlantic Ocean off South America, and the globally distributed common form *T. t. truncatus* (Wells et al., 2019). Based on morphological differences in skull and body size, the subspecies *T. t. nuuanu* has been recently proposed for a smaller form of the offshore bottlenose dolphin inhabiting the eastern Pacific (Costa et al., 2022).

Most information on the distribution and population structure of offshore bottlenose dolphins in the eastern Pacific Ocean comes from research cruises conducted by the US National Marine Fisheries Service (NMFS) from 1986 to 2003 (Hamilton et al., 2009) and from logbooks of tuna fishing vessels operating in the eastern Pacific (Scott & Chivers, 1990). With an estimated population of 243,000 animals (CV = 0.286), the bottlenose dolphin is widely distributed in this region between 25° N and 10° S and structured into two populations, north and south of 5° N (Wade & Gerrodette, 1993). Although the data are inconclusive, this estimate would include mainly the offshore ecotype, as the NMFS cruise coverage area corresponded mostly to open waters. In the southeastern Pacific, coastal and oceanic ecotypes have been recorded (Van Waerebeek et al., 1990; Félix et al., 2018a), as well as an estuarine form with a distinct lineage in the Gulf of Guayaquil, Ecuador (Bayas-Rea et al., 2018). A review of the bottlenose dolphin records in this subregion shows that their distribution is partially continuous along the South American coast from Colombia to southern Chile (Van Waerebeek et al., 2017). The same researchers provisionally identified two offshore stocks in this area, Colombia-Ecuador (associated with the eastern Pacific) and Peru-Chile, and three coastal stocks along the South American coast. A phylogeographic analysis conducted with dolphins stranded on Ecuador's central coast, presumably the offshore ecotype, showed they were most closely related to those in the northeast Pacific (Bayas-Rea et al., 2018), which supports the provisional population structure proposed by Van Waerebeek et al. (2017) for the mainland Ecuadorian offshore ecotype as opposed to that by Wade & Gerrodette (1993).

Abundant information is available on coastal bottlenose dolphins from the inner estuary of the Gulf of Guayaquil in southwestern Ecuador (*e.g.*, Félix et al., 2017, 2022; Félix & Burneo, 2020), but little is known about the offshore ecotype (Castro & Félix, 2021). The few records of offshore bottlenose dolphins off Ecuador come from oceanographic cruises conducted between mainland Ecuador and the Galapagos Islands (1,000 km west of Ecuador; *e.g.*, Clarke et al., 2002; O'Hern et al., 2017). There are also abundant records from researchers and naturalist guides in the Galapagos Islands, where the species is regularly seen throughout the year, although there are more records for the cold season, June–November (Denkinger et al., 2013). Since bottlenose dolphins inhabiting oceanic archipelagos show variable residence patterns and can be either resident or transient (*e.g.*, Silva et al., 2008; Dinis et al., 2016), it is unknown if Galapagos and mainland bottlenose dolphins are part of the same population unit. Based on NMFS surveys, Gerrodette & Palacios (1996) estimated an abundance of 6,091 (95% CI: 2,638–14,065) bottlenose dolphins within the exclusive economic zone (EEZ) of Ecuador, which corresponds to approximately 1.01 million km^2, including the Galapagos Archipelago.

For decades, bottlenose dolphins have been affected by fishing activities off mainland Ecuador (*e.g.*, Van Waerebeek et al., 1997; Castro & Rosero, 2010; Coello et al., 2011; Castro & Félix, 2021), but it is unknown to what extent the population has been impacted. Other cetaceans such as the common dolphin (*Delphinus delphis*) and the pantropical spotted dolphin (*Stenella attenuata*) seem to be more affected by small-scale fishing in Ecuador (Félix & Samaniego, 1994; Coello et al., 2011). However, when population size is taken into account the impact on the bottlenose dolphin is similar, as it is one order of magnitude less abundant than the aforementioned species in the eastern Pacific (Wade & Gerrodette, 1993). Further, bottlenose dolphins have a late sexual maturity and an extended nursing period (see Wells, 1991), making them more vulnerable to fishing activities than other smaller oceanic dolphin species. Considering that the Ecuadorian small-scale fishing fleet included around 30,000 boats 10 years ago (see Herrera et al., 2013), bycatch is the major threat to offshore bottlenose dolphins in the country.

In this study, we provide baseline information on the occurrence, distribution, site fidelity, abundance, and potential threats to offshore bottlenose dolphins off the central coast of Ecuador. The information is based on data mainly collected onboard whale-watching vessels and includes dozens of records gathered by two research groups working in mainland waters. The findings help further our understanding of the population dynamics of this poorly known bottlenose dolphin ecotype in the eastern Pacific.

Material and methods

Study area

The study area covered approximately 4,000 km^2 of the ocean over the continental shelf off Ecuador's central coast (01°36' S, 80°58' W) (Fig. 1). The north and south boundaries were 110 km apart, and the study area extended westward between 15 and

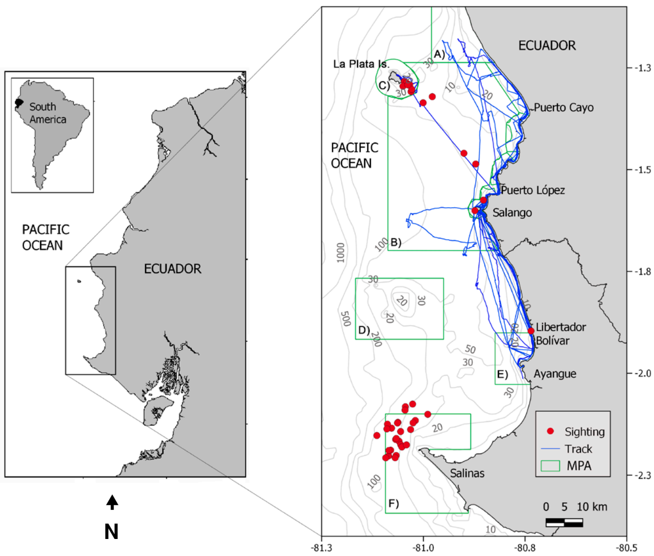

Figure 1. Study area off the central coast of Ecuador. Red dots indicate sites where offshore bottlenose dolphin *Tursiops truncatus* groups were sighted. Green polygons depict the marine protected areas (MPA): A) Pacoche, B) Cantagallo, C) Machalilla, D) Bajo Copei, E) El Pelado, and F) Santa Elena. Blue lines are survey tracks conducted in 2021 and 2022.

30 km depending on the coastal configuration. The depth varied primarily between 20 and 50 m but reached over 100 m at some sites. Because of the continental shelf's narrowness, deep-water vertebrates are regularly found near the coast (Chocho et al., 2021). Further, the oceanography is highly dynamic in the area owing to the presence of the Equatorial Front that separates the high-temperature, low-salinity tropical waters from the north and the low-temperature, high-salinity waters of the Humboldt Current from the south and diverts the flow to the west to become the South Equatorial Current (Wyrtki, 1966). The Equatorial Front moves seasonally north and south along Ecuador's central coast depending on the strength of the Southeast Pacific Anticyclone, causing an annual variation of sea surface temperature between 22° and 28°C (Cucalón, 1996). With some regularity, the area is strongly affected by the El Niño phenomenon, which produces sea surface temperature anomalies of up to +4°C, deepens the thermocline and affects ecosystem-level productivity and dynamics (Wyrtki, 1966).

A cluster of six marine protected areas (MPAs) with different levels of protection and management capacity are located within the study area (Fig. 1). Various marine mammals, such as the bottlenose dolphin, the humpback whale (*Megaptera novaeangliae*), and the South American sea lion (*Otaria flavescens*), are considered conservation-target species in some of the MPAs (MAATE, 2023).

Data collection

The information used in this study was collected by two research teams working 80 km apart that used Puerto López (north) and Salinas (south) as launching sites (Fig. 1). Opportunistic data were obtained onboard whale-watching trips, from 2001 to 2022 during the breeding season of the humpback whale Breeding Stock G (June–October) (*e.g.*, Félix & Haase, 2001; Félix et al., 2011). Several types of vessels with stationary and outboard motors, 8–12 m in length, 75–150 HP, and capacity for 10–30 passengers were used for this purpose. Trips were conducted in a highly variable schedule depending mainly on tourist demand. At Puerto López, vessels combined whale-watching with visits to La Plata Island located 40 km northwest along a fixed route. At Salinas, vessels sailed west or northwest with no specific course until whale groups were spotted. Between 2001 and 2022, 2,329 trips were conducted from Puerto López, and between 2001 and 2015, 939 were made from Salinas. However, the sparseness of the sightings and scarce information on effort from such surveys limited the type of analyses.

Additionally, 26 dedicated coastal surveys to study bottlenose dolphins were carried out from February 2021 to August 2022 departing from Puerto López. Surveys extended along 95 km between Puerto Cayo in the north and Ayangue in the south (Fig. 1). A 12-m boat with twin 150 HP outboard motors and a 2-m height deck was used in these surveys. The activities during this last monitoring period corresponded to 2,358 km and 130 h of navigation. Despite the large number of trips, both opportunistic and dedicated, conducted during the study period, most of the western side of the study area remained unmonitored.

Dolphin sightings were positioned with a GARMIN 60 portable GPS, and information on the survey effort was obtained from its data log. Maps with georeferenced information were created using Q-GIS v. 3.4 (QGIS Development Team, 2018). The depth of each sighting was derived from the General Bathymetric Chart of the Oceans 2020 sea topography layer with a resolution of 460 m, generated by the International Hydrographic Organization (IHO-UNESCO-IOC). Layers with information on Ecuadorian MPAs were downloaded from the Ecuadorian Ministry of Environment, Water, and Ecological Transition's website (https://www.ambiente.gob.ec/areas-prrotegidas/).

Information on group size and composition was collected during sighting periods by experienced marine mammal researchers and volunteers. A dolphin group was defined as all individuals recorded during the sighting period regardless of whether all were engaged in the same activity (Félix et al., 2017). During the trips, groups of both coastal and offshore bottlenose dolphins were recorded, but for the current study, only information on the offshore ecotype was considered. In addition to distribution, the main criterion for differentiating ecotype was dorsal fin shape, which is considerably more falcate in the offshore ecotype, allowing it to be identified in the field with a high level of confidence (Félix et al., 2018a).

Digital cameras with zoom lenses (100–300 and 100–400 mm) were used to photograph dorsal fins for individual identification. More than 4,000 photographs were taken during the study period for this purpose. Nicks on the rear edge of the dorsal fin and other distinguishable characteristics, such as particular pigmentations on the dorsum, were used for identification. Two catalogs were created consisting of individuals containing distinguishable marks, one for the northern zone (Puerto López) and another for the southern zone (Salinas). The quality and size of the photographs in the catalogs vary, with better-quality photographs from the last five years. Additionally, photographs of other parts of the body were used to evaluate the presence of skin lesions or injuries and to calculate the prevalence of scars associated with human activities, and ecological interactions (see Félix et al., 2018b, 2019a).

Site fidelity

Resighting histories of animals were used to understand the tendency of identified animals to return to the same area during the study period. For this purpose, we used two indexes proposed by Ballance (1990): Occurrence (*Oi*) and Permanence (*Pi*). Occurrence was the number of recaptures of an individual over a given period (Morteo et al., 2012):

$$O_i = \sum_{j=1}^{k} C_{i,j}$$

where $C_{i,j}$ is a binary value indicating positive or negative capture (1 or 0) of an individual *i* on the sampling date *j*, and *k* is the total number of samples. Permanence is the proportion of time of an individual *i* in the study area by the time between the capture and last recapture over the sampling period (Balance, 1990). Both O_i and P_i were calculated for each individual and averaged to have population indexes during the study period. Site fidelity indexes were calculated for Salinas and Puerto López independently using all the data obtained through opportunistic and dedicated surveys. In Puerto López, both indexes were also calculated for the last five years (2018-2022) to evaluate changes in time.

Abundance estimation

A preliminary estimate of dolphin abundance in the northern zone (Puerto López) was made with information from nine sightings between March 2021 and August 2022, the years with the highest number of identified individuals. Each sighting was considered a sampling occasion. For this purpose, closed population capture-recapture full likelihood models (Otis et al., 1978) implemented in the software Mark 9.0 (White & Burnham, 1999) were fitted to the data. Full probability models are based on the parameterization of three types of parameters: 1) p = the probability that an animal in the population is captured and marked for the first time; 2) c = the probability that an individual has been captured at least once before; and 3) f_0 = the number of individuals in the population that have not been counted. The closure of the population was tested using the Stanley & Burnham (1999) and Otis et al. (1978) closure tests implemented in the program CloseTest v3 (Stanley & Richards, 2011). Closed population models assume no entry of new individuals or loss due to mortality or emigration, that all animals had the same probability of being captured in the first sample, that marks do not affect catchability, that marks are not lost or overlooked, and that all animals are equally likely to be captured regardless of whether they have been previously captured. The magnitude of the overdispersion of the data or the inflation factor known as $\hat{c}$ (c-hat) is a measure of the lack of model fit, which was estimated using the option "median c-hat" in Mark. After the over-dispersion adjustment, the quasi-likelihood (QAIC*c*) and delta quasi-likelihood (ΔQAIC*c*) values were used for model selection. In general, as $\hat{c}$ increases, the QAIC*c* tends to favor models with fewer parameters (Cooch & White, 2014). Following the recommendation of Burnham et al. (2011) to use an information-theoretic approach (I-T) to model inference, we selected a small number of models based on the ΔQAIC parameter within the two and seven range to obtain an average abundance estimate.

Results

Distribution

Puerto López

Between 2001 and 2022, 22 groups were recorded in the northern part of the study area. Groups were recorded in nine different years, with higher numbers in 2016, 2021 and 2022

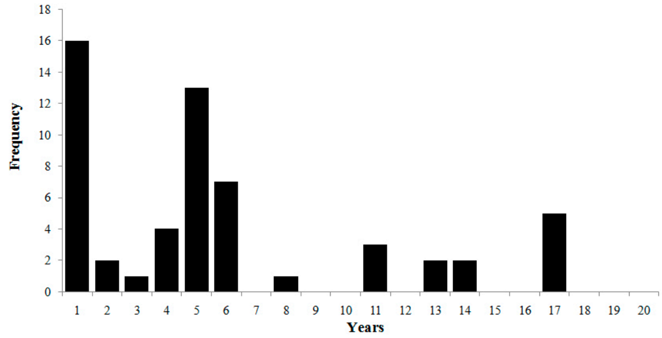

Figure 2. Frequency distribution of between-year resightings of 55 offshore bottlenose dolphins *Tursiops truncatus* at Puerto López, Ecuador, 2001–2022. The x-axis indicates the number of different years dolphins were resighted.

(Table 1). Most groups (61.5%) were recorded around La Plata Island, three along the coast from Puerto López to Libertador Bolívar, and two on the route between Puerto López and La Plata Island (Fig. 1). The average sighting depth was 31.8 m (SD = 13.5, range 3–48 m). Information on group size was available only for three groups recorded between 2021 and 2022 as such data were not regularly taken until dedicated surveys started (mean = 38, SD = 21.5). Six dolphins in a group of 20 animals in April 2022 off Libertador Bolívar were previously known to be the coastal ecotype. Four, including a female with an estimated one-year-old calf and two adult males, were part of a resident coastal bottlenose dolphin community around Salinas, and the other two were immature males associated with a coastal bottlenose dolphin community distributed between Puerto Cayo and Libertador Bolívar (unpubl. data). The sighting occurred 100 m from the shore, and dolphins interacted for at least one hour. This type of mixed group represented 4.5% of the total groups recorded at Puerto López.

Salinas

Twenty-six groups were recorded off Salinas from 2001 to 2022. Groups were recorded only in the ten first years when the effort was considerably higher, mostly in 2007 and 2010 (Table 1). All sightings were made within a 12-km radius around Salinas, of which 22 (85%) were inside the MPA Puntilla de Santa Elena (Fig. 1). The average group size was 38 dolphins, based on 18 groups

Table 1. Number of trips, bottlenose *Tursiops truncatus* dolphin groups, identified individuals, and resightings at Puerto López and Salinas, Ecuador, in the period 2001–2022.

Site and effort	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Total
Puerto Lopez																							
Trips	67	82	91	144	129	101	91	141	101	64	45	69	77	132	132	84	121	85	235	74	62	202	2,329
Groups				3			2	2						1	1	5		1			5	2	22
Identified dolphins				23			7	6						3	9	35		4			99	55	241
Within-year resightings				9			2	0						0	0	17		0			29	3	60
Between-year resightings							1	4						2	5	17		1			27	28	85
Salinas																							
Trips	32	35	30	76	74	96	104	123	105	156	18	21	23	15	18	9						4	939
Groups	1	2	3	1	3	2	5	2	1	6													26
Identified dolphins						3	30	9	1	16													59
Within-year resightings						0	0	0	0	0													0
Between-year resightings							1	1	0	0													2

Table 2. Models run for bottlenose dolphin *Tursiops truncatus* abundance estimates at Puerto López, Ecuador, in the period 2021-2022 and parameter values after over-dispersion adjustments.

Model	$QAIC_c$	Delta $QAIC_c$	AIC_c Weights	Model Likelihood	Number Parameters	QDeviance	-2log(L)
$\{M_t\}$	24.1189	0	0.72074	1	10	29.4285	16.7361
$\{M_{th2}\}$	26.8565	2.7376	0.18336	0.2544	12	28.0706	10.8969
$\{M_0\}$	29.8	5.6811	0.04209	0.0584	2	51.3241	110.8871
$\{M_{bh2}\}$	30.9783	6.8594	0.02335	0.0324	5	46.4532	89.9422
$\{M_b\}$	31.1309	7.012	0.02163	0.03	3	50.6428	107.9573

with such data collected (SD = 46.5, range 5–200). The average sighting depth was 55.4 m (SD = 15.8, range 26–112 m) (Fig. 1).

Site fidelity

Puerto López

A total of 163 different dolphins were identified in the northern area from 2004 to 2022, for which 70 within-year and 102 between-year resightings were obtained. Between-year resightings corresponded to 55 individuals (33.7%) and spanned between one and 17 years (mean = 5.82 years, SD = 5.01) (Fig. 2). The average between-year resighting rate was 1.85 (SD = 1.04, range 1–5). The years with higher resightings both within and between years were 2016, 2021 and 2022. The occurrence (O_i) was calculated at 0.042 (SD = 0.064, range: 0 - 0.28, n = 163) for the whole study period and three times higher for the last five years (2018-2022) (O_i = 0.129, SD = 0.179, range: 0 - 0.7, n = 113). The permanence (P_i) of dolphins during the whole study period was calculated at 0.118 (SD = 0.238, range: 0 - 1, n = 163) and was not different from the value calculated for the last five years (P_i = 0.110, SD = 0.148, range: 0 - 0.62, n=113).

Salinas

A total of 58 individuals were identified off Salinas, but only two between-year resightings were made. Both between-year resightings occurred one year of difference (2006–2007 and 2007–2008). No within-year resightings were found in this area. The occurrence in Salinas was 11 times lower (O_i = 0.003, SD = 0.020, range: 0 - 0.111, n = 58) and the permanence 13.7 times lower than in Puerto López (P_i = 0.008, SD = 0.046, range: 0 - 0.269, n= 58).

Only one dolphin was found in common between Puerto López and Salinas. The individual was recorded first at Puerto López in August and September 2004 and later off Salinas in August 2010. The individual was not subsequently seen.

Abundance

The full parameterized model M_t (N, $p(t) \equiv$ c(t)) best fitted our data (Table 2). The model assumes that the probability that an animal is captured and marked (p) varies with time. However, the rest of the models had ΔQAIC*c* values between two and seven and therefore they may also be model candidates. Since models with heterogeneity (M_{th2} and M_{bh2}) produced unrealistic confidence intervals when averaged, only models M_t, M_0 and M_b were used to obtain a model-averaged estimate. The population around the zone of Puerto López–La Plata Island totaled 138 individuals (95%, CI: 102–172, CV = 0.056). However, this number includes only marked animals, mostly adults and subadults; the number of unmarked animals (calves and some subadults) need to be added to this value. We estimated the percentage of unmarked animals at 18.2% based on the group seen at Salango in 2021 (10/55 dolphins). Thus, the current population in this area would be approximately 163 animals (95%, 120-203).

Ecology

Scars

The prevalence of body scars and depressions in the lumbar and caudal areas associated with fishing gear was evaluated in the group found west of Salango Island in March 2021. Twenty-four of 55 dolphins (43.6%) showed this type of scarring (Fig. 3). In twenty cases, scars were seen on adults, but some were seen on immature animals as well (n = 4). Because not all dolphins' caudal regions could be photographed, scarring prevalence is considered an approximated value.

Crescent scars probably caused by sharks were seen on two dolphins (3.6%). In the first case, the bite was on the upper back behind the dorsal fin, and in the second on the left side of the dorsal fin (Fig. 4). A 5-cm-in-diameter grayish scar without defined borders, resembling a healing wound or a type of discoloration, was seen on the antero-dorsal part of a young dolphin in the

Figure 3. Offshore bottlenose dolphins *Tursiops truncatus* with scars on the lumbar and caudal areas, likely caused by interaction with fishing nets. White arrows indicate where scars or depressions were presumably made by some type of gear.

Figure 4. Two offshore bottlenose dolphins *Tursiops truncatus* with crescents scars presumably caused by shark bites.

Salango group. The remaining scars on the dolphins' bodies were generally rake marks from intraspecific interactions.

Dermal nodules

Semicircular dermal nodules were seen on one immature individual (prevalence: 0.61%, 1/163) close to La Plata Island in August 2022. The nodules extended along both flanks, beginning in front of the dorsal fin and moving toward the lumbar region (Fig. 5). Nodule diameter was estimated at 2–4 cm, and they were mostly rounded with light gray coloration. Some nodules were joined together and more irregularly shaped. Although the photographs show only half of the upper dorsal area, it is estimated that the dolphin had 100–200 nodules.

Figure 5. Dermal nodules in an immature offshore *Tursiops truncatus* bottlenose dolphin around La Plata Island on the central coast of Ecuador.

Epibionts

The presence of the commensal barnacle *Xenobalanus globicipitis* was also assessed in the group at Salango Island in March 2021. Not every animal could be assessed to the same extent, but out of 55 dolphins, 26 (42.3%) had barnacles attached to one or more parts of their body: 15 parts of their body, including the upper edge of the dorsal fin, the trailing edge of the tail, the pedunle (n=1) and the left side of the mouth (n=1; Fig. 6). Eight dolphins had barnacles on both the dorsal fins and the tail, and one also had them in the lumbar area. The number of barnacles varied, with the majority on the tail, although a detailed calculation was not possible. Twenty-four animals with barnacles were adults, but two calves also had barnacles attached to their dorsal fins.

Figure 6. *Xenobalanus globicipitis* barnacles attached to different body parts of offshore bottlenose dolphins *Tursiops truncatus* off Ecuador.

Discussion

Distribution

This is the first study focused on offshore bottlenose dolphins in the continental waters of Ecuador. Although the information did not respond to a systematic effort, two decades of records confirmed the species is distributed widely on the central coast as records were obtained in all surveyed areas. Even though most of the records were seasonally biased towards the period July-September, we also made sightings in March 2021 and April 2022, which indicates that the species is present in the area throughout the year. Other records in April, June, and October from oceanographic cruises off mainland Ecuador (*e.g.*, Clarke et al., 2002; O'Hern et al., 2017), would also confirm this belief. Understanding their population dynamics, habitat use, site fidelity, and interaction with other dolphin communities is essential for guiding and implementing conservation strategies for this population.

The presence of the offshore groups around Salango Island, Salinas, and Libertador Bolívar confirms the sympatric distribution of both the coastal and offshore ecotypes in some areas of the Ecuadorian coast, which is consistent with reports from coastal zones in the northeast Pacific (*e.g.*, Bearzi et al., 2009; Viloria-Gómora & Medrano-González, 2015). Mixed groups of both coastal and offshore dolphins were uncommon (4.5% of the Puerto López groups), which suggests that dolphins of both ecotypes occasionally interact. The interaction between offshore and coastal bottlenose dolphins has been reported in California (Bearzi et al., 2009) and likely also occurs in Argentina (Vermeulen & Cammareri, 2008). Further, during these periods of social interaction, some level of interbreeding between different ecotypes cannot be ruled out. Thus, the sympatric ecology of bottlenose ecotypes has management implications because, if not well defined, it may lead to the misidentification of population units and abundance overestimation.

Site fidelity

Another relevant aspect revealed by this study is the difference in site fidelity exhibited by dolphins inhabiting the north and the south parts of the study area. While in Puerto López calculated site fidelity indexes (*Oi* and *Pi*) suggest that an important proportion of identified dolphins were recorded regularly (33.7 % of dolphins were recorded in more than one year), in Salinas only two between-year resightings were found (3.4%). This and the low rate of matches with the southern zone (one case) suggest some level of population structure and little overlap between these two adjacent dolphin communities. The lower resighting rate off Salinas could partially be because of the low photo identification effort but also because the shelf is narrower, meaning habitat use could differ from that of the wider shelf to the north. Genetic studies are needed to clarify whether dolphins living in both areas can be considered independent population units. It has been established elsewhere that offshore bottlenose dolphins show variable site fidelity and high dispersal (Tezanos-Pinto et al., 2009; Dinis et al., 2016), but high fidelity has been reported in a few areas, such as off the Bahamas (Rossbach & Herzing, 1999), central-north Chile (Sanino et al., 2005), and Hawaii (Baird et al., 2009). A localized upwelling area on the southeastern side of La Plata Island, where most bottlenose dolphin groups were reported, is well-known (Burgos & Gamboa, 2002). Thus, a predictable source of food would explain the regular presence of bottlenose dolphins in this area.

Abundance

We estimated the size of the northern population subunit (La Plata Island–Salango–Libertador Bolívar) to be 163 animals (95%, 120 - 203), but further and more frequent surveys are required to reduce the uncertainty by increasing sample size and reducing the bias associated with natural marks' changing over time. We used capture-recapture closed population models because of the short time between sampling periods, which prevented the introduction of noticeable bias (Hammond, 2018). On the other hand, no sufficient data were available to estimate the abundance around Salinas, but the lack of within-year resightings and the low between-year resighting rate suggest that a larger number of dolphins frequent this area. Further surveys are needed around Salinas to assess aspects such as abundance, distribution, and habitat use.

Ecology

The average group size (38 dolphins/group) was similar to that reported by Gerrodette and Palacios (1996) for Ecuadorian jurisdictional waters (average 31.2 dolphins/group) and by Clarke et al. (2002) aboard oceanographic cruises (average 35 dolphins/group). Bottlenose dolphins in the eastern Pacific are known to have a highly variable group size, which is likely associated with water productivity and prey availability (Scott & Chivers, 1990). Waters off Ecuador's central coast are considered oligotrophic with an annual variation between 0.5 and 1.5 mg chlorophyll α/m^3 (Borbor-Cordova et al., 2019). Ecuador's largest groups of bottlenose dolphins have been recorded in the Gulf of Guayaquil in the southwestern part of the country (Gerrodette and Palacios, 1996; Scott & Chivers, 1990; Hamilton et al., 2009), where productivity is up to three times higher. Our data are concordant with this last as the largest groups were recorded around Salinas, the northern limit of the Gulf of Guayaquil.

The high prevalence of scars on dolphin bodies (45.7%), most likely of anthropogenic origin, is concerning. These scars resembled small depressions and are similar to those left by fishing gear on coastal bottlenose dolphins at other sites in Ecuador (Félix et al., 2019b, 2019c). According to Ecuadorian fishers, bottlenose dolphins are large enough to break nylon monofilament gillnets used regularly in coastal areas in most fishing communities (Herrera et al., 2013). However, gear remains may be towed by animals for a long time and can penetrate the blubber and sometimes the muscle, causing deep scars and appendage mutilation (Félix et al., 2018b, 2019a; Félix, 2021). The prevalence of scars in offshore bottlenose dolphins off Ecuador is higher than other oceanic odontocetes, such as in the southern Caribbean (4.3%) (Luksenburg, 2014) and western Indian Ocean (1–15%) (Kiszka et al., 2008), but consistent with that found in coastal bottlenose dolphins in Ecuador (44.4% at Salinas) (Félix et al., 2018b). The scarring extent is related to the intense fishing activity along the Ecuadorian coast, considered a bycatch hotspot of marine vertebrates (Lewison et al., 2014).

In contrast to the high level of anthropogenic-related scarring, dolphins showed a low level of scars from sharks (3.8%) - which is generally used as a proxy of predation level - compared to bottlenose dolphins in Moreton Bay, Australia (36.6%) (Corkeron et al., 1987), Florida (22–31%) (Wilkinson et al., 2017) and Bahamas (29%) (Melillo-Sweeting et al., 2022). This low predation scarring would be related to reduced shark populations in Ecuadorian waters due to fishing activities. Between 2008 and 2012, 1.3 million sharks (30 different species, mainly alopiids and carcharhinids) were landed by Ecuadorian artisanal fishers (Martínez et al., 2015). A high proportion of this shark catch occurred outside the EEZ, possibly because of the depletion of the stocks in coastal waters. Thus, bottlenose dolphins' low prevalence of scars from interactions with sharks in Ecuador could indicate fishing pressure on large pelagic fish. On the other hand, the low proportion of shark scars in Ecuadorian offshore bottlenose dolphins may be caused by the lack of shark species that prey on dolphins such as bull (*Carcharhinus leucas*) and white sharks (*Carcharodon carcharias*) among others (see Heithaus, 2001).

A low prevalence of skin infections was found in this dolphin population. The sole case was in a young animal with abundant cutaneous nodules on most of the dorsal and lumbar regions (0.61%). Such a condition is uncommon in cetaceans but has been observed in orcas (*Orcinus orca*) in Brazil and Irrawaddy dolphins (*Orcaella brevirostris*) from Southeast Asia and diagnosed as fibropapillomas (Van Bressem et al., 2014, 2015). The low prevalence of skin diseases in Ecuadorian offshore bottlenose dolphins is consistent with previous skin disease evaluations in South American cetaceans in which a lower prevalence was found in offshore species compared to coastal species, likely related to poorer water quality in coastal areas (Van Bressem et al., 2015). For instance, 44% of coastal bottlenose dolphins at Salinas showed evidence of the skin disorder lobomycosis-like disease (Félix et al., 2019a), which was absent in the offshore dolphins in the current study. On the other hand, the prevalence of the epibiont (*X. globicipitis)* found in the current study is within the highest-known range for the species (*e.g.*, Kane et al., 2008; Gómez-Hernández et al., 2020). As a commensal organism found on the trailing edges of cetacean appendages, *X. globicipitis* can also occasionally be found on the mouth, as with one dolphin at Salango. This barnacle has been reported in 22 cetacean species in the eastern Pacific, primarily in areas of increased productivity, and its presence provides useful information on environmental conditions, host susceptibility, and other related ecological aspects (Kane et al., 2008).

Management considerations

Offshore bottlenose dolphins in Ecuador had been poorly understood due to the lack of information on basic aspects such as distribution and abundance. Despite their distinct ecological requirements and divergent evolutionary trajectories, in Ecuador all bottlenose dolphin populations have been traditionally assessed together and included in the same conservation category. However, environmental authorities have been receptive to assessing the status of the mainland offshore bottlenose dolphin separately from the inshore form and of the Galapagos offshore form in a recent review of the International Union for Conservation of Nature Red List of Mammals of Ecuador (Tirira, 2021). Although the mainland offshore ecotype is still classified as "data deficient," this is a step in the right direction. Our study contributes to filling gaps in population structure and occurrence on Ecuador's central coast, but additional efforts are needed to define the boundaries between the different population units, the nature of the interaction with coastal dolphins, and to address threats. Additionally, more systematic surveys are required to improve data collection concerning photo identification and tissue samples for genetic studies. We encourage environmental authorities to support such research along the entire coast of Ecuador to improve our knowledge of this ecotype and subsequently develop effective conservation strategies.

The existing network of MPAs on mainland Ecuador created in 2017 by the Ministry of Environment represents an opportunity to raise awareness and promote bottlenose dolphin conservation. In this study, we found that the species was mostly seen within the limits of several MPAs on Ecuador's central coast. We recommend that such MPAs include the bottlenose dolphin as a conservation target and initiate monitoring programs to generate information on this and other marine mammal species. Similarly, tourist boats operating within MPAs may join this effort and record sightings in logbooks, as occurs in the Galapagos Islands, where data on marine mammals have been collected chiefly by tourist guides for decades (Denkinger et al., 2013). We would like to highlight the Ecuadorian humpback whale-watching programs' contribution to collecting information on cetacean species, which has improved our understanding of the cetacean community in the area and their social and ecological interactions (*e.g.*, Félix et al., 2007; Castro et al., 2017). However, thus far, all the data have been collected directly by scientists. We propose that MPAs coordinate a logbook program involving all authorized tour operators within their jurisdiction to report on marine mammal species during their trips. Studies have shown citizen science to be effective at helping scientists collect information on marine mammals in developing countries (*e.g.,* García-Cegarra et al., 2021; Mwango'mbe et al., 2022). The contribution of such a program would considerably increase the number of records of offshore bottlenose dolphins and other cetaceans, as dozens of whale-watching boats are working in Ecuadorian MPAs.

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