

**NOTE**

# From coastal to offshore: The case of an inshore bottlenose dolphin that joined an offshore pod

Fernando Félix<sup>1,2</sup>  | Cristina Castro<sup>3</sup>  |  
Marie-Françoise Van Bresse<sup>4,5</sup>  | Luna Barragán<sup>3</sup>  |  
May Platt<sup>3</sup>  | Koen Van Waerebeek<sup>4,5</sup>

<sup>1</sup>Associate Researcher, Pontificia Universidad Católica del Ecuador (PUCE), Quito, Ecuador

<sup>2</sup>Museo de Ballenas, Salinas, Ecuador

<sup>3</sup>Pacific Whale Foundation-Ecuador, Puerto López, Ecuador

<sup>4</sup>Cetacean Conservation Medicine Group, Peruvian Centre for Cetacean Research/Centro Peruano de Estudios Cetológicos (CEPEC), Museo de Delfines, Lima, Peru

<sup>5</sup>Biodiversity Unit, ProDelphinus, Lima, Peru

## Correspondence

Fernando Félix, Bellavista Mz 38 V17, Guayaquil, Ecuador.

Email: [fefelix90@hotmail.com](mailto:fefelix90@hotmail.com)

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The common bottlenose dolphin (*Tursiops truncatus*) is widely distributed across tropical and temperate waters worldwide (Wells et al., 2019; Wells & Scott, 2018). Within its distribution range, several morphotypes and ecotypes are associated with coastal, estuarine, and oceanic environments, where the dolphins exploit diverse ecological niches (e.g., Fruet et al., 2017; Louis et al., 2021; Natoli et al., 2004; Tezanos-Pinto et al., 2009; Van Waerebeek et al., 1990, 2017). The ecotype that inhabits the nearshore and inland estuarine waters are known as the inshore or coastal form, distinguished morphologically and ecologically from the offshore or oceanic ecotype, the former likely resulting from relatively recent colonization processes. In some regions, however, different ecotypes have sympatric distributions and occasionally interact (e.g., Bearzi et al., 2009; Félix & Castro, 2023; Vermeulen & Cammareri, 2008; Viloria-Gómora & Medrano-González, 2015). Currently, the Marine Mammal Society Taxonomy Committee (2024) recognizes only one species and four subspecies: *T. t. gephyreus* in the Southwest Atlantic, *T. t. nuuanu* an offshore form in the Eastern tropical Pacific, *T. t. ponticus* in the Black Sea, and the nominal common bottlenose dolphin *T. truncatus*. However, there is a consensus that the species requires further taxonomic studies for its proper characterization.

Beyond ecological specialization, offshore and inshore bottlenose dolphins exhibit differences in morphology and social behavior. The most notable distinctions between ecotypes involve variation in external coloration (Viloria-Gómora & Medrano-González, 2015), dorsal fin shape (Félix et al., 2018; Morteo et al., 2017; Simões-Lopes et al., 2019), skull morphology (e.g., Dromby et al., 2023; Mead & Potter, 1993; Ott et al., 2016; Perrin et al., 2011; Van Waerebeek et al., 1990), and parasitic load (Mead & Potter, 1993; Van Waerebeek et al., 1990). Coastal bottlenose dolphins tend to be resident within well-defined home ranges, typically forming small groups of up to two

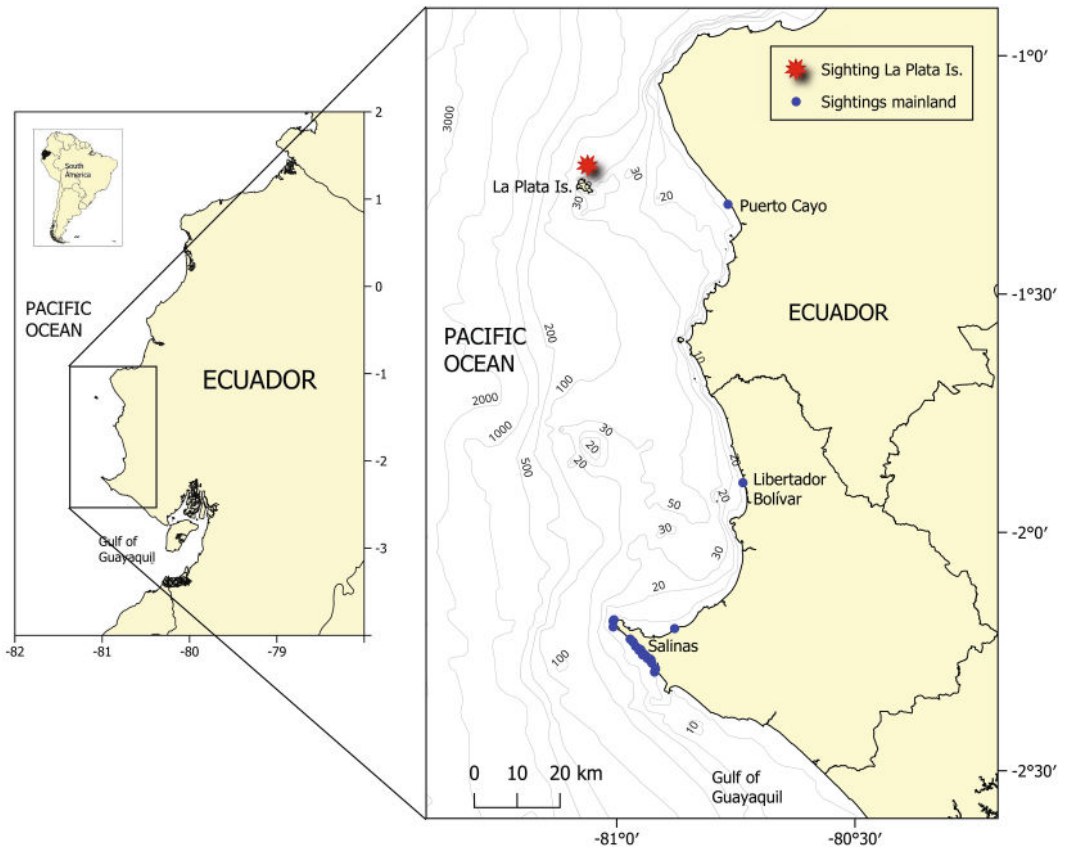
dozen individuals, while offshore bottlenose dolphins have an extensive range and may aggregate in groups numbering up to several hundred individuals (e.g., Scott & Chivers, 1990; Vilorio-Gómora & Medrano-González, 2015; Wells & Scott, 2018). Offshore populations also exhibit greater gene flow with other populations leading to higher genetic diversity compared with the coastal ecotype, which is characterized by highly structured populations and low genetic diversity (e.g., Bayas-Rea et al., 2018; Fruet et al., 2017; Natoli et al., 2004; Sanino et al., 2005; Tezanos-Pinto et al., 2009).

Similar to a few other regions, three ecotypes of bottlenose dolphins are found along the coast of Ecuador: (1) the offshore ecotype inhabits the outer continental shelf and slope, and open, oceanic waters (Félix & Castro, 2023; Van Waerebeek et al., 2017); (2) the nearshore ecotype inhabits the coastal border, extending up to approximately 1 km from the shore (Castro & Félix, 2021; Félix, Van Bresseem, & Van Waerebeek, 2019); and (3) the estuarine ecotype that is resident in the inner estuary of the Gulf of Guayaquil in the southwest of the country (Bayas-Rea et al., 2018; Félix, 1994). A molecular study demonstrated a lower diversity of haplotypes in the inner estuary population than those in the outer estuary and the offshore ecotype, with a single haplotype (Hap-7) predominating and widely spread within the inner estuary (Bayas-Rea et al., 2018). Skull shape variations also confirm high divergence and habitat specialization in the estuarine population (Dromby et al., 2023). Offshore bottlenose dolphins in the Southeast Pacific can be distinguished at sea by their falcate dorsal fins, which contrast with the more triangular dorsal fins of inshore dolphins (estuarine and nearshore) (Félix et al., 2018). While groups of the offshore ecotype have occasionally been recorded in coastal areas of central Ecuador, there have been no sightings of coastal groups venturing into offshore waters. Similarly, coastal dolphins have not been observed within the distribution range of the estuarine ecotype nor have estuarine dolphins been spotted in coastal areas along the central coast of Ecuador, despite extensive research efforts, including photo-identification of individuals, in the past 10 years (Castro & Félix, 2021; Félix et al., 2022; Félix, Van Bresseem, & Van Waerebeek, 2019).

Ecological differentiation among bottlenose dolphin ecotypes in Ecuador is marked also by the presence of lobomycosis in coastal and estuarine populations but absence in the offshore ecotype (Van Bresseem et al., 2024). Lobomycosis, a mycotic dermal disease, manifests as single or multifocal light gray to whitish nodules and plaques that may ulcerate, grow over time, and ultimately lead to the animal's death (Van Bresseem et al., 2015, 2024). Its prevalence ranges from 5.1% to 13% in the estuarine form and is even higher in the nearshore (coastal) community at Salinas in the northern Gulf of Guayaquil, reaching 44.4% (Félix, Zavala, & Centeno, 2019).

On August 19, 2024, during a cetacean research trip off the central coast of Ecuador, we encountered a group of 110–120 offshore bottlenose dolphins traveling westbound along the north side of La Plata Island (1°16.13' S, 81°3.74' W) (Figure 1). The island is located 24 km from the nearest point on the coast and lies at the edge of the continental shelf. The depth on the north and east sides ranges from 20 to 30 m, but it increases sharply on the west side, reaching 200 m just 7 km from the island. This group of dolphins was identified as part of a known community of offshore bottlenose dolphins that the authors have monitored for two decades. In 2022, this oceanic community was estimated to comprise 163 individuals (95% CI: 120–203) and has demonstrated high site fidelity over time (Félix & Castro, 2023). We photo-identified 85 dolphins, including 58 recaptures, 27 new individuals, and 24 calves, based on their dorsal fins during the sighting. Notably, one of the recaptured dolphins was an inshore bottlenose dolphin identified as S20, an adult female from a community residing near Salinas (2°11.77' S, 80°58.82' W), approximately 100 km to the south (Figure 1) (Félix, Van Bresseem, & Van Waerebeek, 2019). S20 and her calf, estimated about 3 years old (originally documented in 2022, see below), appeared well integrated into this offshore group, swimming alongside other mothers and their calves.

Salinas is located on a narrow peninsula that constitutes the westernmost point of continental Ecuador, toward the Pacific Ocean and the northern border of the Gulf of Guayaquil (Figure 1). Between April 2010 and March 2018, S20 was recorded 22 times, being one of two mothers with calves in this reduced community of nine inshore bottlenose dolphins (Félix, Van Bresseem, & Van Waerebeek, 2019). The Salinas dolphin community inhabits approximately 40 km of coastline, covering both sides of the peninsula, but they concentrate activities along the southern coast of the peninsula (Figure 1). The first time S20 was observed outside her community's home range was on April



**FIGURE 1** Distribution range of inshore-type dolphin S20 on the central coast of Ecuador. Blue dots indicate where coastal sightings of S20 were made. Red dot indicates the site of the sighting just north of La Plata Island.

23, 2022. She was seen in Puerto Cayo, about 100 km north of Salinas, accompanied by her calf, then estimated to be 1 year old, an adult female (ID S10), and an adult male (ID S6), both from the Salinas community. The following day, these four dolphins were observed interacting with 14 offshore bottlenose dolphins near Libertador Bolívar, a fishing village 65 km south of Puerto Cayo (Figure 1). This event was previously reported by Félix and Castro (2023) and represented the first time that dolphins of two different ecotypes were documented interacting in Ecuador. These sightings, far beyond the dolphins' home range, indicated that something unusual was happening with the Salinas dolphin community. However, no further monitoring has been conducted around Salinas since 2018, and the current status of this dolphin community remains unknown.

A comparison of the dorsal fin shape of S20 and some members of the former Salinas community with the dorsal fins of the offshore dolphins she joined is shown in Figure 2. The morphological differences mostly consist of the greater falcate shape of the offshore dolphins' dorsal fins than those of the inshore Salinas community. This distinction aligns with previous findings on the differences between both ecotypes of Southeast Pacific bottlenose dolphins (Félix et al., 2018).

Besides the unique markings on her dorsal fin, S20 exhibits characteristic granulomatous skin lesions associated with lobomycosis. Figure 3 illustrates the progression of the disease since July 2016 when S20 was part of the Salinas community. At that time, two whitish granulomas were visible on the rear right flank: a larger one on the lower back and two smaller ones approximately 30 cm forward (Figure 3a). Photographs B and C, taken at La Plata Island in 2024, revealed significant changes. The whitish skin lesion on the rear flank had increased in size by three to four



**FIGURE 2** Comparison of mostly triangular dorsal fins of the Salinas (nearshore ecotype) bottlenose dolphin community (below), including S20 (extreme right) and more falcate dorsal fins (Félix et al., 2018) of some of the offshore pod members that S20 joined on August 19, 2024 (above).



**FIGURE 3** Progression of lobomycosis skin disease on the right flank of bottlenose dolphin S20. Photograph (a) was taken on July 30, 2016, in Salinas, and photographs (b, c) on August 19, 2024, at La Plata Island. It demonstrates the chronic nature of lobomycosis. Arrows highlight areas on the animals' body where cutaneous lesions caused by lobomycosis have developed.

times (Figure 3b), while the anterior granulomas appeared to have fused and grew to nearly three times their original size (Figure 3c). Additionally, new whitish nodules had developed between the original two, indicating further cutaneous spread of the disease. Lobomycosis expands slowly during the initial years of infection but, with time, the

disease may develop more rapidly due to immunological depression associated with age or environmental factors (Van Bresseem et al., 2024).

Inshore bottlenose dolphins live in communities within well-defined territories, forming strong social bonds that often last a lifetime (Wells, 1991, 2014; Wells & Scott, 2018). This appears to have been the case with S20, an adult female observed from 2010 to 2018 within the Salinas community and which was consistently seen associated with another adult female (S10) (Félix, Van Bresseem, & Van Waerebeek, 2019). S20 and S10 were also observed together in April 2022 near Puerto Cayo and Libertador Bolívar, although they were not associated during the sighting at La Plata Island. Thus, the bond between S20 and S10 endured for at least 12 years. The question then arises: What led S20 and other members of the Salinas community to leave their home range and move 100 km north in 2022, with S20 ultimately joining a group of oceanic dolphins? The social organization, distribution, and movement patterns of inshore bottlenose dolphins are influenced by a range of biological and ecological factors, including kinship, sex, age, prey availability, predation pressure, and changing environmental conditions due to seasonal variability and the tidal cycle, among others (e.g., Di Giacomo & Ott, 2016; Louis et al., 2018; Morteo et al., 2012, 2014; Wells et al., 1987). Like other coastal dolphins worldwide, bottlenose dolphins face threats from human activities such as fishing, maritime traffic, and habitat degradation due to pollution (e.g., Bechdel et al., 2009; Félix et al., 2018; Kiszka et al., 2008; Reeves et al., 2013; Van Waerebeek et al., 2007) that may alter the spatiotemporal distribution patterns of dolphins (e.g., Bridge et al., 2023; Morteo et al., 2012). It is unclear whether environmental or demographic factors disrupted the Salinas community's social structure. However, with only nine members in 2018 of which four had lobomycosis, including seriously affected high-rank male S4 (Félix, Zavala, & Centeno, 2019), the long-term viability of the community was already at risk.

The movement of females S20 and S10 northward along the coast in 2022 suggests that after the collapse, remaining members of the Salinas community extended their range along the coastal border, possibly in search of integration into another inshore dolphin community. Alternatively, they could have moved southward to the inner estuary of the Gulf of Guayaquil, where at least five dolphin communities inhabit estuarine waters (Félix, 1994; Félix et al., 2022). Their northward movement, rather than southward, implies that low salinity might have posed a barrier. Skin lesions and changes in blood biochemistry have been reported in bottlenose dolphins exposed to low salinity (Deming et al., 2020; Duignan et al., 2020; Geraci et al., 1986; McClain et al., 2020). Even estuarine bottlenose dolphins are sensitive to extended low salinity conditions. Félix (1994) observed changes in the distribution of estuarine dolphins near the mouth of the Guayas River, in the inner estuary of the Gulf of Guayaquil (Figure 1). Dolphins moved away from the area during heavy rainy seasons for several months. Likewise, Van Waerebeek et al. (2003) reported a sharp decline in sightings of resident common bottlenose dolphins in the Gambia River estuary (West Africa) in 1999, after more than a third of dolphins were affected by “creamy-white skin lesions” on their back and dorsal fin. The lesions had disappeared when the dolphins reappeared months later, presumably after moving out to sea. We suggest that a severe drop in salinity of the estuarine habitat due to unusually heavy seasonal rains causing flooding in The Gambia from June to September 1999 (FAO, 1999) may also have played a role.

It is also possible that the estuarine communities were less receptive to integrating new dolphins that did not belong to the communities from the inner estuary. A process of fusion between communities has recently been observed within the inner estuary, but not with nearshore dolphins. The high genetic diversity observed in offshore bottlenose dolphins (e.g., Louis et al., 2021; Natoli et al., 2004; Tezanos-Pinto et al., 2009) suggests a high level of social permeability, which S20 may have exploited. Female inshore bottlenose dolphins typically exhibit strong site fidelity and low immigration rates (Félix & Burneo, 2020; Natoli et al., 2005; Wells & Scott, 1990). Female dispersal could be even more reduced if other dolphin communities are not nearby. Castro and Félix (2021) monitored the area between Puerto Cayo and Libertador Bolívar, where S20 was recorded, and estimated the encounter rate at .0051 dolphins/km of survey, 29 times lower than the encounter rate in Salinas with its small dolphin community. Therefore, it is likely that S20 joined a group of oceanic dolphins due to the absence of a neighboring inshore community to migrate to.

The arrival of female S20 in this oceanic *T. truncatus* community has health implications. Caused by the yeast *Paracoccidioides ceti*, lobomycosis is likely transmitted by contact with an infected individual through cutaneous injuries, such as bites (Van Bresseem et al., 2024). Thus, in the Gulf of Guayaquil, males are at higher risk than females because they form long-lasting alliances and frequently interact with each other (Félix, Van Bresseem, & Van Waerebeek, 2019). As S20 is a reproductive female, she may infect offshore dolphins during mating and other social interactions and introduce the disease to this population. In the Gulf of Guayaquil, low-rank old males are mostly responsible for lobomycosis dissemination of the disease, as they have larger home ranges than high-rank males (Félix, Zavala, & Centeno, 2019). Similarly, transient dolphins are suspected to play a role in the disease expansion along the coast of Brazil (Van Bresseem et al., 2015). Lobomycosis is rare among oceanic dolphins, with only three cases reported in North Carolina, USA (Rotstein et al., 2009). It has not been detected in 221 offshore *T. truncatus* photo-identified off the coast of Ecuador (Félix & Castro, 2023) nor was it observed in dozens of *T. truncatus*, both offshore and inshore ecotypes, bycaught off Peru and examined freshly dead between 1985–2000 (Van Waerebeek et al., 1990, 2017). Further surveys are necessary to examine if lobomycosis will be transmitted to other individuals in the offshore population or if a stronger immunity possibly linked to higher genetic diversity and lower anthropogenic contamination may protect them against the disease. Migrant dolphins like S20 may be responsible for expanding lobomycosis to coastal and offshore/oceanic populations. Although lobomycosis may negatively affect small communities of coastal dolphins already burdened by various human-induced stressors (Van Bresseem et al., 2024), its potential encroachment on offshore populations also impacted by anthropogenic activities should not be overlooked. It currently appears unfeasible to address or mitigate the risk of lobomycosis transmission, as no experimental treatments have been attempted in wild populations, only in captivity (e.g., Esperón et al., 2012; Minakawa et al., 2016; Ueda et al., 2013). Monitoring this case could provide valuable insights into the disease pathogenesis, epidemiology, and potential risks affecting this offshore population. The ecological plasticity exhibited by S20 suggests that gene flow between inshore and offshore ecotypes may be bidirectional. While genetic evidence indicates that offshore bottlenose dolphins have given rise to inshore populations through multiple founding events worldwide (Louis et al., 2021; Natoli et al., 2004; Nykanen et al., 2019), there is no documented evidence, to the authors' knowledge, that gene flow is also occurring in the opposite direction. Given that S20 is a reproductive female, gene flow from inshore to offshore bottlenose dolphins seems inevitable. In our catalog of approximately 200 offshore bottlenose dolphins from central Ecuador, two other individuals have triangular dorsal fins, a characteristic typically associated with inshore dolphins. This suggests that the case of S20 may not be the first in the area. Similarly, Félix et al. (2018) documented a landed offshore bottlenose dolphin in Peru with a triangular dorsal fin, which deviated from the typical falcate pattern observed in the rest of Peruvian offshore dolphins. Although the socio-ecological conditions in S20's community may be unique, similar dynamics could occur in other regions, with offshore populations potentially integrating individuals from declining inshore communities. This phenomenon could explain why a common haplotype in the coastal population was found in one offshore bottlenose dolphin in the Northeast Atlantic (Louis et al., 2014). The case reported here has implications for population management and taxonomic characterization of wild bottlenose dolphin populations and warrants further research.

## AUTHOR CONTRIBUTIONS

Fernando Félix: conceptualization, investigation (field), writing original draft. Cristina Castro: investigation (field), review and editing. Marie-Françoise Van Bresseem: interpretation of data, review and editing. Luna Barragán: investigation, review and editing. May Platt: investigation, review and editing. Koen Van Waerebeek: interpretation of data, review and editing.

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## ORCID

Fernando Félix  <https://orcid.org/0000-0001-7881-3114>

Cristina Castro  <https://orcid.org/0000-0002-5166-0389>

Marie-Françoise Van Bresseem  <https://orcid.org/0000-0003-4399-3084>

Luna Barragán  <https://orcid.org/0000-0002-8123-5957>

May Platt  <https://orcid.org/0000-0002-8008-3082>

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