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Fusion of Communities, the Response of Estuarine Bottlenose Dolphins to Population Decline in the Gulf of Guayaquil, Ecuador

Fernando Félix

Museo de Ballenas. Av. General Enríquez Gallo 11-09. Salinas, Ecuador.

Corresponding author (Email: fefelix90@hotmail.com)

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Abstract – Changes in the social structure of two neighboring communities of estuarine bottlenose dolphins in Ecuador were assessed over 14 years (2011–2024). During this period, 632 surveys were conducted, covering a cumulative distance of 23,171 km. A total of 133 distinct individuals, representing all age and sex classes, were recorded. The annual abundance of dolphins decreased from 50 in 2014 to 24 in 2024, coinciding with a decline in the proportion of non-resident individuals, from 35% to 0%. Changes in the social structure were analyzed across three periods: 2011–2015, 2016–2019, and 2020–2024. Pairwise cluster analyses revealed two distinct communities (El Morro and Posorja) in the first two periods, which merged into a single community in the third period. Significant social changes were observed during this process as the two communities adapted by sharing spaces and resources, altering spatiotemporal patterns, and increasing their time together to benefit from the fusion. Female mixed groups increased from 0% to 77.8%, the inter-community association rate rose from 0.04 to 0.74, and the average group size grew from 8.07 to 11.48 dolphins/group. Reproductive parameters, including calf survival rates and the fertility of Posorja females, improved following the fusion. These findings reveal a high degree of social flexibility within this population, suggesting that even though inshore bottlenose dolphins typically form discrete social units, these structures can adapt and reorganize under certain demographic or social pressures. Given the historical and emerging threats to this population, understanding the drivers of these social dynamics is critical for the long-term conservation of this endangered population.

Keywords – *Tursiops truncatus*, Social behavior, Reproductive parameters, Conservation, Ecuador

The social behavior of mammals is shaped by genetic and ecological factors that determine the complexity of interactions within the social network and maximize survival and fitness (Clutton-Brock, 2021; Crook et al., 1976). Environmental changes, such as habitat degradation and climate disruption, can lead to population fluctuations and heightened vulnerability, often resulting in sudden demographic imbalances that are not always well understood (Colchero et al., 2018; Testard et al., 2021; Wild et al., 2019). Changes in social structure within populations may occur during adaptation to the new conditions but can go unnoticed in the absence of contextual information. Unlike short-term studies, long-term studies, for example with chimpanzees *Pan troglodytes* (Pusey et al., 2007), elephants *Elephas maximus* (Fritz, 2017), mountain gorillas *Gorilla beringei beringei* (Steklis and Steklis, 2008), common bottlenose dolphins *Tursiops truncatus* (Wells, 2018) and orcas *Orcinus orca* (Parsons et al., 2009), provide critical insights by allowing researchers to track changes in stable social groups in relation to environmental fluctuations across generations. Such studies have been crucial to understanding life-history traits and evolutionary processes and finally providing essential data for conservation efforts.

The common bottlenose dolphin is widely distributed in temperate and tropical waters worldwide, inhabiting pelagic and coastal environments, including oceanic islands, continental shelves, coast bays and estuaries (Wells et al., 2019). Its ecological flexibility to adapt to different environments has given origin to well-differentiated forms along much of its distribution range that have been grouped into two main categories inshore and offshore ecotypes. The inshore ecotype is found in estuaries, bays, and lagoons, while the offshore ecotype occupies neritic and pelagic waters (Well et al., 2019). Contrary to the offshore form, inshore dolphins show population differentiation at small geographic scales, low genetic diversity, and restrained home ranges (Fruet et al., 2017; Louis et al., 2014; Lowther-Thieleking et al., 2015; Natoli et al., 2004; Richards et al., 2013; Rosel et al., 2009; Sellas et al., 2005; Tezanos-Pinto et al., 2009). The inshore ecotype also includes estuarine populations that inhabit brackish waters and exhibit even smaller home ranges than other inshore populations, primarily due to habitat specialization, making them highly vulnerable to human activities (e.g. Félix et al., 2022; Fury and Harrison, 2008; Harzen, 1998; Mazzoil et al., 2008).

Most of our knowledge about the social behavior of bottlenose dolphins has been generated by long-term studies in Sarasota Bay, Florida (USA) and in the Indian Ocean bottlenose dolphin *Tursiops aduncus* in Shark Bay, Australia (Connor et al., 2019; Wells, 2014). Although some differences in social behavior are evident between bottlenose dolphin species/populations due to different environmental conditions associated with social behavior and seasonal shifts, other aspects such as long-term site fidelity, high degree of sociability, long nursing period, and organization in multigenerational family groups are common to most populations around the world (Connor et al., 2000; Wells 2019). Bottlenose dolphins live in societies known as fission-fusion in which their members join and split fluidly (Connor et al., 2000; Lusseau, et al., 2006; Wells et al., 1987). Adult females are the nucleus of the community with a larger social network around which other members associate according to sex, physical maturity, kinship and social status (Félix et al., 1997; Wells, 2014; Wells et al., 1987). Related females stay together as a family in multi-generational groups organized in bands (Duffield and Wells, 1991; Wells et al., 1987). Adult males also develop strong affective bonds with other males from puberty, creating pairs or alliances facilitating access to females or to improve social status when adults (Connor et al., 2000; Duffield and Wells, 2023; Félix, 1997; Gerber et al., 2022, Wells et al., 1987; Wiszniewski et al., 2012). Young individuals leave the family group during adolescence and return years later as adults (Wells et al., 1987). Maternal investment and long lifespans play a key role in fostering and maintaining strong social relationships over time and contribute to the stability of the social system (Wells, 2014). Gender parity or a slight bias towards females has been reported in stable bottlenose dolphin populations (Fruet et al., 2015; Wells and Scott, 1990). However, this may not be the case in populations showing depressed demographic parameters (Félix and Burneo, 2020).

A resident population of estuarine bottlenose dolphins inhabits the inner estuary of the Gulf of Guayaquil in southwestern Ecuador, and which I have been studying for 35 years (Félix 1994; Félix, et al., 2020, 2022). Molecular studies show that they are genetically distinct from other nearby coastal populations, have low genetic variability, and high level of inbreeding (Bayas-Rea et al., 2018). This distinctiveness results from geographical isolation due to ecological factors characteristic of the inner estuary, particularly its lower salinity and high productivity (Stevenson, 1981). As in other inshore bottlenose dolphins (e.g., Fruet et al., 2017; Mazzoil et al., 2008; Sellas et al., 2005; Wells et al., 1987), the population in the inner estuary is structured in semi-closed communities within small home ranges that overlap at their borders despite habitat uniformity (Félix, 1997; Félix & Burneo, 2022). Although no evident physical or ecological barriers exist, the home ranges of this population appear to be defined by physiographic features, such as islands and channels, and generally defined by the movements of adult females and their calves, as some adult males extend their range when seeking breeding opportunities in neighbor communities (Félix et al., 2019). Between 13 and 25% of the recorded dolphin groups are individuals belonging to two or more neighboring communities (Félix, 1997; Félix & Burneo, 2020). Typically, groups comprise up to two dozen individuals, but larger groups can occasionally be observed

(Félix 1994). Social groups maintain different degrees of stability, with members of some social units found regularly together for days or weeks and containing all age and sex classes, while other dolphins with weaker bonds stay short and involve mostly adult males (Félix 1997; Félix et al., 2017).

The bottlenose dolphin population inhabiting the inner estuary of the Gulf of Guayaquil is currently experiencing a decreasing trend, with dolphin community size reduced by an average of 53% over the past thee decades (Félix et al., 2017, Félix and Burneo, 2020). It is estimated that around 200 dolphins could remain, but an updated evaluation of the whole estuary is required to determine population status. The decreasing trend has also changed the structure of the communities, which are now much smaller, and the average group size has been reduced by 46% (Félix et al., 2017). It is estimated that the communities on the western side of the estuary could disappear within a time equivalent to thee generations (40 to 70 years) if current conditions persist (Félix and Burneo, 2020). The causes of this population decline are similar to those affecting other marine megafauna species, including interaction with fisheries, collisions with ships (Félix, 2021; Félix et al., 2018; Van Waerebeek et al., 2007), and habitat degradation due to pollution in its various forms (wastewater and industrial waste, persistent organic matter, eutrophication, plastic waste, noise, heavy metals, among others) (Jiménez and Álava, 2014, Ormaza et al., 2022, 2024; Twilley et al., 2001). Human activities are modifying social behavior in this population by reducing opportunities for socialization, forcing emigration to other less deteriorated areas, and modifying the hierarchical structure within communities, which could accelerate their decline (Félix, 2021). The social organization of the population in communities is key to understanding why the impacts caused by human activities are differentiated. While some communities are less impacted, others face intensive deterioration exacerbated by habitat degradation and greater exposure to environmental stochasticity.

In this article, I analyzed medium-term changes in the social structure of two neighboring communities of bottlenose dolphins in the inner estuary of the Gulf of Guayaquil, which are subjected to strong anthropogenic pressure. The goal was to quantify the effect of population decline on their social structure and assess whether this compromises their long-term survival. As the number of individuals declined in both communities, a proportional reduction in social network size was expected. Alternatively, dolphins might increase social connectivity with other communities to maintain group cohesion, potentially leading to more mixed-group associations. The analysis shows that dolphins exhibit high flexibility in expanding their social networks, which has led to improvements in demographic parameters and created new opportunities for conservation.

Methods

Ethics Statement

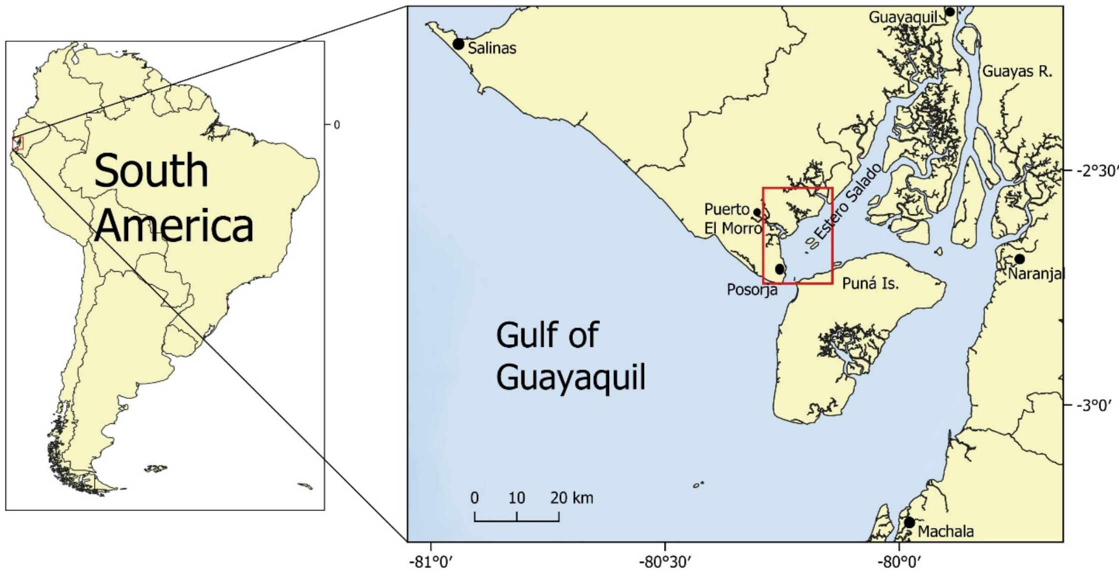
This research was authorized by the Ministry of Environment of Ecuador though permits N004-IC-FAU-DPG/MAE, N006-2018-IC-FLO/FAU-DPAG/MAE, N018-2019-IC-FLO/FAU-DPAG/MAE, MAAE-ARSFC-2021-1776, MAATE-ARSFC-2023-2943 and MAATE-ARSFC-2024-0389.

The Study Area

The study area is situated in the Gulf of Guayaquil, a productive tropical estuary in southwestern Ecuador, spanning 12,000 km^2 (Figure 1). This region is characterized by a seasonal rainfall pattern, with a short warm and rainy season from January to April and an extended dry season from May to December. During these periods, significant seasonal shifts occur in salinity, primary productivity, nutrient levels, and, to a lesser extent, temperature and pH (Stevenson, 1981). Salinity varies annually between 19 and 36 ppt, while surface temperatures range from 22 to 30°C (Twilley et al., 2001). The inner estuary experiences a semi-diurnal tidal regime with 2.5 m tides and currents up to 3 knots, which plays a key role in estuary dynamics (Stevenson, 1981).

Figure 1

The Study Area



Note. The study area in the southwest of Ecuador (red square). The map also shows the location of Ecuador in northwest South America.

The study area covers approximately 55 km^2 on the western side of the inner estuary (centered at 2º39'S, 80º13'W), extending along 22 km on the west side of the Estero Salado channel, between Posorja to the south and the Sabana Grande to the north. It includes thee secondary channels, Morro, Ceibo, and Sabana Grande, that branch from Estero Salado and are frequented by dolphins, particularly near their mouths (Figure 1). With a width of up to 15 km in this area, the Estero Salado extends 70 km inland. Approximately 50 km to the east, the Guayas River, the estuary's largest freshwater source, flows counter to the Estero Salado. Between these channels lies a vast delta of islands and waterways. Most of the study area falls within the El Morro Mangrove Refuge (REVISMEM), a 10,230 ha marine protected area where the bottlenose dolphin is a major conservation target (Ministerio del Ambiente del Ecuador, 2010).

Surveys

Boat trips have been conducted since 2005 as part of a long-term study of the bottlenose dolphin population in the inner estuary. Beginning in 2011, these surveys became more regular, with gradual increases in survey frequency (see Table 1). The boats used were 6–8 m in length with outboard engines (48-150 HP), departing from Posorja (2011–2014) and subsequently from Puerto El Morro, 8 km upstream. Most trips were opportunistic, using tourist boats, though some dedicated research trips covered areas beyond the scope of this analysis. Survey distances varied from 20 to 100 km, with durations between 2 and 7 hours, depending on the trip type. Surveys commenced near the departure port, with dolphin searches extending outward to the Estero Salado. If the trip departed from Posorja, the direction was north toward El Morro; if it departed from El Morro, the direction was south toward Posorja, continuing until a group of dolphins was found. If no dolphins were found in this section, the boat moved north along the Estero Salado to survey the El Ceibo and Sabana Grande channels. Surveys were conducted with similar intensity throughout the year. Additional details on survey methodology is documented in Félix and Burneo (2020) and in Félix et al. (2022).

A group following sampling method was used once dolphins were located (Mann, 1999). A group of dolphins was defined as all animals observed during the sighting period, generally performing similar activities and moving as a unit with similar speed and direction (Félix et al., 2017). Data collected included behavioral state, group size, and composition. Group size was estimated in the field and then verified after photo-ID analysis. Individual dolphins were classified into thee classes: adults, subadults, or calves based on their relative size (Félix 1997; Félix & Burneo, 2020). Larger animals were classified as adults, smaller animals around 2 m in length were deemed subadults, and smaller animals regularly associated with an adult, presumably, the mother, as calves.

Cameras (18–24 megapixels) with 70-300 mm and 100-400 mm zoom lenses were used to take photographs of dorsal fins and other characteristic body parts. Both the shape and the notches on the posterior edge of the dorsal fins were used for individual identification, but also temporal scars product of teeth rakes and sharp objects (see previous work Félix, 1997; Félix and Burneo, 2020; Félix et al., 2017). The best quality photographs regarding focus and angle were used to create a catalog regularly updated as new distinctive features appeared. Each dolphin was assigned an alphanumeric identification code. The sightings were georeferenced using a Garmin 64 GPS and the route information was subsequently used to estimate the sampling effort and build distribution maps using QGIS v.3.4 (QGIS Development Team 2018).

Population Demographics

Dolphin Population

The area is inhabited by two resident population units (Félix et al., 2017, 2022), hereafter referred to as communities (*sensu* Well et al., 1987). These communities were named Posorja and El Morro, based on their distribution areas. Both exhibit strong intra-group affinity and limited home ranges, but have distinct demographic profiles (Félix & Burneo, 2020). Community membership was inferred though pairwise association analysis, which quantifies the strength of associations between pairs of individuals (Félix et al., 2017; Félix et al., 2022). For both dolphin communities, 95% of home ranges were estimated at 23.5 km^2 and 44.8 km^2, respectively, with 11.2 km^2 overlap (Félix et al., 2022).

Age and Sex Determination

Individuals were assigned to one of three age categories (adults, subadults, or calves) according to their relative size and their life histories (Félix, 1997; Félix et al., 2017; Félix & Burneo, 2020). As some individuals were recorded since they were calves or juveniles and changed their class with time, the age class was assigned on an annual basis. The sex of the animals was determined by using photographs of the dolphin's anogenital area, molecular methods (Bayas et al. 2018), and using indirect information based on breeding condition and behavior. Adult females were closely and regularly associated with a calf at some point in their lives and males never associated specifically with a calf during the study period but regularly associated with another adult male of similar characteristics (Félix et al., 2019).

Reproductive Parameters

To evaluate changes in reproductive conditions of both communities, five reproductive parameters were evaluated over the three periods of the study: 1) the number of adult females; 2) the total number of offspring; 3) female fertility (offspring per female); 4) survival to one year of age; and 5) calf survival at weaning.

Abundance

Since all dolphins in the study area were identified though natural marks, including calves and immature animals, the population size was calculated yearly as the number of individuals recorded in that year. Mark-recapture models were used in the past to estimate population abundance in the area and population parameters calculated to assess population trajectories (Félix & Burneo, 2020; Félix et al., 2017).

However, those estimates only included marked individuals, leaving out many youngsters and calves. Annual variation in population size, residence level, and age/class composition provides valuable insights into social structure dynamics.

Community Structure and Membership

Residency and Site Fidelity

Sighting histories were used to calculate residency and site fidelity for each identified individual following the definitions of Balance (1990) and Morteo et al. (2012) with adaptations to the study. Two indices were calculated "residence" and "permanence." The annual residency level is the number of times an individual was recorded relative to the number of groups observed in the year. Animals with a value less than 0.05 (5%) were considered non-residents. Permanence is the number of days (converted to years) between the first and last sighting. Dolphins were assigned to one of four categories: 1) Uncommon, when individuals were observed only within one year; 2) Low, when individuals were seen between one and four different years; 3) Medium, when individuals were seen between four and nine different years; and 4) High, when individuals were seen in more than nine years.

Social Structure Analysis

Dolphin social structure was assessed based on the frequency individuals were found together though hierarchical cluster analysis using the half-weight index implemented in the software SOCPROG (Whitehead, 2009). This index is appropriate when there are sources of bias associated with identifying individuals for different reasons such as if pairs are more likely to be scored when together than when separate (Cairns & Schwager, 1987). This index measures association strength between individuals based on group co-occurrence frequency, ranging from 0 (no association) to 1 (always together). The analysis included 790 groups with two or more individuals. Individuals considered non-residents were excluded from the analysis. Dendrograms comparing association indices were created for different periods. A cophonetic correlation index indicates how well the dendrogram reflects the association indexes in the matrix. A cophonetic coefficient greater than 0.8 indicates a good match (Bridge, 1993).

SOCPROG allows for exploring the possibility that the population can be divided into clusters by selecting option Modularity 1 when performing the cluster analysis. Association indices are higher among individuals of the same cluster and lower among individuals of different clusters. Modularity is the difference between the proportion of the total association within clusters and the expected proportion explored, given the added associations of different individuals (Newman, 2006). A value of modularity above 0.3 is usually considered useful for indicating divisions of the population (Newman, 2004). In addition, a test for preferred/avoided associations using 1000 permutations implemented in SOGPROG to test the null hypothesis that individuals associate with the same probability with other individuals, given their availability, was used.

To complement the hierarchical cluster analysis, the lagged association rates (LARs) were modeled with SOCPROG. LAR analyses address the temporal pattering scales in social relationships describing how they change with time (Whitehead, 1995). LAR is an estimate of the probability that if two individuals are associating now, they will still be associated various time lags later (Whitehead, 1995, 2008). LAR curves were smoothed changing the number of potential associations over which the lagged association rate and its associated lag is calculated. Precision for LARs were obtained with the jackknife procedure in which the analysis is run several times omitting one or more sampling periods each time (Efron & Stein, 1981). The default value 1, jackknifing on each sampling period, was used.

LAR plots describe the types of associations between individuals in society, such as closed non-interacting units, casual acquaintances, constant companions plus casual acquaintances, rapid disassociation plus preferred companions, constant companions plus casual acquaintances plus mortality, and cyclic sociality plus mortality (Whitehead, 2008). Exponential models, in which lagged association rates are built from processes whose effects (forming or breaking an association) are equally likely to occur in any time interval, were used to fit the LAR data in SOCPROG. The quasi-Akaike Information Criterion (QAIC) was used for model selection (Burnham and Anderson, 2002). The model with the minimum QAIC was selected.

Spatial Analysis

Survey tracks and sighting positions logged with a Garmin 60 GPS were used to estimate the effort and relative group density using vectorial tools implemented in the software Q-GIS. Tracks were segmented to exclude off-effort periods (sightings). A polygon data layer of 250 m x 250 m grid cells (0.062 km^2) covering the study area was used to calculate individual cell effort units. The total length of survey tracks was calculated in each cell using the geoprocessing tool "intersect". Then the number of groups was calculated in each cell using the data management tool "join attributes by location". Finally, the relative abundance of dolphin groups per unit of effort in each cell (groups/km of survey) was calculated using the "field calculator" tool. Maps of relative abundance and distribution were also created with Q-GIS.

Results

Efforts

Over the study period (2011-2024), 632 surveys were conducted, covering 23,171 km. The monitoring time amounted to 1,639.2 h, including 694.6 h of direct observation of dolphins. A total of 886 groups and 8,155 dolphins were recorded. Detailed data on annual monitoring effort and relevant information on dolphin groups are shown in Table 1.

Due to irregular monitoring effort across the study period, thee distinct time frames were established to analyze dolphin social structure: 2011-2015, 2016-2019, and 2020-2024. The 2011-2015 period was characterized by a low level of monitoring, except for 2014, with 64 surveys and 78 sightings. In the period 2016-2020, monitoring was more homogeneous, and the number of trips increased 2.9 times compared to the previous period. In the 2020-2024 period, monitoring effort doubled compared to 2016-2019, though it was less uniform, especially in 2020.

Table 1

Annual Effort

Item	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	Total
Trips	5	4	9	42	4	51	40	58	38	19	38	100	173	51	632
Survey time (h)	13.8	7.9	39.4	139	6.8	106	120	248	167	53.9	82.6	204	350	99.7	1,639.2
Sighting time (h)	2.7	3	12.9	17.8	2.4	39.6	47.1	137	86.8	28.1	48.5	86.3	139	44.2	694.6
Distance (km)	147	80	496	2,123	77	1,418	2,038	3,129	2,376	952	1,145	2,777	5,012	1,401	23,171
Groups	6	5	13	49	5	62	84	122	79	25	67	122	188	59	886
Total dolphins	40	60	118	335	55	470	497	850	484	215	608	1255	2341	827	8,155

Note. Annual effort and number of groups and dolphins observed during the study period (2011-2024).

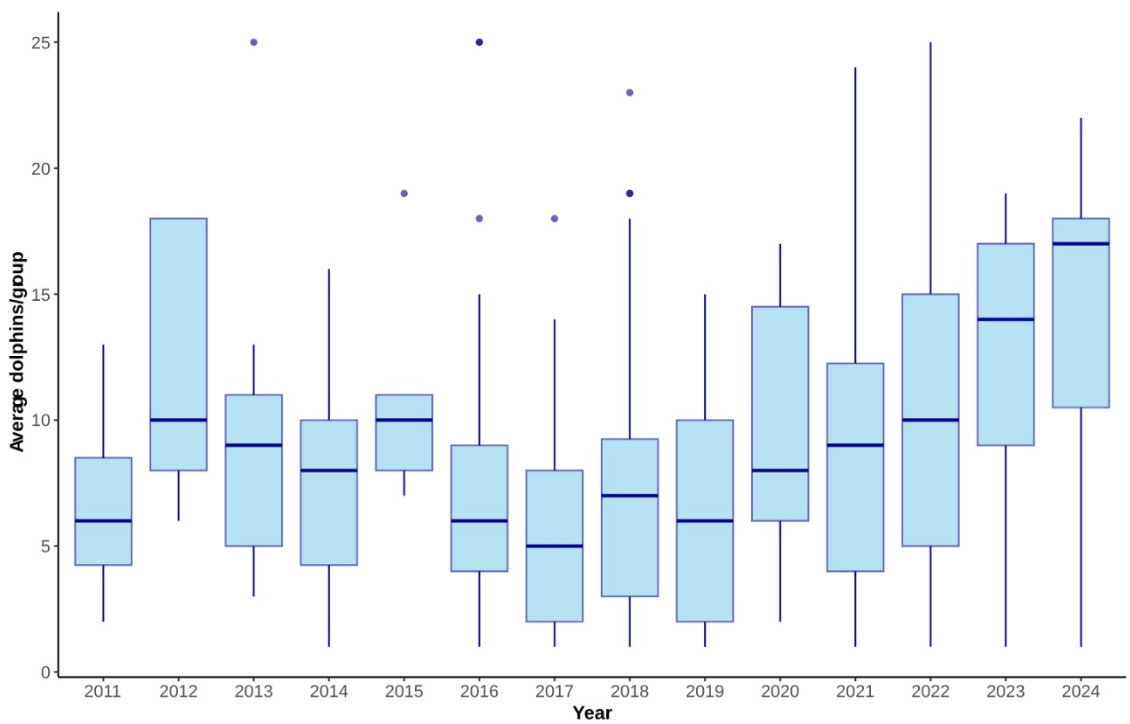
Population Demographics

Group Size

The average group size was 9.21 dolphins per group (SD = 4.65, n = 886), though there was considerable annual variation throughout the study (see Figure 2). In the first period (2011-2015), the average group size was 8.07 dolphins per group (SD = 4.45) and remained relatively stable across years despite uneven survey effort. During the second period (2016-2019), the average group size decreased to 6.55 dolphins per group (SD = 4.21) and also showed little annual fluctuation. In the third period (2020-2024), the average group size steadily increased to 11.48 dolphins per group (SD = 5.83), a significant difference compared to the earlier periods (ANOVA: $F = 59.7$, $p < .001$, df = 2, 892).

Figure 2

Annual Group Size Variability During the Study Period (2011-2024)



Reproductive Parameters

In both communities, a decline in the number of adult females was observed due to population decrease, but the decline was more pronounced in the Posorja dolphins (from 5 to 3) compared to El Morro (from 4 to 3) (Table 2). The number of females decreased in both communities during the third period. Despite Posorja having a higher number of females, El Morro produced 22% more offspring (18 vs. 14). In Posorja, calf production remained relatively constant across the three periods, while in El Morro, calf production increased significantly during the second period, primarily because two females with 1.5-year-old calves gave birth to new calves and were raising two calves simultaneously.

The fertility of El Morro females was 18% higher than that of Posorja females (4.31 vs. 3.66 calves per female) (Table 2). However, an improvement in fertility was noted in both communities during the last two periods. The survival of calves to one year in the El Morro community was, on average, 42% higher than in Posorja (0.73 vs. 0.42). In Posorja, calf survival to one year showed a dramatic improvement, increasing by 100% in the second period and 230% in the third period. Survival to one year was more stable in El Morro (ranging from 0.62 to 1). Calf survival at weaning improved in both communities during the last period. In Posorja, survival at weaning increased by 250% (0.2 to 0.5), and in El Morro by 120% (0.35 to 0.8) (Table 2).

Overall, the El Morro dolphins exhibited better reproductive parameters than the Posorja dolphins. While El Morro showed higher and more stable values, the improvements in female fertility and calf survival at one year and at weaning in the last two periods were notable in the Posorja dolphins.

Table 2

Evolution of Four Reproductive Parameters for the El Morro and Posorja Dolphins in Each Sampling Period

Posorja		Period		Total
Parameter	2011-2015	2016-2020	2021-2024	Periods
Adult females	5	3.75	3	3.92
Calf production	5	5	4	14
Fertility (number calves/female)	1	1.33	1.33	3.66
Calf survival (1 year)	0.2	0.4	0.66	0.42
Calf survival (weaning)	0.2	0.2	0.5	0.29
El Morro		Period		Total
Parameter	2011-2015	2016-2020	2021-2024	Periods
Adult females	4	4	3.2	3.71
Calf production	3	8	5	18
Fertility (number calves/female)	0.75	2	1.56	4.31
Calf survival (1 year)	1	0.62	0.75	0.73
Calf survival (weaning)	0.33	0.38	0.8	0.5

Abundance

Despite the number of dolphins recorded during the surveys, only 133 unique individuals, including all age and sex classes, were found within the study area. This indicates that most records correspond to the same animals. Table 3 shows the annual abundance of dolphins identified by age class and sex. There was a weak positive relationship (r = .132) but not significantly between the number of unique dolphins and effort (km of survey) ($p > 0.65$).

During the 2011-2015 period, annual dolphin numbers ranged from 16 to 50, with 2014 showing a notable increase likely due to a 2.33-fold rise in survey effort compared to the first three years. In 2015 the effort was reduced tenfold, and the dolphin abundance dropped to one third.

In the 2016-2019 period, the highest abundance was recorded in 2016 with 59 dolphins, although it was not the year with the highest effort (see Tables 1 and 3). Dolphin abundance remained similar until 2018 when 50 animals were recorded followed by a sharp 34% decline (50 to 33 dolphins) between 2018 and 2019, despite the effort in 2019 being like 2017 (Table 1). The abundance continues decreasing gradually in the 2020-2024 period from 34 in 2021 to 24 in 2023 (2020 was an atypical year with low effort). Given that survey effort doubled in this last period compared to the previous one (Table 1), the decline cannot be attributed to reduced effort.

The most notable changes occurred in two age and sex categories “adult males” and “unknown sex adults”. Between 2016-2019 and 2020-2024, the average number of adult males dropped from 17.5 to 7.8, and unknown-sex adults from 8.75 to 0.6. On the other hand, subadult males and calves increased slightly in the last period. Between 2017 and 2019, only five new non-calf individuals were recorded in the study area, four of which were observed once. Since May 2019, all new individuals corresponded to calves and sub-adults of the mothers already identified. Overall, during the study period, adults accounted for 73.7%, subadults 9.5% and calves 16.7% of the population.

Table 3

Annual Abundance

Age/Class Group	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	Total
Adult males	9	9	18	18	8	19	20	21	10	6	9	9	8	7	Adult males
Adult females	9	6	7	10	5	13	8	8	7	7	8	8	6	6	Adult females
Unknown sex adult	9	8	11	16	1	14	9	9	3		3				Unknown sex adult
Subadult males	1	1		1		2	2	2	2	2	4	4	2	3	Subadult males
Subadult Females					1	2	1	1	2	1	1		2	3	Subadult Females
Subadult unknown sex			1				1	3	2						Subadult unknown sex
Calves	2	4	6	5	1	9	5	6	7	9	9	9	5	5	Calves
Total	30	28	43	50	16	59	46	50	33	25	34	30	23	24	30

Note. Annual abundance of dolphins based on age and class during the study period.

Community Structure and Membership

Residency

The annual number of resident and non-resident (non-calf dolphins) was calculated over the study period using a threshold of 5% presence in recorded groups (Table 4). Due to low survey effort in certain years (2011-2013 and 2015), it was not possible to distinguish between residents and non-residents. In 2014, non-resident groups constituted 35% of sightings. In the 2014-2019 period, the annual proportion of non-resident animals remained relatively stable (47-49%) but dropped to 15% in 2019. In the third period (2020-2024), non-resident dolphins dropped to 0 in 2020, rose to 15%, and then gradually declined back to 0 by 2024. Resident dolphins also decreased by an average of 8.8% when comparing 2016-2019 to 2020-2024, indicating a declining trend in both resident and non-resident categories.

Overall, 44 dolphins were classified as residents, with eight remaining in the area throughout the study and recorded repeatedly. Twenty-two dolphins shifted from resident to non-resident status and eventually disappeared from the study area. Three dolphins transitioned from non-resident to resident status, including one sub-adult male and two adult males, and stayed though the end of the study in 2024. Forty-four animals were recorded as non-resident, of which 36 (81.8%) were observed only once.

Table 4

Variability in the Annual Residence Level of Non-Calf Dolphins During the Study Period (2011-2024)

Category	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Residents	28	24	37	31	14	27	21	22	18	18	21	22	17	19
Non-residents	0	0	0	17	0	24	19	21	4	0	4	1	1	0
Total	28	24	37	48	14	51	40	43	26	18	26	23	18	19
Proportion non-resident				0.35		0.47	0.48	0.49	0.15	0	0.15	0.04	0.06	0

Note. The proportion of non-resident dolphins was calculated for years with sufficient data.

Permanence

The average permanence of non-calf individuals (n = 109) during the study period was 3.84 years (SD = 4.31, range 0 - 13.4 years). Table 5 shows the number of dolphins according to the level of permanence within the study area. The "Uncommon" category (n = 45, 41.2% of the total) includes individuals recorded once or a few occasions within the same year. In 39 cases (86.7%) their age class and/or sex could not be determined. The "Low" category (n = 20) included two adult males, one adult female, and five subadults, though the majority were of undetermined sex (n = 12, 60%). In the "Medium" category, adult males were the dominant class (44.8%), followed by similar proportions of adult females, subadults and animals of unknown sex (17.2 - 20.7%). This category included adult males recorded since the beginning of the study who later died or emigrated, lower-status males, and five females (P4, P33, P56, ES108 and ES136) who were initially present but died or emigrated to another community. It includes two subadults (P95, ES151) who subsequently died or emigrated, and thee subadults (P106, ES158, ES159) born, weaned, and still alive by the end of the study. The "High" category includes seven adult males and seven females presented early in the study and consistently recorded in the area, as well as one subadult male born in 2012 (see Table 5). This category accounted for only 13.7% of the total non-calf animals recorded in the study.

Table 5

Permanence During the Study Period

	Males		Females		Unknown		Subadults	
Permanence level	n	%	n	%	n	%	n	%
Uncommon (<1 years)	2	4.4	3	6.7	39	86.67	1	2.2
Low (1-4 years)	2	10	1	5.0	12	60	5	25.0
Medium (4.1-9 years)	13	44.83	5	17.2	5	17.24	6	20.7
High (> 9 years)	7	46.67	7	46.7			1	6.7

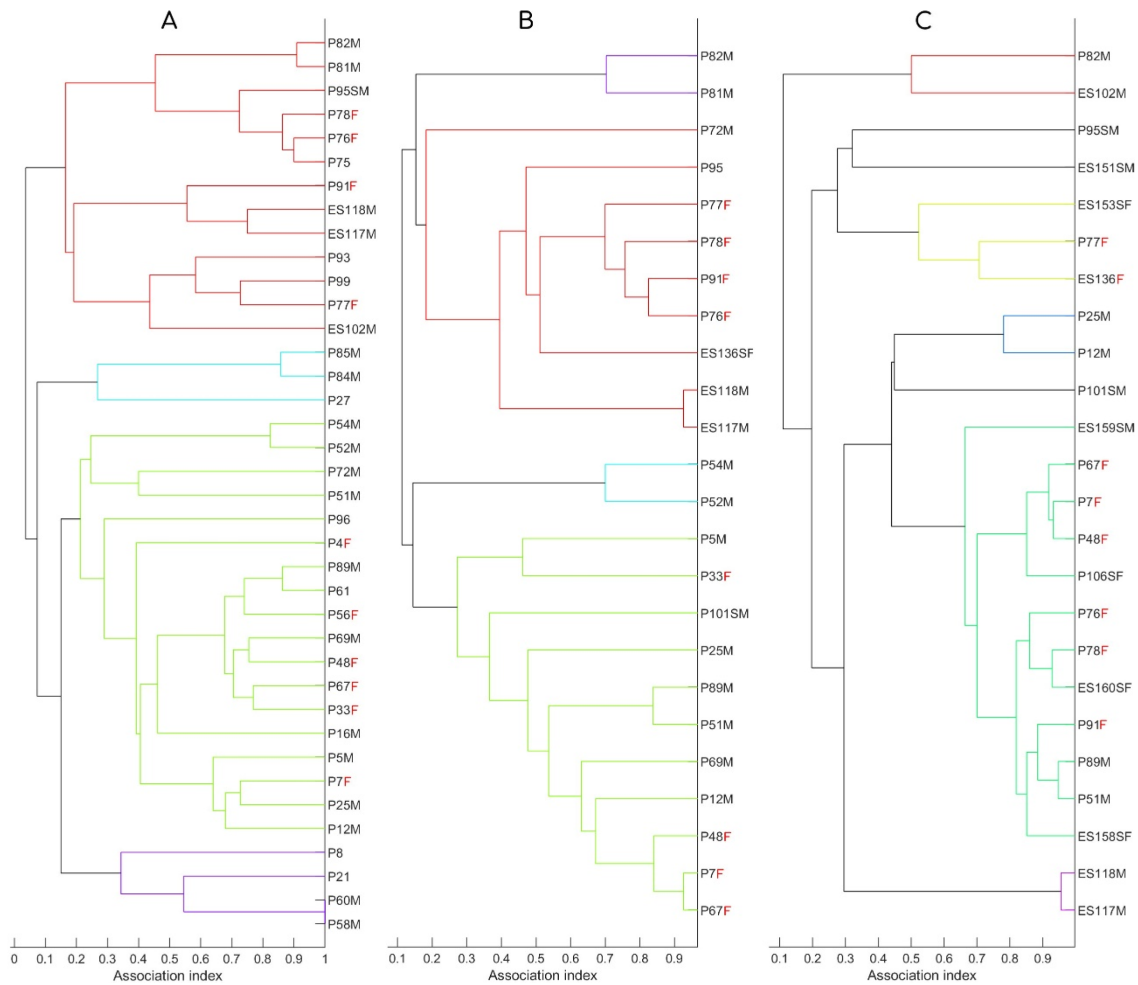
Note. Number and proportion of individuals by age and sex classes according to their permanence during the study period.

Community Membership

Non-calf animals classified as residents were included in the hierarchical cluster analyses. Community membership was assigned to each individual according to the cluster to which they were automatically grouped based on modularity, using the software SOCPROG. Dendrograms for each period illustrated changes in social structure over time (Figure 3). Table 6 gives a summary of dolphins' presence across the periods.

Figure 3

Cluster Analysis Based on Pairwise Associations with Non-Calf Resident Individuals in the Thee Periods the Study was Divided: A) 2011 - 2015 (n = 38); B) 2016 - 2019 (n = 24); and C) 2020 - 2024 (n = 24)



Note. M = adult males. F = adult females, SF = subadult female, SM = subadult male. Adult females are highlighted in red for better visualization.

Table 6

Summary of Life Histories of Resident Dolphins in Both Communities Across the Three Periods of the Study

Community	Dolphin ID	Period 1	Period 2	Period 3	Status
El Morro	ES102M	■		■	Unknown
	ES117M	■	■	■	Alive
	ES118M	■	■	■	Alive
	ES136F		■	■	Emigrated
	ES151SM			■	Unknown
	ES153SF			■	Unknown
	ES158SF			■	Alive
	ES159SM			■	Alive
	ES160SF			■	Alive
	P75	■			Unknown
	P76F	■	■	■	Alive
	P77F	■	■	■	Dead
	P78F	■	■	■	Alive
	P81M	■	■		Unknown
	P82M	■	■	■	Alive
	P91F	■	■	■	Unknown
	P93	■			Unknown
	P95SM	■	■	■	Unknown
	P99	■			Unknown
Posorja	P4F	■			Unknown
	P5M	■	■		Unknown
	P7F	■	■	■	Alive
	P8	■			Unknown
	P12M	■	■	■	Alive
	P16M	■			Unknown
	P21	■			Unknown
	P25M	■	■	■	Dead
	P27	■			Unknown
	P33F	■	■		Dead
	P48F	■	■	■	Alive
	P51M	■	■	■	Alive
	P52M	■	■		Emigrated
	P54M	■	■		Unknown
	P56F	■			Unknown
	P58M	■			Dead
	P60M	■			Unknown
	P61	■			Unknown
	P67F	■	■	■	Alive
	P69M	■	■		Unknown
	P72M	■	■		Dead
	P84	■			Emigrated
	P85	■			Unknown
	P89M	■	■	■	Alive
	P96	■			Unknown
	P101SM		■	■	Alive
	P106SF			■	Alive

Note. A blue square indicates the presence of an individual during a given period. The rightmost column, "Status", provides information on each individual's fate by the end of the period: alive, dead (if the carcass was found or photographed), emigrated (if the dolphin is alive but living in another community) and unknown (if no information is available). Adult males are labeled with "M", adult females with "F" and subadults with "S".

Period 2011-2015

Two large and two small clusters indicate that the population in the study area during this period included individuals from at least two communities (Figure 3A). The large cluster in the upper part of Figure 3A represents the El Morro community and includes 13 animals: five adult males, four adult females, one sub-adult male and thee animals of unknown sex. This cluster shows that females P76 and P78 had a stronger affinity with the male pair P81-P82, while female P91 with the pair ES117-ES118, and female P77 with two individuals of unknown sex P93 and P99.

The second large cluster in Figure 3A represents the Posorja community and includes 18 animals: ten adult males, six adult females, and two animals of unknown sex. Within the Posorja community, four females (P33, P48, P56, P67) showed strong affinity with each other, as well as with males P89, P69, and P16, along with another individual of unknown sex (P61). Female P7 showed a strong association with the male pair P12-P25 and male P5, while female P4 did not display a preference for any specific male. Two smaller clusters with 3 and 4 individuals are also associated with the Posorja cluster; four of these individuals were identified as adult males, and thee as animals of unknown sex. Their low level of affinity suggests that these animals may belong to other neighboring communities. The overall association index for this period was 0.16.

The sex ratio (M:F) in the El Morro community was 1.5:1 and in the Posorja community 2.16:1. Four mixed groups (5.9% of the total) containing at least one member of the other community were recorded in this period. Only adult males were found in groups with females from the other community. On thee occasions, males from El Morro were observed with Posorja females, and one occasion, a male from Posorja was observed with El Morro females. The average association index between Posorja and the El Morro communities was very low 0.04 (Figure 3A).

Overall, the Posorja community was larger, had a higher proportion of males, and displayed more social flexibility with dolphins from other communities than the El Morro community. The division of the population into two communities was supported by the values of the cophenetic correlation coefficient (0.89) and modularity (0.33). The preference/avoidance test indicated that associations were not random (p = .001).

Period 2016-2019

Like the previous period, two large clusters were identified: El Morro with 11 animals and Posorja with 13, representing an overall decrease of 37% (from 38 to 24 individuals) (Figure 3B). Most absences were among adult males, animals of unknown sex, and one adult female (P4). A pair of males outside the large cluster (P81-P82) was associated with the El Morro community, while another male pair (P52-P54) was associated with the Posorja community. All animals observed in this period had been part of the same cluster in the previous period, except for male P72, who migrated from Posorja to El Morro. Additionally, one new animal was included in each community: subadult female ES136 in El Morro and subadult male P101 in Posorja. Both were considered calves in the previous period and were not included in earlier analyses. In both clusters, adult females now exhibited a higher affinity for each other. In the El Morro community, the male pair ES117-ES118 showed a stronger affinity with five females (association index 0.40), displacing the male pair P81-P82, which had only marginal associations with females during this period (0.15). In the Posorja community, the male pair P12-P69 gained status, showing a higher affinity with three adult females (P7, P48, and P67) compared to the male pair P51-P89 (0.67 vs. 0.54, respectively). The male pair P5-P25 lost status, while pairs P52-P54 and P84-P85 maintained a low status. Female P33 from Posorja, who died in January 2018, appeared separated from the other adult females in the cluster (Figure 3B). The overall association index was similar to the previous period, at 0.15.

The sex ratio (M:F) in the El Moro community decreased to 1.25:1, while in the Posorja community it increased to 2.25:1 during this period. The proportion of mixed groups increased significantly to 27.7% (n = 79) ($X^2 = 9.93$, $p < .001$). On 47 occasions, males from one community were temporarily associated with females from the other community, while on 27 occasions (9.4%) females from both communities were observed in the same group, and on five occasions (1.7%) the mixed group included immature males from the other community.

The dendrogram still shows two well-defined communities, although the association index between them increased threefold to 0.12. The gregariousness indices revealed a high cophenetic correlation coefficient (0.908), while the modularity index was slightly below the threshold (0.292). The preference/avoidance test also indicated that associations were not random in this period (p = .001).

Period 2020-2024

During this period, cluster analysis shows a significant shift in social structure. Only one large cluster with 15 individuals is present, characterized by high affinity among members and including females from both communities and two male pairs (P12-P25 and P51-P89) (Figure 3C). Four additional small clusters, each with varying degrees of affinity, are associated with this large cluster. Although the total number of animals remained the same (n = 24), notable changes in composition and a generational shift were observed. Five adult males disappeared (P5, P54, P69, P72, and P81). Male P72 was confirmed dead in 2017, and similar fates are likely for three others, as their male alliances (P52-P54, P81-P82, and P12-P69) were broken. Six new animals appeared in the dendrogram, including one adult male (ES102) and five sub-adults who were calves in the previous period (ES151, ES153, ES159, P106, and ES158). Additionally, sub-adult female ES136 had her first calf and attained adult female status.

Within the large cluster, females displayed high affinity within their original community (> 0.85) and also with females from the other community (0.74). Among males, the alliance between P51 and P89 strengthened, making them the highest-ranking males in the new, unified community (average association rate 0.70). In contrast, the previously dominant male pair ES117-ES118 from the El Morro community lost status (association rate 0.29). The newly allied males P12-P25 also held a low status. The smaller clusters at the top of Figure 3C include two low-status males (P82 and ES102), two adult females, P77 who died in 2022, and ES136, who migrated to another community across the estuary after losing her two-month-old calf, and thee sub-adults (P95, ES151, and ES153) who were no longer recorded after 2022. The overall association index doubled in this period, reaching 0.33.

The sex ratio (M:F) in this period shifted considerably from previous periods, approaching parity at 1.14:1. Likewise, the proportion of mixed groups increased significantly to 77.8% (n = 341) (X^2 = 178.2, p < .001). Most mixed groups involved adult females from both communities (54.1%), followed by only males (17.8%) and only immatures (5.9%). Most of the mixed groups involving females also included males, immatures, or both. Thus, in this period the El Morro and Posorja communities had merged possibly because of the demographic changes at the end of the second period. This fusion of communities is confirmed by the gregariousness indices, which show a high cophenetic correlation coefficient (0.959) but a low maximum modularity value (1.05), indicating a lack of support for more than one community in the area. The preference/avoidance test also showed that associations were not random (p = .001).

Lagged Associate Rates Analysis

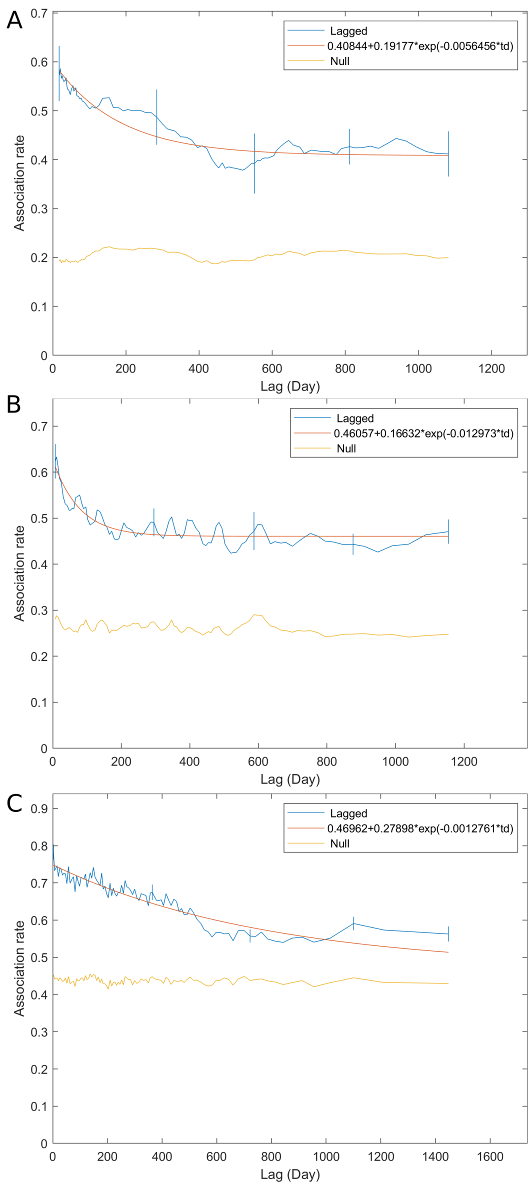
The calculated values for LARs across the three periods exhibit similar trends: an initial decline followed by stabilization above the null association rate curve (the threshold for random associations) (Figure 4). The data were best described by the exponential model

$$a2+a3*\exp(-a1*td)$$

rapid dissociation plus preferred companions plus casual acquaintances, where $a1$, $a2$, and $a3$ are parameters of the model (set with value 0.5) and td the lag value. Such a pattern is characteristic of societies with stable social units that dissolve after certain lag periods, yet exhibit a tendency for individuals to preferentially associate with previous companions rather than random. The time-predicted LARs varied across periods, reflecting differences in social structure. In the first two periods, LARs declined within the first 100 days, likely due to the presence of non-resident and low-ranking animals. Another decline occurs around day 400, with association values stabilizing between 0.43 and 0.45. In contrast, LARs for the third period showed no sharp initial drop but rather a gradual decline extending to day 500, followed by a pronounced decrease before stabilizing at an association value of 0.58. This suggests that dissociation during the last period would be primarily driven by mortality or emigration. LARs calculated are well above the null association rates and extended beyond three years in the first two periods and beyond four years in the third, anticipating long-term non-random associations. Overall, the predicted LARs confirm an increased level of social association in the third period with the fusion of both communities.

Figure 4

Lagged Associate Rates (LARs)



Note. Lagged associate rates (LARs) calculated (blue line) and modeled (orange line) for the thee periods: A (2011 - 2015), B (2016 - 2019) and C (2020 - 2024). The bottom yellow line corresponds to the null association rates. Vertical bars over the LARs curve plot represent the jackknife error bars (± 1 estimated standard error).

Spatial Analysis

Distribution

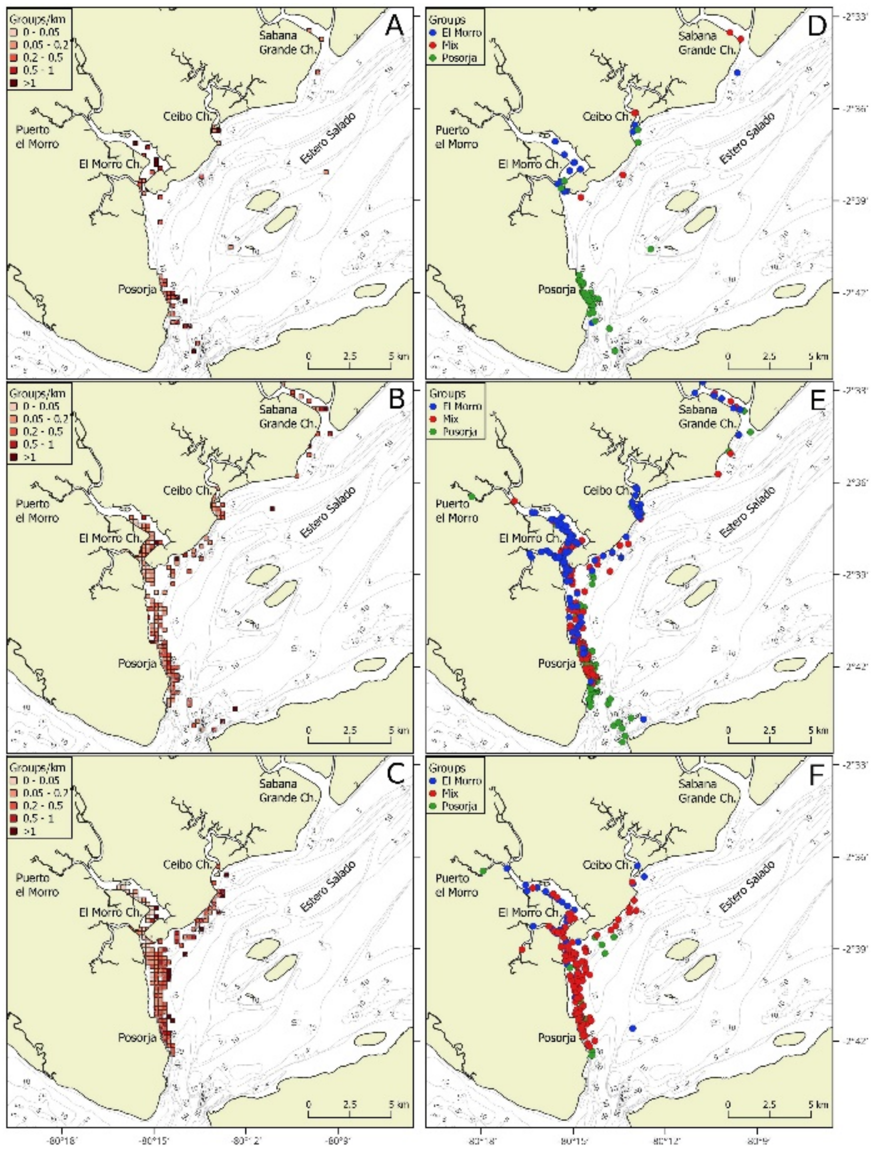
Changes in social structure and demography were accompanied by shifts in dolphin distribution over time. In the first period (2011 – 2015), the distributions of groups from both communities were well differentiated. Groups from the El Morro community were observed primarily within the Morro Channel and along a 15 km stretch northward in the Estero Salado, with concentrations near the entrances to the Ceibo and Sabana Grande channels. In contrast, groups from the Posorja community were mainly recorded along a 5 km section of the port, extending southeast to the eastern side of the Estero Salado (see Figure 5A and 5D). During this period, a spatial separation of approximately 5 km existed between the communities, with very few dolphin groups observed in this area.

Both communities maintained the same core distribution areas in the second period (2016 – 2019). However, the Posorja dolphins expanded further north, while the El Morro dolphins showed a reduced presence in their original area, resulting in increased spatial overlap between the two communities. During this period, spatial separation between the communities nearly disappeared (see Figures 5B and 5E).

Dolphin distribution changes became more pronounced in the third period (2020 – 2024). The previous spatial separation between the communities is no longer observed, with a continuous distribution between Posorja and the El Morro Channel. The area that previously shown low usage by both communities now exhibits the highest density of dolphin groups (see Figure 5C and 5F). Additionally, there is reduced use of the El Morro Channel, increased activity in the Estero Salado between the El Morro and Ceibo channels, and an absence of groups in the Sabana Grande channel. Changes were also observed to the south, with reduced usage of the area around Posorja and no recorded groups southeast of this area.

Figure 5

Relative Abundance of Dolphin Groups Weighed by Survey Effort Across the Thee Periods the Study was Divided: (A) 2011 - 2015, (B) 2016 - 2019, And (C) 2020 - 2024, and Distribution of Groups According to Community Membership in the Three Periods: (D) 2011 - 2015, (E) 2016 - 2019 and (F) 2020 - 2024



Note. The cell grid size is 250 × 250 m. Colors indicate intensity according to the density scale in figures A, B, and C. Dots in Figures D, E, and F represent dolphin groups recorded in the area, with colors indicating their community membership: El Morro (blue), Posorja (green), and mixed (red).

Discussion

Changes in the social structure of two neighboring communities of estuarine bottlenose dolphins on the western side of the inner estuary of the Gulf of Guayaquil reveal a highly dynamic demography that included abundance decline, shifts in residence and habitat use patterns, and the fusion of two neighboring communities. These changes occurred over a period equivalent to just over half a generation (21 years in bottlenose dolphins, Taylor et al., 2007) and demonstrates a high degree of social fluidity that challenges the semi-closed social structure characteristics of inshore bottlenose dolphin populations (Connor et al., 2000; Wells et al., 1987; Wells, 2014). Long-term studies of coastal cetaceans including bottlenose dolphins and orcas (*Orcinus orca*) have demonstrated that their social structure at individual level is dynamic and responds to demographic and environmental changes, while the overall structure of communities remains relatively stable though generations (Parsons et al., 2009; Wells, 2018). However, changes in the social structure can be exacerbated by habitat degradation or extreme climatic events that may threaten population survival (e.g., Alter et al., 2010; Desforges et al., 2018; Félix and Burneo, 2020; Jefferson et al., 2006; Wild et al., 2019).

Abundance

A significant change in dolphins' abundance was the sudden decrease at the end of the second period from 50 dolphins in 2018 to 33 in 2019 (34% decline), with resident dolphins decreasing by 18% (from 22 to 18) and non-residents by 81% (from 21 to 4). Despite a 34% reduction in survey effort (see Table 1), this decrease is unlikely due to effort, as similar effort in the years 2014 and 2017 yielded thee times more non-residents. Additionally, in the third period, non-resident dolphins continued declining while resident ones stabilized, even as effort doubled. Thus, abundance decline appears due to non-residents ceasing to visit the area and to a lesser extent to a few residents that abandoned the area. It is common to find non-resident animals within resident communities of coastal and estuarine bottlenose dolphins (e.g., Fury & Harrison, 2008; Titcomb et al., 2015; Wells et al., 1987; Zolman, 2002) as it was observed regularly in the study area between 2011 and 2019. The decrease in non-resident animals affected the gene flow from neighboring communities, which is key to maintaining genetic heterogeneity (Duffield & Wells, 1991; 2023; Wells et al., 1987). According to Duffield and Wells (2023), about 26% of the calves born to Sarasota females were sired by non-Sarasota males. Thus, the interruption of the exchange of dolphins from neighboring communities would further increase the risk of extinction for this population, although its impacts can only be assessed in the medium and long term.

Possible explanations for the abrupt decrease in abundance in 2018-2019 include environmental changes, shifts in human activities, and changes in social behavior. The study area is highly dynamic, with a wide tidal range and seasonal rainfall causing fluctuations in temperature, salinity, and pH (Stevenson, 1981), which intensify during El Niño Southern Oscillation (ENSO) periods. This was the case in 2018–2019, when colder conditions prevailed early in 2018 (La Niña), followed by warmer conditions later in 2018 and into the first half of 2019 (El Niño). However, a stronger El Niño in 2015 had no similar effect on dolphin abundance in the area. Pollution in the Estero Salado has degraded water quality, with heavy metals and eutrophication levels exceeding those typical of balanced environments (Ormaza-González et al., 2022, 2024). Excess nutrients may lead to toxic red tides, as previously detected in the Gulf of Guayaquil (Borbor-Córdova et al., 2019). Although high dolphin mortality has been linked to toxic red tides in other areas (e.g. Fire et al., 2015; Flewelling et al., 2005), red tides alone are unlikely to explain the absence of dolphins in the study area, as they would impact both residents and non-residents alike.

Changes in artisanal fishing and traditional maritime activities were not assessed, but no evident shifts were observed in the area during the study. Posorja is one of Ecuador's main fishing ports and the intense maritime activity has been linked to high rates of scarring and mortality in dolphins (Félix et al., 2018; Félix & Burneo, 2020). The Ecuadorian pelagic fleets have maintained a similar size in the last ten years with approximately 260 vessels for small pelagic fish and 110 tuna vessels (Canales et al., 2021; Ministerio de Producción, Comercio Exterior, Inversiones y Pesca, 2024). Small-scale fishing in El Morro primarily focuses on harvesting shellfish and shrimp. These negative factors have persisted over time with little change. However, the decline of abundance in the study area coincides with the construction of a container port facility in Posorja, where piling and the construction of a 500-meter dock began in January 2018. Although the potential impact of the dredging and piling phases is recognized in the environmental impact study (Cardno, 2016), no mitigation measures for dolphins were proposed or implemented during port construction. Port activities may affect the social behavior, physiology, and distribution of small cetaceans by increasing stress levels (e.g., Marley et al., 2017; Piwetz, 2019; Würsig & Greene, 2002) and may be responsible for the differing reproductive parameters and rates of sociality between the El Morro and Posorja dolphins (Félix & Burneo, 2020; Félix et al., 2022). Whether the construction and operation of the port caused a differentiated impact affecting mostly non-resident dolphins cannot be established with certainty. Since the port was built within an important area of the Posorja community's home range, resident dolphins may be more resilient to the increased activity during the construction phase due to habituation.

A third potential cause of the abandonment of dolphins from the study area could be linked to a rigid hierarchical structure, leading non-resident dolphins and resident low-ranking males to seek better reproductive opportunities elsewhere. Before the study began, the area may have hosted larger communities with more reproductive females, attracting males from other communities. Over time, however, conditions deteriorated, skewing the sex ratio towards males, a trend that became more pronounced in the second study period, ultimately skewing the male-to-female ratio to 2.25:1 in Posorja. In other wild bottlenose dolphin populations, gender parity or a female-biased ratio is more common (Fruet et al., 2015; Manlik et al., 2016; Wells & Scot, 1990). The situation worsened with the disappearance of female P4 in 2016 and the death of female P33 in 2018 in Posorja, increasing competition among males for the few remaining females. This competition likely led to agonistic interactions, sometimes resulting in the death of rival males (see Parsons et al., 2003). During this time, at least thee male alliances dissolved, likely due to the death of one partner. Left without a partner, these males may have to seek another partner in other communities with less competition. By the end of the second period, resident male pairs P12-P69 and P51-P98 had consolidated their dominance over non-resident males.

This hypothesis is supported by recent monitoring in another dolphin community near the Naranjal River, approximately 50 km east of the study area, which the author has conducted over recent years. Between 2019 and 2024, 22 dolphins previously observed in Posorja and El Morro as either residents or non-residents were recorded in this area. The Naranjal dolphin community, thee times larger than the Posorja-El Morro, appears to be drawing dolphins from other communities, including nine females from three different communities, likely facing similar demographic challenges (F Félix, unpublished information). Naranjal is thought to offer better conditions than Posorja and El Morro, which may explain why dolphins have not returned to the study area. However, some may eventually return, as seen in the case of female P3, who was resighted in the area after 11 years before leaving again (Félix and Burneo, 2020). Wells and Scott (1990) documented a similar case of an individual resighted after eight years, suggesting that some dolphins may periodically shift their core habitats.

Community Fusion

Although the movement of adult males, and occasionally sub-adults, between Morro and Posorja was observed throughout the study period—including the emigration of an adult male identified as P72 to Morro—the fusion of both communities began only when females from each community started associating. This gradual process took about three years to consolidate. The first groups containing females from both communities were recorded in December 2017, six years after the study began, when females from Morro were observed within the Posorja dolphins' home range. The next mixed group was observed in January 2018, followed by thee more in March 2018. They were not seen again until June, after which nine more sightings occurred though December 2018. In 2019, females from both communities were observed together five times (6.3% of the groups). At that time, there were no indications that the communities would merge. A kind of territorial behavior was recorded earlier when large groups of two communities met in another part of the estuary (Félix, 2001). However, by 2020, the proportion of mixed female groups rose sharply to 28%, reaching 34% in 2022 and 68% in 2023. By the study's final year (2024), groups with females from both communities accounted for 73%. This fusion marks a milestone in the demographic dynamics of the Posorja and El Morro communities, likely a response to the observed population decline. LARs analysis supports a long-term stability in the new community favoring non-random associations. Unlike the findings in this study, a reduction in social cohesion in orcas has been associated with population decline (Parsons et al., 2009). Interestingly, increased affiliative connections were observed in rhesus macaques (*Macaca mulatta*) in Puerto Rico after a hurricane devastated the island where they live (Testard et al., 2021), suggesting that social animals may exhibit different adaptive responses to adversity.

To the best of the author's knowledge, there are no precedents for the fusion of adjacent depressed communities in other social coastal cetacean species. However, Wells (2003) described the growth of a successful female band in Sarasota between 1993 and 1994, which later split into smaller units and eventually expanded its home range into areas formerly occupied by less successful female bands. In this case, the band likely grew due to favorable reproductive conditions rather than though fusion, but the social structure was not maintained over time and eventually split apart. While population size and social structure of bottlenose dolphins are largely influenced by available resources (Louis et al., 2014; Wells et al., 1987; Wiszniewski, et al., 2009), for the Morro and Posorja dolphin communities, and likely for other communities within the inner estuary, resource availability does not seem to be a concern, given the high productivity of the area (Borbor-Córdova et al., 2019; Chinacalle-Martínez, 2021; Stevenson, 1981). This is also demonstrated by the fusion process occurring simultaneously within the Naranjal dolphins on the opposite side of the estuary, resulting in a larger community.

The fusion of communities was accompanied by a significant increase in group size, from 6.5 dolphins per group (SD = 4.21) in the second period to 11.48 dolphins per group (SD = 5.83) in the third period, suggesting that group size may be key for community survival. Although an optimal group size based in part on the need for protection from predators, resource competition, and socializing has been proposed for bottlenose dolphins elsewhere (Wells et al., 1987; Connor, 2019), this would not entirely apply to dolphins in the inner estuary of the Gulf of Guayaquil. Dolphins in the study area currently do not have natural predators and dolphin groups in the area were larger in the past (Félix, 1994; Félix et al., 2017, 2018). Thus, dolphin group size in the study area would be largely influenced by the need for social affiliation and learning, including protection from human-related threats, such as entanglement in nets and collisions with boats, factors that may take an even larger toll than predation does in other populations (see Félix, 2021; Félix et al., 2018). The fusion would provide increased stability for members of both communities by strengthening social bonds and facilitating social learning and cultural transmission, favoring adaptation and resilience (Wells, 2003; Whitehead et al., 2019). An example of cultural transmission between both communities is a behavior known as rope rubbing (Félix, 2015). This play behavior, where dolphins rub their bodies against mooring buoy ropes, has been observed among Posorja dolphins where fishing vessels are moored. However, on 24 October 2024, it was also observed for first time in an El Morro adult female (P76) following two Posorja males.

While the medium-term benefits of this fusion remain to be fully evaluated, certain short-term improvements in reproductive parameters have been observed, such as higher calf survival rates in both communities and increased fertility among Posorja females. Improved survival rates are crucial for population viability (Manlik et al., 2016) and may help to stop the current population decline trend. The fusion also creates a more supportive environment for subadults, eliminating the need to migrate to other communities for social interactions. This likely explains the observed higher proportion of immature individuals in the third period (see Table 2). These findings align with studies in Sarasota Bay, where calves raised in larger, more stable groups showed higher survival rates (Wells, 2000).

Distribution and Habitat Use

The fusion of both communities also altered each community's spatiotemporal use patterns within their respective home ranges. Following the fusion, both communities reduced their use of traditional foraging areas and began to use and share other areas. Posorja dolphins used to feed in the port area, where scavenger fish were attracted by raw discharges from fish processing plants (Félix et al., 2022), resulting in concentrated sightings around the docks during the first two periods (Figure 3A). For the El Morro dolphins, a preferred feeding site was a secondary channel branching off from the El Morro channel, where fish gather near the shore, particularly at low tide (Félix et al., 2022; Jiménez and Álava, 2015). After the fusion, Posorja dolphins reduced their presence near the fishing docks and extended their feeding area northward, reaching the areas where Morro dolphins frequently fed, particularly at the entrances of the El

Morro and Ceibo channels. El Morro dolphins also significantly reduced their use of the El Morro Channel for shore fishing. Consequently, members of both communities began to share feeding areas, a pattern not observed in the study's first two periods.

Both communities, however, still maintain some individuality in their patterns of distribution and habitat use. Females from Morro occasionally enter the central and southern parts of Posorja, where fishing fleets and most plants are located, and they have not been observed southeast of Posorja, on the eastern side of the Estero Salado. Conversely, females from Posorja have never been observed entering the Morro and Ceibo channels, remaining instead at the entrances. When dolphins from the El Morro enter the Morro or Ceibo channels, primarily to feed, the group often splits, with those from Posorja returning to their traditional areas of distribution.

Management Implications

The case of bottlenose dolphins in the Gulf of Guayaquil highlights the importance of considering social behavior in managing wild populations to enhance resilience. Identifying patterns of spatiotemporal distribution, habitat use, and demography is insufficient for species with intricate social structures such as those involving hierarchies, complex mating systems, tight family bonds, and cultural learning, all of which are crucial for the survival of social or population units. Certain human activities are already affecting the social dynamic of dolphins in the Gulf of Guayaquil, particularly gillnet fisheries, with unpredictable consequences (Félix, 2021). Fishing nets may be a primary factor in the recent absence of dolphins from other communities within the study area over the past five years, raising concerns about the interruption of genetic flow, a key factor for the survival of small dolphin populations (Chen, et al., 2017; Duffield & Wells, 2023). Establishing net-free corridors to connect dolphin communities on both sides of the estuary could help reinitiate movement to Posorja and El Morro. The northern side of Puná Island to the east of the study area serves as a natural passageway between the eastern and western parts of the estuary but is under intense fishing pressure (personal observations by the author). Regular assessments of the proportion of non-resident animals could help gauge the effectiveness of these measures.

Similar assessments should extend to other sites in the inner estuary to determine the potential risks of gene flow interruption in other dolphin communities. In parallel, annual evaluations of association indices should be conducted to monitor the social cohesion of communities and detect whether they are undergoing fusion, fission, or remain stable. Currently, the fusion of the Posorja and El Morro dolphin communities is not the only reorganization occurring within the inner estuary of the Gulf of Guayaquil. In the northeast, around the Naranjal area, females from communities with traditional home ranges in the northern and southeastern parts of the estuary are also converging. Recent monitoring indicates a decrease in dolphin density in the north-central estuary, with an apparent shift toward the northeast (F. Félix, unpublished). A comprehensive evaluation is necessary to fully understand the current demographic dynamics of bottlenose dolphins in the inner estuary to develop strategies to prevent further decline. Early identification of these social processes can inform timely and targeted management strategies.

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