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Article

On the Biology of the Coastal Spotted Dolphin *Stenella attenuata graffmani* (Lönnberg, 1934) in Pacific South America

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Abstract

Knowledge on the biology of the coastal spotted dolphin *Stenella attenuata graffmani* from western South America, one of the least studied delphinid taxa, is summarized for the first time. Information was obtained largely opportunistically during field research targeting other species or during whale watching. Life history is discussed including distribution (Colombia, Ecuador, Peru, Chile), external morphology and pigmentation, cranial characteristics, reproduction and growth, feeding, behavioral ecology, parasites and pathology, but also genetic diversity, population structure and fisheries interactions. As a (sub)tropical dolphin its habitual austral range is the Piura Department, northern Peru, but under El Niño conditions it can reach Lima Province (Cerro Azul at 13°02'S). No evidence was found for Chile. The coastal subspecies is heavily spotted and substantially bigger, as reflected in body length and all cranial measurements. Condylobasal length, mandibular ramus length and height do not even overlap with the offshore *S. a. attenuata* morph. Phylogenetic analysis of the hypervariable part of mtDNA control region, revealed Ecuadorian coastal spotted dolphins to be distributed across seven different clades, with most belonging to the three largest clades, while only one haplotype was found in each of the remaining four. This pattern suggests a complex evolutionary history, possibly indicating substructures within the population or an ongoing evolutionary process. The presence of haplotypes in multiple clades may reflect high genetic diversity, likely influenced by dolphin migration between nearby geographic areas, facilitating haplotype exchange and contributing to the observed distribution.

Keywords: Delphinidae; life history; Colombia; Ecuador; Peru; SE Pacific; bycatch; distribution

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Introduction

The oceanic dolphin genus *Stenella* Gray, 1866 (Delphinidae) has been well-studied in the offshore Eastern Tropical Pacific (e.g. Douglas et al., 1984; Dizon et al., 1994; Hohn et al., 1985; Gerrodette and Palacios, 1996; Perrin, 1975, 2001, 2018; Gerrodette and Forcada, 2005) but received minimal focussed attention in coastal Pacific South America (e.g. Dizon et al., 1994; Van Waerebeek et al., 1998; Hamilton et al., 2009). Specifically, the distribution and biology of the pantropical spotted dolphin *Stenella attenuata* (Gray, 1846) from coastal waters of western South America, i.e. Colombia, Ecuador, Peru and Chile, has not been studied in any detail, partially due to a scarcity of documented cases, until recently (Londoño, 2005; Valencia, 2006; García et al., 2006, 2008; Hamilton et al., 2009; Martínez et al., 2021; Cortez-Casamayor et al., 2024).

Swedish zoologist Einar Lönnberg (1934) described a new delphinid species *Prodelphinus graffmani* from a spotted dolphin captured by J. Holger Graffman in nearshore waters 20 miles north of Acapulco, Guerrero, Mexico (Figure 1). Taxonomist William Perrin (1969, 1975), followed by Rice (1998), synonymized *Prodelphinus graffmani* (Lönnberg, 1934) with *Stenella attenuata* (Gray, 1846). Subsequently, Perrin (2001) then designated two subspecies, a cosmopolitan pelagic Gray's pantropical spotted dolphin *Stenella attenuata attenuata* (Gray, 1846) (hereafter: SAA) and an eastern Pacific coastal spotted dolphin *Stenella attenuata graffmani* (Lönnberg, 1934) (hereafter: SAG), or briefly, coastal spotted dolphin (Dizon *et al*., 1994; Carwardine, 2020). In Latin America they are referred to as *delfín manchado costero* or *delfín moteado costero.* Castro and Van Waerebeek (2019) first assigned heavily spotted stranded specimens in Ecuador as SAG. No other *S. attenuata* subspecies have been described world-wide.

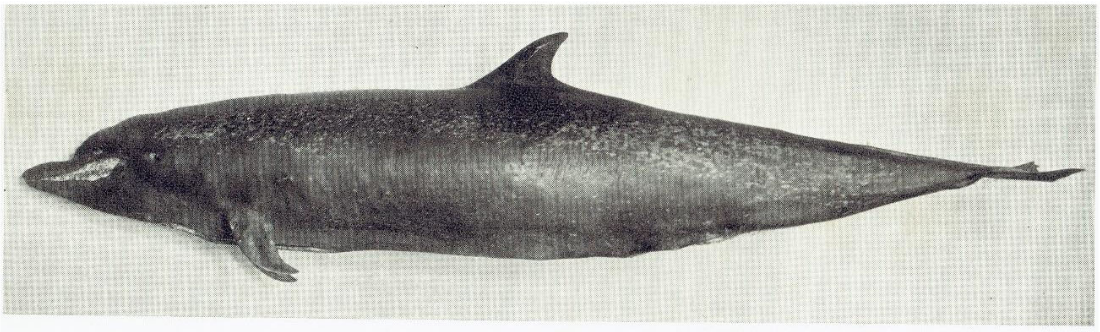

Figure 1. Holotype specimen of the stocky and heavily spotted *Stenella graffmani* Lönnberg (1934) from Acapulco, Mexico. The left-side mandibular and labial damage, due to firearm shots, exposes underlying connective tissues (pale colouration). Reproduced from Lönnberg (1934) [1].

The distribution of SAG in the NE Pacific has been characterized as coastal and inshore waters within about 25 km from land, between the Gulf of California and Colombia (Perrin, 1969, 1975, 2018; Rice, 1998; Flórez-González et al. 2004; Jefferson *et al*., 2015). A continuous distribution is supported along the coasts, with observations from Ensenada (31º30'N), NW Baja California, Mexico (Vidal *et al*., 1993), Guaymas, Gulf of California (Mexico), Guatemala (Ortiz-Wolford *et al*., 2021), El Salvador (Ibarra-Portillo *et al*., 2020), Nicaragua (de Weerdt, 2021), Costa Rica (Rodríguez-Fonseca and Cubero-Pardo, 2001), Panama (Aguilar *et al*., 1997; Justines, 1997; García *et al*., 2008) and Colombia (Perrin, 2018; Hamilton et al., 2009).

SAG individuals of the eastern Pacific are heavily spotted, significantly more than SAA offshore stocks, hence the dorsal cape may be practically obliterated by dense lightly-colored spotting in large individuals. Spotting may extend to dorsal fin and flippers. The smallish dorsal fin is strongly falcate and relatively narrow (Perrin, 1969, 1975, 2001; Carwardine, 2020). All mensural cranial characters of the coastal form are substantially greater than those of offshore stocks, concomitant with the larger body size. SAG has slightly lower tooth counts while tooth width is significantly greater (Perrin, 1969, 1975, 2001; Douglas *et al*., 1984; Perrin *et al*., 1987, 1994).

Based on haplotypic diversity, it was proposed that SAG distributed along the Eastern Pacific is divided into four different populations: northern Mexico, Central America, Costa Rica and Ecuador, being the southern populations that diverged first from the offshore form (Escorza-Treviño et al., 2005). These authors included seven spotted dolphin samples (unknown subsp.) from unspecified

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[1] Published in Arkiv för Zoologi which has ceased to exist. It was a Swedish scientific journal on zoology published between 1903 and 1974.

locations in Ecuador and pooled them with specimens from Panama. However, they admitted that some structure might exist within this area which could be unveiled as the sampling gaps are filled (Escorza-Treviño et al. 2005). Since the latter study included few samples from Ecuador, further efforts are needed to properly characterize the southern population molecularly. The northern Mexican stock did not significantly differentiate from offshore (SAA) animals and further sampling was recommended (Escorza-Treviño et al. 2005).

In the Southeast Pacific, *Stenella attenuata* has been briefly reported from captures and strandings in Ecuador and Peru (Félix and Samaniego, 1994; Van Waerebeek and Reyes, 1994; Chiluiza *et al.*, 1998; Félix et al., 2011; Castro and Van Waerebeek, 2019). Spotted dolphins accounted for 9.42% of the stranding records on the coast of Ecuador between 1996 and 2009 and recorded throughout the year with no seasonal pattern (Félix et al., 2011). The species is observed with regularity over the shelf on the central coast of Ecuador between Isla de la Plata (01º15´S) - Puerto López (01°33'S) and Salinas (02º10'S) (FF and CC, unpublished information) although most probably its distribution is continuous along the entire coast of the country. *Stenella attenuata* is observed in waters of the Colombian Pacific throughout the year; however, its relative abundance is higher during the first quarter, when ocean productivity is greater (Rodríguez-Rubio *et al*., 2003). During research cruises conducted in both semesters between 2006 and 2009, *S. attenuata* exhibited the second highest relative abundance (0.21 groups/100 km), after the striped dolphin *Stenella coeruleoalba*, and was associated with waters characterized by higher chlorophyll-a concentrations and a stronger, shallower thermocline (Herrera, 2009). In Colombia, *Stenella attenuata graffmani* is resident in the waters surrounding Gorgona Island and is present year-round, typically in small groups of up to ten individuals, although it is occasionally observed forming herds of more than one hundred individuals (Capella *et al*., 2014). It can also be found at the Negritos shoals in Bahía Málaga, the Gulf of Tribugá and Cupica, and the Utría Bight (Herrera *et al*., 2011a).

Life history, genetics and population structure information are essential for developing conservation and management strategies. Here we compile spotted dolphin records from Peru, Ecuador and Colombia, hence update distribution range and status, document (scarce) natural history information, and review literature. We also include a genetic analysis (mtDNA) of samples collected in central Ecuador aiming at defining stock identity and population structure.

Material and Methods

Study Area

The study area that was examined for potential SAG records comprises the western South American (WSA) coast including continental shelf waters from Chocó, northern Colombia, Ecuador, Peru extending for approximately 8,000 km, to southern Chile (Figure 2). The climate across this vast region ranges from tropical in the north (Colombia and Ecuador), subtropical in northern and central Peru, temperate in southern Peru and most of Chile, and subantarctic in southern Chile. Surface circulation in the north is dominated by the North Equatorial Current and North and South Equatorial Counter currents, while from Ecuador to southern Chile it is influenced by the Peruvian or Humboldt Current (Wyrtki, 1966). In addition to seasonal shifts in the position of the Intertropical Convergence Zone, the region is regularly affected by El Niño–Southern Oscillation (ENSO) events (NOAA, 2025). During its warm phase (El Niño), sea surface temperature can rise by up to 4 °C above the mean, whereas during its cold phase (La Niña) it may fall by up to 2 °C below the mean (Fiedler, 2002). This cycle is also associated with changes in winds, rainfall, thermocline depth, circulation, and biological productivity, with significant effects on the distribution of marine species, including seabirds, small pelagic fish, and marine mammals (Barber & Chávez, 1983; Ramírez & Urquizo, 1985; Fiedler, 2002).

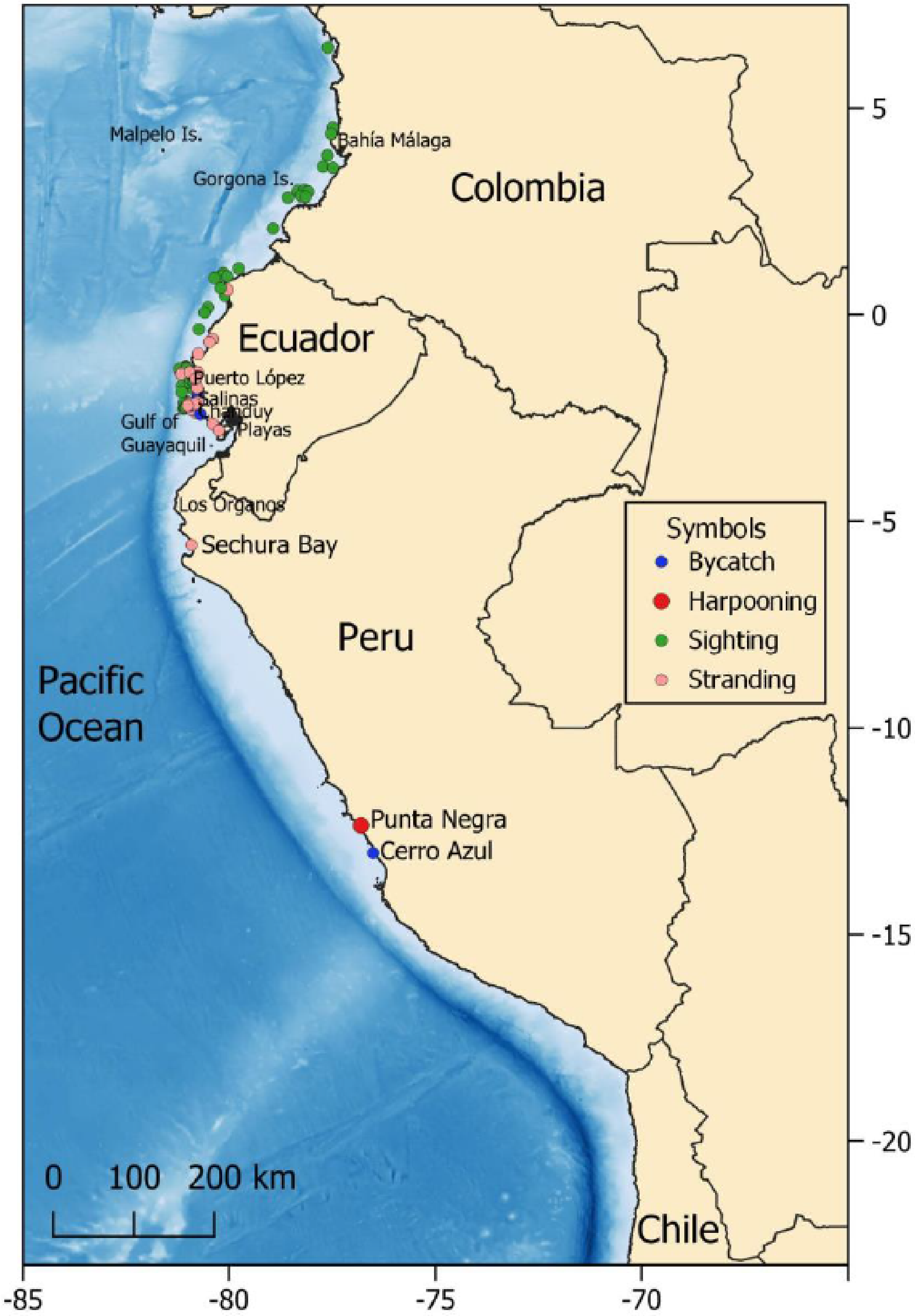

Figure 2. The Southeast Pacific region and records of SAG in the period 1986-2024. Record from Colombia were obtained from the scientific literature.

Source of Data

While significant information is available on natural history parameters, and especially morphological variation and reproductive biology, for the SAA offshore ETP populations (e.g. Hohn et al., 1985; Perrin and Hohn, 1994; Perrin *et al*., 1987; Perrin, 1975, 2001), equivalent knowledge for the SAG subspecies remains minimal (Douglas et al., 1984; Perrin, 2018). Original data utilized in this paper are derived mainly from spotted dolphin specimens bycaught in small-scale fisheries (Van Waerebeek et al., 1988; Félix and Samaniego, 1994; Van Waerebeek and Reyes, 1994) and stranding surveys implemented along much of the Peruvian and Ecuadorian coasts in 1985–2017 (e.g. Chiluiza *et al*., 1998; Félix *et al*., 2011; Castro and Van Waerebeek, 2019; Van Waerebeek *et al*., 2018; and others see below). Of skulls curated at Museo de Ballenas, Salinas, at the Parque Nacional Machalilla, Puerto López (Ecuador) and at Museo de Delfines, CEPEC, Pucusana, Peru, standard cranial measurements were taken with callipers (to nearest 0.5 mm) according to Perrin (1975), with a few additions, ensuring optimal comparability with published data from the ETP.

Sighting data off central Ecuador were collected during commercial whale watching trips and research surveys targeting humpback (*Megaptera novaeangliae*) and Bryde's whales (*Balaenoptera edeni/brydei*) (Félix et al., 2025). Sightings in Colombia have been conducted aboard oceanographic vessels of the General Maritime Directorate (DIMAR) during ERFEN cruises, as well as from smaller research vessels, tourism boats, and fishing vessels (Herrera, 2009; Herrera and Flórez-González, 2018; Herrera et al., 2007, 2011b). Off northern Ecuador and off Colombia equivalent data were collected by the Southwest Fisheries Science Center (SWFSC) during the Eastern Tropical Pacific Cetacean and Ecosystem surveys conducted between 1986 and 2005 (Hamilton et al., 2009) and were downloaded from the Ocean Biodiversity Information System (OBIS).

Genetic Analysis

Twenty-nine skin samples, collected from 2006 to 2024 on the central coast of Ecuador, were used for genetic analysis (Table S1). Dolphins were thought to be SAG and included stranded (n= 13) and free-ranging (n= 16) individuals. Samples were collected by swabbing the dorsolateral region using a 3 m extendable tube with a 5 cm-wide strip of #35 sandpaper at the tip, a modified version of the technique described by Bayas-Rea et al. (2018). This technique enabled sampling of dolphins both above and below water. Small epidermal tissue samples, ranging from a few mm^2 to approximately 1 cm^2, were collected and preserved in 95% ethanol. All genetic analyses were conducted at the Molecular Laboratory of the Pontificia Universidad Católica del Ecuador (PUCE), Quito.

DNA was extracted, and the hypervariable region of mtDNA control region (CR) (~602 bp; n = 21 and ~727 bp; n = 8) was amplified using two primer sets: (1) H00034 (Rosel et al., 1994) and L15824 (Rosel et al., 1999) and (2) t-pro-whale and Dlp8G (Dalebout et al., 1998). Forward and reverse strands of each sequenced sample were manually edited and aligned to obtain a consensus sequence using MEGA 11 (Tamura et al., 2021). To validate sequence identity, all consensus sequences were evaluated with the BLAST algorithm in GenBank (Altschul et al., 1997). Finally, multiple sequence alignment for each marker was performed using CLUSTAL W, implemented in MEGA 11 (Tamura et al., 2021). Since sequences varied in length, all molecular analyses were based on a 405 bp truncated alignment. Genetic diversity was estimated by calculating the number of haplotypes using DNAsp v6 (Rozas et al., 2017). Haplotype diversity (h), nucleotide diversity (π), Tajima's D test (Tajima, 1989), and Fu's Fs test (Fu, 1997) for selective neutrality were estimated using Arlequin v3.5 (Excoffier & Lischer, 2010). Significance of both neutrality tests was assessed through randomization (10,000 iterations).

To investigate the phylogeographic relationships among Ecuadorian haplotypes and other populations of *S. attenuata* elsewhere, 101 mtDNA CR sequences from different geographic regions available in the GenBank database were included (Courbis et al., 2014; Escorza-Treviño et al., 2005; Leslie et al., 2016; Oremus et al., 2015), along with 27 sequences obtained from this study (Table S2). Genealogical relationships were inferred using a median-joining network implemented in Network v.10 software (Bandelt et al., 1999). To infer phylogenetic relationships, Bayesian inference with

MrBayes v.3.2.7 was used (Ronquist et al., 2012). The analysis included 57 mtDNA CR sequences of *S. attenuata* (accession numbers in Table 1) (Escorza-Treviño et al., 2005; Leslie et al., 2016), along with two sequences of *S. longirostris* (NC_032301.1 and KX857382.1), one sequence of *S. coeruleoalba* (NC_012053.1), one sequence of *S. frontalis* (NC_060612.1), and one sequence of *Lagenorhynchus albirostris* (NC_005278.1) as an outgroup. The best-fitting model for nucleotide evolution (HKY+I+G) was inferred under the AICc criterion using jModelTest v.2.1.10 (Darriba et al., 2012). Posterior probabilities of the tree and parameters in the evolutionary model were approximated using Markov Chain Monte Carlo (MCMC). Two independent runs of four chains were carried out for 5,000,000 generations, with a 100,000 burn-in and sampling every 5,000 generations. The effective sample size (ESS > 200) values were evaluated using Tracer v.1.6 (Rambaut et al., 2018) to ensure adequate mixing and convergence of the posterior distribution and parameters. Additionally, the potential scale reduction factor (PSRF = 1) and the average standard deviation of split frequencies between chains (≤ 0.01) were examined. The phylogenetic tree was visualized and edited using Fig (Tree) v.1.4.2 (Rambaut, 2014).

Table 1. Stranding records, chronologically ordered, of *S. attenuata graffmani* on the coast of Ecuador, 1993–2021.

Date	Site	Position	Sex	Length (cm)	Source
5/10/1993	San Vicente	3º35'S. 80º24'W		212	Chiluiza et. al. (1998)
21/11/1993	Anconcito	2º22'S, 80º47'W			Chiluiza et. al. (1998)
5/4/1994	Montañita	1º49'S 80º45'W		204	Chiluiza et. al. (1998)
30/4/1995	Libertador Bolívar	1º56'S, 80º44'W			Chiluiza et. al. (1998)
12/7/1995	Olón	1º50'S, 80º34'W		191	Chiluiza et. al. (1998)
2/9/1995	Playas	2º37'S, 80º23'W			Chiluiza et. al. (1998)
3/9/1995	Monte Verde	2º03'S, 80º44'W			Chiluiza et. al. (1998)
25/5/2007	Ayangue	1º58'S, 80º45'W	M	» 200	Félix et al. (2011)
14/4/2006	Mar Bravo	2º15'S, 80º56'W		190	Félix et al. (2011)
23/12/2002	San José	1º46'S, 80º46'W	M	193	Félix et al. (2011)
21/3/2004	Mar Bravo	2º13'S, 80º57'W		»120	Félix et al. (2011)
14/9/2004	Punta Carnero	2º17'S, 80º54'W			Félix et al. (2011)
19/9/2004	Mar Bravo	2º14'S, 80º56'W	F	228	Félix et al. (2011)
11/11/2005	Playa FAE	2º11'S, 80º59'W		>200	Félix et al. (2011)
16/2/2006	Punta Carnero	2º17'S, 80º54'W	M	92	Félix et al. (2011)
18/11/2006	Mar Bravo	2º16'S, 80º55'W	M	181	Félix et al. (2011)
2/12/2006	Mar Bravo	2º15'S, 80º55'W	F	218	Félix et al. (2011)
13/5/2007	Diablica	2º18'S, 80º54'W			Félix et al. (2011)
13/1/2008	Mar Bravo	2º14'S, 80º57'W	F	186	Félix et al. (2011)
31/10/2009	Punta Carnero	2º17'S, 80º54'W	F	179	Félix et al. (2011)
2/1/2010	Mar Bravo	2º15'S, 80º56W		195	This report
1/5/2015	Diablica	2º17'S, 80º54W		» 200	This report
31/8/2017	San Pablo	2º06'S, 80º44W	F	190	This report
27/6/2018	Cauchiche	2º48'S, 80º14'W			This report
10/7/2021	Mar Bravo	2º14'S, 80º57'W			Chocho et al. (2023)

Results and Discussion

Distribution Off Western South America

Colombia

Perrin (1975) indicated that the southernmost known specimen of *S. attenuata* (USNM 258641) from Colombia was collected at Isla Gorgona (03°0′N, 78°20′W), one of the earliest specimens. Valencia (2006) studied the behavior of spotted dolphins around Isla Gorgona, without discussing subspecific status. García *et al*. (2006) reported 11 sightings of SAA and indeterminate subsp. and one confirmed sighting of SAG (n= 3) in Colombian waters, including towards Malpelo Island

(04°00′12″N, 81°36′27″W), ca. 500 km offshore. A follow-up abstract indicated the high risk of fisheries interactions for coastal spotted dolphins (García *et al*., 2008). The pantropical spotted dolphin was the third most abundant cetacean recorded and the second delphinid after the striped dolphin (*Stenella coeruleoalba*) in both coastal and oceanic waters of Colombia during surveys conducted between 2001 and 2010 from the mainland to Malpelo Island (Herrera et al., 2011 b).

Palacios *et al*. (2012) estimated abundance of *S. attenuata* in the Colombian EEZ, without distinguishing between subspecies. In contrast with common bottlenose dolphin *Tursiops truncatus* (Montagu) that occurred nearshore, Londoño (2005) did not observe spotted dolphins inside Bahía Málaga (03°58′N, 77°19′W), Valle del Cauca Department, but at a mean distance from the coastline of 9.1 km (range 1–30 km), indicating separate habitats. Herrera et al. (2011 b) also indicate that it is possible to find the species in the external part of the bay at Negritos Bank. Only one small group (n=5) was sighted at 1 km from shore, while mean group size was 22 (range 2-100). Spotted dolphins were present off Bahía Malaga in both dry and wet seasons and presumably year-round. A similar situation was found in the Parque Nacional Utría, Chocó Department (Suárez, 1994). However, in none of these studies was it attempted to distinguish between coastal and oceanic subspecies. SAG would have a continuous distribution along the entire coast of Colombia according to sightings registered by the SWFSC (Hamilton et al., 2009) (Figure 2).

Ecuador

Stenella attenuata has a regular occurrence in offshore waters off Ecuador (Tables 1 and 2; Figure 2), but there is no indication of abundance in coastal waters. However, Gerrodette and Palacios (1996) estimated the abundance of spotted dolphins within the Ecuadorian EEZ at 1,864 animals (CI 95% 567-6427), remaining unclear what proportion corresponds to the coastal SAG. The species has been reported also off the Galápagos Islands (Perrin *et al*. 1987; Day, 1994; Palacios and Salazar, 2002; Denkinger et al., 2013) especially outside the Galápagos Marine Reserve (40 nm offshore) where it was regularly seen in mixed aggregations with spinner dolphins (*Stenella longirostris*) (Palacios and Salazar, 2002) and would correspond to the offshore subspecies. Among the four small odontocete species captured in artisanal drift gillnets in 1993, only 2% were identified as *S. attenuata* (Félix and Samaniego, 1994). In contrast, Castro and Rosero (2010) reported that spotted dolphins accounted for 22% of the cetacean bycatch from small-scale fishing fleets along the central coast of Ecuador. This discrepancy is likely related to the fishing depth at which different fleets operated, as the continental shelf is narrower in some areas. Most probably virtually all specimens bycaught in the Ecuadorian small-scale fisheries belong to SAG.

Table 2. Sightings of *S. attenuata graffmani* (n=59) on the central coast of Ecuador, 2000–2024.

Date	Position	Group size	Remarks
23/7/2000	1°18'S, 81°02'W	6-10	With humpback whales
2/7/2002	2º09'S, 81º02'W		With humpback whales
1/8/2003	2º16'S, 81º06'W	30-40	Feeding
23/9/2004	2º15'S, 81º04'W	~100	With humpback whales
2/10/2004	2º06'S, 81º00'W	100-200	Several subgroups
14/8/2005	2°08'S, 80°53'W	60-80	
18/8/2005	2°11'S, 81°01'W	~80	
21/8/2005	2°10'S, 80°58'W	~60	Feeding
9/7/2007	2°08'S, 81°00′W	3	Feeding
15/7/2008	2°10'S, 81°00′W	~30	
11/8/2008	2°06'S, 81°03'W		With humpback whales
11/7/2010	2°09'S, 80°59′W	50-100	

28/7/2010		80-100	
29/7/2010	2°08'S, 81°01'W	~50	
4/8/2010	2°11'S, 80°58'W	~60	
5/8/2010		~40	
12/8/2010	2°07.'S, 81°05'W		With humpback whales and common bottlenose dolphins
13/8/2010	2°12'S, 81°03'W	300-400	
14/8/2010		60-80	
23/8/2010	2°13'S, 81°03'W	6-8	With humpback whales
19/9/2010	2°08'S, 81°00’W	15-20	
2021-03-05	1°36'S, 81°00'W	15-20	
2022-03-25	1°47'S, 80°51'W	~100	
2022-12-20	1°26'S, 80°56'W	4	
2023-01-22	1°23'S, 81°04'W	18-20	
2023-02-25	1°27'S, 80°59'W	~200	Feeding
7/3/2023	1°19'S, 80°58'W	~200	
8/3/2023	1°24'S, 80°58'W	~100	Feeding
26/2/2024	1°25'S, 81°07'W	~500	
28/2/2024	1°25'S, 81°08'W	~500	
14/3/2024	1°26'S, 80°59'W	~200	Feeding , with Bryde's whales
14/3/2024	1°33'S, 81°11'W	~500	Feeding
17/3/2024	1°19'S, 80°59'W	~200	Feeding
3/4/2024	1°24'S, 81°11'W	~50	
11/4/2024	1°21'S, 80°57'W	~20	
11/4/2024	1°16'S, 81°04'W	~50	
18/4/2024	1°25'S, 80°57'W	~200	
18/4/2024	1°35'S, 80°53'W	5	With Bryde's whales
1/5/2024	1°25'S, 80°56'W	~300	
2/5/2024	1°25'S, 80°55'W	~300	Feeding
4/6/2024	1°26'S, 80°54'W	10	With Bryde's whales
27/7/2024	1°33'S, 80°56'W	~300	With humpback whales
15/8/2024	1°19'S, 81°00'W	~20	With humpback whales
17/8/2024	1°24'S, 80°57'W	~20	
19/8/2024	1°21'S, 80°59'W	~200	
24/8/2024	1°16'S, 81°02'W	~200	
26/8/2024	1°25'S, 80°56'W	~20	With Bryde's whales
3/6/2024	1°35'S, 80°52'W	~200	Feeding
8/9/2024	1°25'S, 80°56'W	~100	
11/9/2024	1°24'S, 80°54'W	~200	
20/9/2024	1°26'S, 80°54'W	~20	
20/9/2024	1°26'S, 80°55'W	~20	

21/9/2024	1°23'S, 80°58'W	~200	
21/9/2024	1°24'S, 80°57'W	~200	Feeding
22/9/2024	1°25'S, 80°56'W	~100	Feeding
1/10/2024	1°28'S, 80°52'W	~200	With humpback whales
19/10/2024	1°17'S, 81°1'W	10	
26/10/2024	1°24'S, 80°55'W	3	
28/10/2024	1°26'S, 80°54'W	5	

The neritic subspecies seems to primarily occur over the shelf along the ocean-exposed central provinces of Santa Elena and Manabí, although this could be explained by the lower research effort in northern Ecuador and the southwestern Gulf of Guayaquil, the most productive zone along the Ecuadorian coast (Chinacalle et al., 2021). No SAG catches were reported, for example, for the southern port of Puerto Bolívar (Van Waerebeek *et al*., 1997) but some remains were found in the northeastern part of the gulf, at Playas (Chiluiza et al., 1998).

Peru

The first specimen records of SAG in central and northern Peru date from, respectively, 1986 and 1989, (Table 3), decades before free-ranging animals were sighted in northern Peru (Pacheco et al., 2019; Martínez et al., 2021; Cortez-Casamayor, 2024). Among thousands of small cetaceans taken in Peru's mostly small-scale coastal fisheries, examined in 1985-2010 (e.g. Read *et al*., 1988; Van Waerebeek *et al*., 1988, 1994; Reyes, 2009; Mangel *et al*., 2010; Tzika *et al*., 2010), only four individuals of *S. attenuata* were authenticated (Table 3). Stranding surveys in southern and south-central Peru (Tacna and Ica Departments) did not encounter any spotted dolphin records (Van Waerebeek and Reyes, 1994; Van Waerebeek *et al*., 2018; Reyes, 2009; Pizarro-Neyra, 2010; Pizarro-Neyra *et al*., 2021; Santillán, 2021). Surveys of beaches and fishing ports in Peru's three northern coastal departments, *i.e.* Tumbes, Piura and Lambayeque (Van Waerebeek *et al*., 1988; Van Waerebeek and Reyes, 1994; unpublished CEPEC archives) yielded a single skull from Bahía Sechura in 1989 (Table 3).

Table 3. Specimen records of *S. attenuata graffmani* from Peru, ordered chronologically. Abbreviations: Standard body length (SL), Not available (NA).

Specimen	**Date**	**Location**	**Coord.**	**Sex, maturity**	**SL (cm)**	**Circumstances**	**Voucher, Museo de Delfines, CEPEC**
KVW-343	20/04/1985	Landed at Cerro Azul port, Lima Department	13°02'S, 76°29'W	Adult female (lactating)	211	Gillnet bycatch	skull
KVW-344	20/04/1985	Landed at Cerro Azul port, Lima Dept.	13°02'S, 76°29'W	Female. Small calf. Milk in stomach.	106	Gillnet bycatch, landed with KVW-343	skull
AJR-036	24/02/1986	Taken at Punta Negra, landed at Pucusana port, Lima Dept.	12°22'S, 76°48'W	Male. Sexually immature; cranially subadult	188	Harpooned; collected by A.J. Read	skull
KVW-1999	28/12/1989	Playa Michallo, Bahía Sechura (sur), Piura Dept.	05°35'S, 80°57'W	Sex unknown; cranially mature	NA	Beach pick-up (Santiago Zambrano)	skull

Seasonal observer effort from humpback whale-watching trips in nearshore waters off El Ñuro (04°14'S, 81°10.5'W) and Los Órganos (04°29.5'S, 81°20.778'W), Piura Province, did not result in any spotted dolphin sightings in winter and early spring months (Silva-Buse, 2016; Pacheco et al., 2019). However, in 2018-2019, a single spotted dolphin was sighted among a short-beaked common dolphin *Delphinus delphis* pod off Los Órganos thrice, in September, October and January (Martínez et al.,

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2021). The peculiarity of these encounters suggests these are most likely re-sightings of a single individual. The habitual southern range of SAG is probably Piura, with the cold coastal Humboldt Current acting as barrier. The three capture records in central Peru, in February and April 1986, occurred during the rapid warming phase of an exceptionally lengthy 1986-1988 El Niño event (NOAA, 2025). An increase of 85% in sightings of spotted dolphins in northern Peru was associated with warm waters intrusion during a strong El Niño event in 2023 (Cortez-Casamayor et al., 2024). The documented austral range for SAG is off Cerro Azul (13°02’S) at the southern end of the Lima Department, based on a net-entangled mother-calf pair (Figure 3). The veteran fisher who hand-harpooned AJR-036 from a pod of three animals just off the beach of Punta Negra, Lima, (Table 3) emphasized that he had ‘never seen dolphins of this type before’.

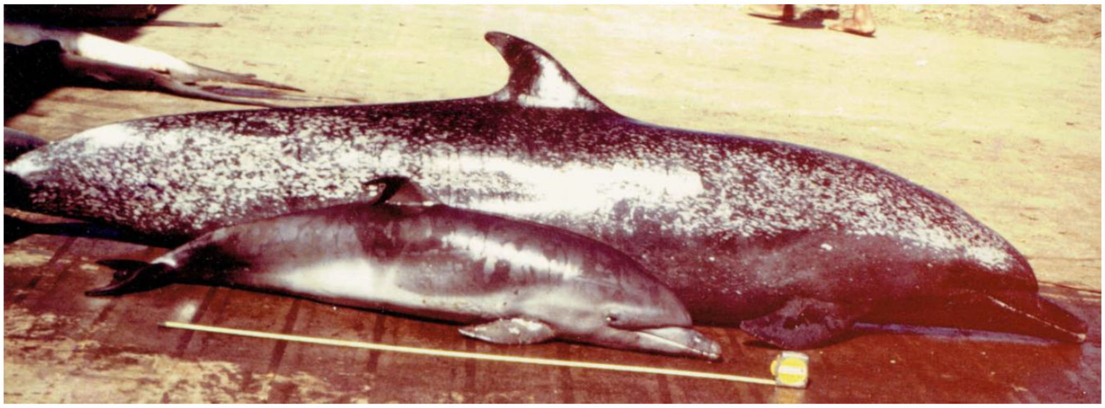

Figure 3. Southernmost record of *Stenella attenuata graffmani* in the SE Pacific: adult female (KVW-343) with calf (KVW-344) landed at Cerro Azul artisanal port in Lima Department, Peru.

Chile

Although Sielfeld (1980) reported no *S. attenuata* specimens in Chilean collections, he later listed *S. attenuata* for the country, without supporting evidence (Sielfeld, 1983). A cetacean manual (Cárdenas *et al.*, 1986) stated that the spotted dolphin was ‘probably’ present in littoral waters of northern Chile. The primary range of the oceanic SAA was mapped to range south to the Peru-Chile border (18°21’S) (Jefferson *et al*., 2015; Perrin, 2018) while Rice (1998) indicated ‘about 35°S off Talca’ as southern range. However, all these remained without specific, authenticated records. Two authoritative national reviews of Chilean cetaceans (Aguayo, 1975; Aguayo *et al.*, 1998a) did not include the species. Also, no spotted dolphins were encountered offshore, between Valparaiso (33°00’S,71°37’W) and Easter Island (27°09’S,109°W), during five sighting surveys in winter months (Aguayo *et al.*, 1998b). Comprehensive field work in 1986-1988 and 2017-2021, including vessel-based surveys, stranding and bycatch monitoring in the Antofagasta region, were also negative for *S. attenuata* (Guerra-Correa *et al*., 1987; Findlay *et al*., 1998; García-Cegarra et al., 2021). The same results were found during dolphin surveys off central and southern Chile (e.g. Findlay *et al*., 1998; Gibbons, 2010; Schweber and Thomas, 2010; Gibbons and Waring, 2013; Siciliano and Higuera, 2015). We are confident that *S. attenuata*, and especially SAG is normally absent from Chile’s coastal waters. A far offshore summer presence of SAA off northern Chile, beyond the 200 nm EEZ, remains a possibility.

Life History

Pigmentation, External Morphology

Perrin (1969, 1975) described the strong developmental and individual variation in coloration found in SAG specimens from the ETP off Central America. He grouped individuals in five general categories of increasing spotting concurrent with larger body size: Newborn stage, Two-tone, Speckled, Mottled and Fused stage in the largest dolphins (see Figures 1-14 in Perrin, 1969). The degree of body spotting in *S. attenuata* diminishes in animals the further west one goes in the ETP (Perrin, 1975; 2018). The coastal morphotype encountered in Peru and Ecuador (Figure 4) shows heavy spotting fully congruent with the Eastern Pacific SAG holotype (Figure 1). An adult female (Figure 3) and subadult male in Peru showed heavy white mottling on dorsum, flanks, tailstock and anogenital area. The lower half of the head, rostrum (minus white lips and tip), flippers and anterior ventral field was dark gray (Figure 6). Two calves that lacked any spotting (Two-tone stage), had grey upper flanks and dorsal field while the abdomen was whitish with a white anogenital blaze (Figures 3 and 5). They closely resembled a calf Indo-Pacific bottlenose dolphin *Tursiops aduncus,* due to the more attenuate rostrum compared to *T. truncatus*.

A subadult male (AJR-036; Table 3) showed darker spots on a dark background of upper rostrum, flanks, abdomen, dorsal fin and flippers. A few lighter spots were present on the upper flanks. Dark bands extended from rostrum, around eyes and towards the blowhole. All three Peruvian animals had pale lips, and a smallish, falcate dorsal fin. Adult animals photographed at sea in Ecuador also show white lips and most have a pronounced narrow, falcate dorsal fin, although there exists important individual variation in dorsal fin shape (Figure 4). An adult female had a slight postanal keel (Figure 3). Males of adult size, from Ecuador, had a more pronounced postanal keel (Figure 7).

Figure 4. Photographs of three adult *S. a. graffmani* taken on the central coast of Ecuador in which the heavily spotted pattern is evident. Note the important variation in dorsal fin shape, with the strongly falcate morph (bottom) commonly seen.

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Figure 5. A calf of SAG with no spots on the body leaping by its mother.

Figure 6. Adult coastal spotted dolphin photographed off Ecuador showing a dark rostrum with white lips.

Figure 7. An adult male SAG showing a pronounced postanal keel.

In central Peru, a male of 188 cm (standard body length, SL) had a body mass of 84 kg. The SL of specimens collected in Ecuador ranged between 92–228 cm, with females ranging 179-228 cm and males 92-200 cm (Table 3). In the NE Pacific, average lengths of adult male coastal and offshore subspecies were 223 cm (range 197–246) and 200 cm (range 166–240), respectively (Perrin, 2001). Average lengths of adult females were 207 cm (range, 179–227) and 182 cm (range, 163–215), coastal and offshore respectively (Perrin, 2001). The Peruvian adult female (211 cm; 99 kg) and the Ecuadorian females thus cluster with the ETP coastal stock. In the Gulf of California, males measured 146–227 cm (n=9) and females 182–221 cm (n=6) (Vidal et al., 1993). No adult males have been collected in Ecuador for comparison.

Cranial Characteristics

The earlier studies of geographic variation in cranial morphology of eastern Pacific *S. attenuata* integrated relatively large samples (e.g. Perrin, 1975; Perrin et al., 1994), however they did not include coastal specimens from South America. Here we present descriptive statistics of standard craniometrics for 9 SAG skulls (8 adults, 1 subadult) from Ecuador and Peru (Table 4), including mean, SD, minimum and maximum values, subsample sizes (because variable), both for absolute measurements (in mm) and the same expressed as percent of condylobasal length (% CBL). For comparison, equivalent data for SAA from the offshore ETP (Perrin, 1975) are juxtaposed, based on 65–70 adults (Table 4).

Table 4. Standard craniometrics of adult specimens of *S. a. graffmani* compared to equivalent data for a large sample (n= 75-80, depending on variable) of *S. a. attenuata* presented by Perrin (1975). Values in blue indicate non-overlapping between the two morphs. % CBL = percent of condylobasal length. .

	***Stenella attenuata graffmani* (Peru, Ecuador; Coastal)**										***S. attenuata attenuata* Offshore, ETP (Perrin, 1975**	
	Craniometrics in mm					% CBL	% CBL	% CBL	% CBL			
VARIABLE	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	**Mean**	**Range**
Condylobasal length	428.9	10.6	410.5	440.0	9	100.0	0.0	100.0	100.0	9	389.9	356-411
Rostrum length from base	249.6	6.8	237.6	257.7	9	58.2	0.8	56.9	59.6	9	232.2	210-249
Rostrum width at base (min)	93.1	3.5	87.4	99.1	8	21.7	1.1	20.7	24.1	8	82.1	82-100
Rostrum width at base (s.l.)	97.8	3.0	93.2	101.1	5	23.0	0.7	22.3	24.1	5	na	na
Rostrum width at 60mm	65.6	2.9	60.8	69.9	9	15.3	0.7	14.4	16.0	9	55.4	46-63
Rostrum width at ¼ Length	64.7	2.3	61.0	67.8	9	15.1	0.6	14.2	16.0	9	na	na
Rostrum width at ½ Length	49.5	2.5	47.3	54.9	8	11.6	0.6	11.1	12.7	8	40.8	35-48
Rostrum width at ¾ Length	36.4	3.4	32.4	43.8	9	8.5	0.8	7.7	10.1	9	28.4	23-36
Premx Width at ½ Length	27.4	1.9	25.6	31.1	9	6.4	0.4	5.9	7.4	9	22.2	17-28
Tip rostrum to ext. nares	288.3	9.0	273.9	298.4	9	67.2	0.8	66.1	68.6	9	271.3	245-294
Tip rostrum to int. nares	297.8	9.3	285.3	305.0	5	69.0	0.9	67.4	69.8	5	272.9	243-293
Preorbital skull width	159.4	4.9	150.5	165.6	8	37.1	0.9	35.8	38.3	8	146.0	134-163
Postorbital skull width	182.3	6.1	171.6	190.6	7	42.5	1.2	41.0	44.1	7	164.2	151-178
Zygomatic skull width	181.5	5.5	173.4	191.3	9	42.3	1.2	40.0	43.7	9	163.0	148-177
Parietal skull width	147.7	5.7	140.8	157.1	9	34.4	1.1	33.1	35.8	9	137.6	129-150
Maximum width premax.	71.9	2.9	67.5	76.6	9	16.7	0.4	16.1	17.4	9	64.9	57-71
External nares width	46.8	2.3	44.1	51.6	9	10.9	0.5	10.0	11.7	9	41.5	37-47
Internal nares width	51.8	3.2	47.6	58.1	7	12.1	0.8	11.3	13.8	7	36.4	40-54
Temporal fossa length	87.6	3.6	83.0	92.4	8	20.4	1.1	18.9	22.5	8	67.6	56-77
Temporal fossa width	62.0	3.6	56.3	67.8	9	14.5	1.0	12.9	16.1	9	52.8	46-63
Max. length left pterygoid	70.5	5.3	66.0	78.1	4	16.2	1.1	15.6	17.8	4	62.8	55-76
Length mandibular condyle	25.9	2.7	22.0	28.0	4	5.8	0.7	5.0	6.3	3	na	na
Length fossa mandibularis	117.9	5.8	112.4	126.0	4	27.1	1.0	26.6	28.6	4	104.0	90-124
Length symphysis mandibularis	66.1	3.3	61.2	68.2	4	15.2	0.9	14.0	16.1	4	na	na
Orbital length	54.1	3.0	49.3	58.2	8	12.6	1.0	11.2	13.9	8	47.0	44-53
Antorbital process length	39.3	4.1	33.5	45.7	8	9.1	0.9	7.7	10.5	8	35.6	30-42
Length upper tooth row	217.0	7.0	203.4	225.0	9	50.6	0.9	49.5	52.0	9	201.8	180-220
Length lower tooth row	216.9	8.1	205.8	227.0	5	49.8	1.4	48.3	51.7	5	195.8	177-220
Ramus length	366.8	8.4	354.0	376.0	6	84.6	0.9	83.7	85.8	5	328.5	296-347
Ramus height (coronoid process)	66.4	2.5	64.2	70.8	6	15.3	0.6	14.6	16.2	5	56.8	50-62
N° alveoli upper left (UL)	36.4	2.1	33	39	10	na	na	na	na	na	41.5	37-48
N° alveoli upper right (UR)	35.8	1.9	33	39	10	na	na	na	na	na	41.4	37-47
N° alveoli lower left (LL)	36.4	0.9	35	37	5	na	na	na	na	na	40.4	34-45
N° alveoli lower right (LR)	37.2	0.8	36	38	5	na	na	na	na	na	40.6	34-46
Tooth width transverse (max)	4.9	0.6	4.0	5.3	4	1.1	0.1	0.9	1.2	4		
Alveolus width	6.1	0.5	5.5	6.7	6	1.4	0.1	1.3	1.6	6		
Bulla length	31.9	0.8	31.1	32.6	3	7.4	0.2	7.1	7.5	3	29.9	29-33
Bulla width	19.1	2.7	17.2	21.0	2	4.4	0.5	4.1	4.8	2		
Periotic length	28.1	0.9	27.3	29.1	3	6.5	0.1	6.4	6.6	3	26.9	25-30
Height braincase	117.1	6.5	107.2	130.5	9	27.3	1.6	25.6	30.9	9		
Length braincase	130.1	4.5	121.7	135.0	9	30.3	1.1	28.1	31.6	9		
Maximum width nasals	44.3	1.8	41.5	46.1	7	10.4	0.3	9.9	10.7	7		
Maximum width palatines	37.3	2.8	33.3	41.5	9	8.7	0.6	7.9	9.6	9		
Max. span occipital condyles s.s.	89.0	2.7	86.0	93.6	6	21.0	1.0	20.0	22.8	6		
Max. span occipital condyles s.l.	95.8	3.3	90.5	101.3	9	22.4	1.1	20.6	24.1	9		
Width foramen magnum	38.4	3.9	34.0	43.1	6	8.9	0.8	7.8	10.0	6		
Height foramen magnum	37.4	2.6	33.6	40.8	6	8.8	0.7	8.0	9.9	6		
Height supraocc. crest	na	na	na	4.5	3	0.4	0.6	0.0	1.1	3		
Width at posterior borders of temp	129.4	6.8	120.0	140.7	6	30.0	1.4	28.6	32.5	6		

Jointly with graphic evidence (Figure 8), such information is immensely helpful in the (sub)species identification of dolphin skulls, especially those that are damaged or of unknown origin. To allow statistical analysis, however, our preliminary sample will need to be increased with additional skulls from South America. Also, access to raw craniometric data from Central and North America will be required. However, a simple comparison of means and ranges for adult skulls (Table 4) shows that, for all variables, the SAG skulls from South America are consistently larger than the offshore SAA collected by Perrin (1975). Three cranial variables, the CBL, mandibular ramus length and ramus height do not even have overlapping ranges, so important are the differences in size (Table 4). With a few measurements individual skulls can readily be assigned to their respective subspecies. Similarly, skulls from inshore specimens in the Northeast Pacific are also substantially larger than those from offshore areas of the ETP (Perrin, 1975; Douglas *et al*. 1984; Perrin and Hohn, 1994; Perrin, 2018). Perrin (1975) reported that tooth width is the character of the skull where the greatest divergence is found between (northern) inshore and offshore forms, with SAG having the widest teeth. Our sample (lacking teeth) does not allow evaluation. There are other significant differences in the feeding apparatus of the two forms, with offshore specimens having a more attenuate rostrum, smaller temporal fossa and smaller teeth (Perrin, 1975), which also explains the differences in size (non-overlapping) of the mandibles between the southern SAG and SAA (this paper). Our findings are consistent with the conclusions by Perrin (1975), that the significant variations suggest feeding differences between inshore and offshore morphs.

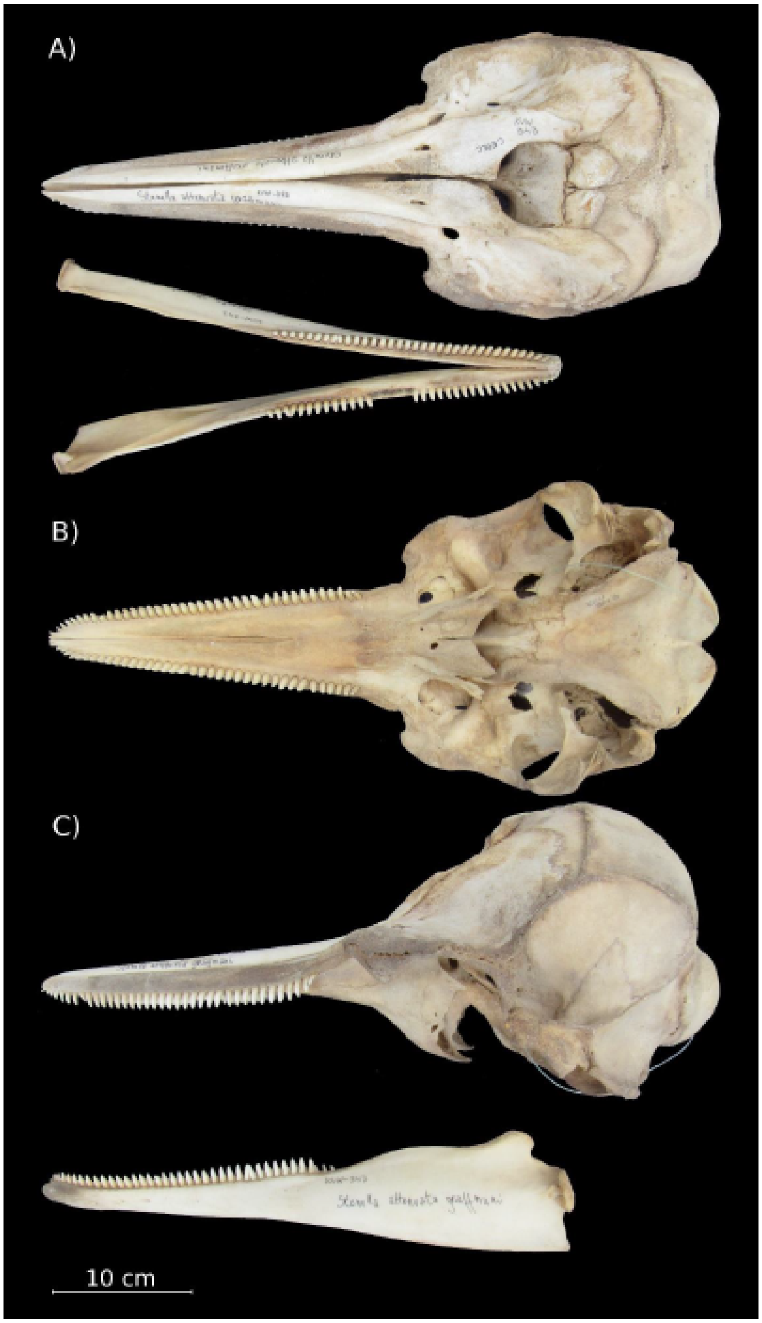

Figure 8. SAG skull curated at CEPEC, Peru. A) dorsal view and mandibles, B) ventral view, C) lateral vie and left mandible.

Reproduction and Growth

The reproductive biology of both male and female *S. attenuata* from the Eastern Tropical Pacific is supported by large sample sizes (Hohn et al., 1985; Myrick et al., 1986; Kellar et al., 2013). No information is published on reproductive parameters of the SAG subspecies in South America. In Peru, one small calf (KVW-344) without neonatal folds measured 106 cm for a weight of 19 kg, while a 84 cm near-term foetus from Ecuador, collected from a 218 cm female, is conserved in formalin at the Museo de Ballenas, Salinas. This suggests that length at birth for SAG may approach 90–95cm. Neonates of SAA in the ETP measure some 80-85 cm (Perrin and Hohn, 1994; Perrin, 2018) or 83.2–85.4 cm (Hohn and Hammond, 1985), smaller than those of the coastal stock.

A lactating female of 211 cm (KVW-343; Table 3) with abundant milk in its mammaries, presented only two corpora albicantia, one regressing, in the right ovary, and was thought to be still young. The left ovary was smooth, without corpora. Ovary dimensions were 40 x 13 x 7 mm (left) and 50 x 21 x 19 mm (right). Largest diameters of uterine horns measured 21 mm (left) and 36 mm (right). The female calf (KVW-344) with unerupted teeth had milk in its forestomach and oesophagus. It showed a healed umbilicus and lacked foetal rostral hairs and foetal folds. Age was estimated as a few months, hence the 20 April capture date was consistent with a summer parturition. Its smooth, fully immature, ovaries measured 17 x 9 x 6 mm (left) and 17 x 8 x 6 mm (right).

The macroscopic absence of sperm in both epididymides of a 188 cm male (AJR-036, Peru) confirmed its sexual immaturity. Its testes measured 97 x 17 x 12 mm (left) and 103 x 10 x 15 mm (right), with a mass of 34 g and 33 g, respectively.

Feeding

Nothing has been published on the diet of SAG in South America. The forestomach contents of an immature male (AJR-036) from Peru consisted of undigested fish flesh, small fish bones (possibly Peruvian anchovy *Engraulis ringens*) and small squid beaks. Nine otoliths were retrieved from 6 unidentified small fish remains. The main and pyloric stomachs, which were empty, weighed 390 g and 190 g respectively. Perrin (1975) indicated that morphological differences in the feeding apparatus, including tooth width (wider in SAG), length and width of temporal fossa (larger in SAG) suggest feeding differences between inshore and offshore populations of the ETP. Interestingly, in a case of parallel evolution, significantly wider teeth also differentiate inshore from offshore forms of common bottlenose dolphins in the eastern Pacific. The two forms show discrete diets (Walker, 1981; Van Waerebeek et al., 1990).

In Ecuador, SAG has been observed feeding on small pelagic fish, on occasions with large aggregations of marine bird flocks including blue-footed booby *Sula nebouxii*, red-footed booby *Sula sula*, and frigate birds *Fregata* sp., among others, as well as with other species of cetaceans, including Bryde's whales and common bottlenose dolphins (Félix et al., 2025). On two occasions, prey was identified as anchovies (*Anchoa* sp.) but it is not discarded that SAG targets other small pelagic fish such as mackerel (*Scomber japonicus*) or sardines (*Opisthonema* spp.), which are more abundant in Ecuadorian coastal waters than anchovies (Romero *et al*., 2020). Feeding behavior was observed on 11 occasions (18.6% of sightings) in Ecuadorian waters between 18 and 57 m in depth (mean= 46.75, n=4). Empty stomachs were found in a fresh adult female and an immature male, both stranded in 2006.

Helminth Parasites and Pathology

There is no published information available on parasites, epibionts and diseases of SAG. Here we present some initial findings.

Peruvian specimens

An adult female was infested with five *Anisakis* sp. nematodes in the forestomach and one in the pyloric stomach. We found no helminth parasites in the gastrointestinal tract of the subadult male AJR-036. Its kidneys were also unaffected. The female KVW-344 presented a moderate infestation of small-sized *Nasitrema* sp. trematodes in the cranial sinuses while its calf had none. The subadult male's sinuses were infested with the same trematode. Its pterygoid bones showed some fenestration, but any potential link is unclear. Fully adult skull KVW-1999 had (anteriad) several maxillary alveoli filled-in with trabecular osseous tissue, presumably age-related.

None of the appendages of the three freshly dead individuals examined in Peru (Table 3) carried semi-stalked barnacles *Xenobalanus globicipitis*, although this phoront is very common in other Peruvian small odontocetes (e.g. Van Waerebeek et al., 1993; Reyes and Van Waerebeek, 1995). Also, no whale lice (Cyamidae) were found. All three animals had good body condition and no macroscopic pathologies were observed. However, due to the extensive spotting, certain dermatopathies e.g. poxviral tattoo skin disease, cutaneous herpes and papillomaviral warts (e.g. Van Bressem *et al*., 2007, 2009) could have escaped detection in the field.

Ecuadorian specimens

In Ecuador, only a handful of the hundred SAG recorded and photographed at sea carried *X. globicipitis* in their dorsal fins (less than 2%), although a high proportion of photographs were of insufficient quality for an exact evaluation. Anyhow, this datum indicates a low prevalence of the semi-stalked barnacle in SAG on the central coast of Ecuador, contrasting with the offshore common bottlenose dolphin which shows a prevalence of 42.3%, primarily on the dorsal fin (Félix and Castro, 2023), but only 4% in offshore *T. truncatus* of Peru (Van Waerebeek et al., 1990). The sampling period (because of possible seasonality), speed of travel and feeding ecology (cf. depth of diving) may all play an important role. Deep-diving Ziphiidae and *Globicephala* spp., for instance, do not carry *Xenobalanus* barnacles (KVW, unpublished data).

We recorded two cases of unusual barnacle infestation. The first case involved a calf with (reddish) stalked barnacles *Conchoderma auritum* in its mouth (Figure 9a), probably attached to exposed teeth due to a mandibular deviation or fracture. The second case was an immature dolphin that had an unusually high number (estimate n= 25) semi-stalked barnacles attached to its dorsal fin (Figure 9b). The animal appeared unhealthy and swam slowly, which may explain the unusual number and large size reached by the barnacles in this specimen. Additionally, an animal stranded in 2017 was found with five *X. globicipitis* barnacles along the trailing edge of the tail flukes.

Figure 9. Two extreme cases of SAG dolphins infested with the stalked barnacles *Conchoderma auritum* in the mouth of a calf (left) and the semi-stalked barnacle *X. globicipitis*: on the dorsal fin of an immature animal (right).

Behavioral Ecology

Except, perhaps, for a limited study at Gorgona Island (Valencia, 2006) of an indeterminate form, but probably SAG, the behavioral ecology in South America remains unstudied. As off California, habitat of SAG in Pacific South America is thought to be largely limited to neritic waters and in northern part of South America (Colombia, Ecuador) may appear partially sympatric with the offshore ecotype of *T. truncatus* (Van Waerebeek et al., 2017; Félix and Castro, 2023). However, competitive exclusion may force upon a parapatric distribution.

In Colombia, Herrera et al. (2011b) reported spotted dolphins in deep waters around Malpelo Island and also over the shelf, suggesting that both subspecies could be recorded in their surveys from mainland to Malpelo Island. At Gorgona Island, individuals are frequently sighted in small herds with an average group size of eight dolphins. Groups with small calves are observed year-round, suggesting that reproduction occurs continuously in the region (Capella et al., 2014). On the central coast of Ecuador SAG groups have been recorded in depths ranging from 10 to 718 m (mean 75.8 m, SD = 124), with 60% of the sightings at depths between 30 and 60 m and only 5.6% in waters deeper than 100 m (Figure 10). Since most sightings in Ecuador were made onboard whale-watching boats, there is a sampling bias towards coastal areas. In the southern part of Ecuador SAG has been recorded in the outer estuary of the Gulf of Guayaquil but not in the inner estuary where inshore type *T. truncatus* is resident (e.g. Félix, 1997), suggesting that SAG avoids brackish waters.

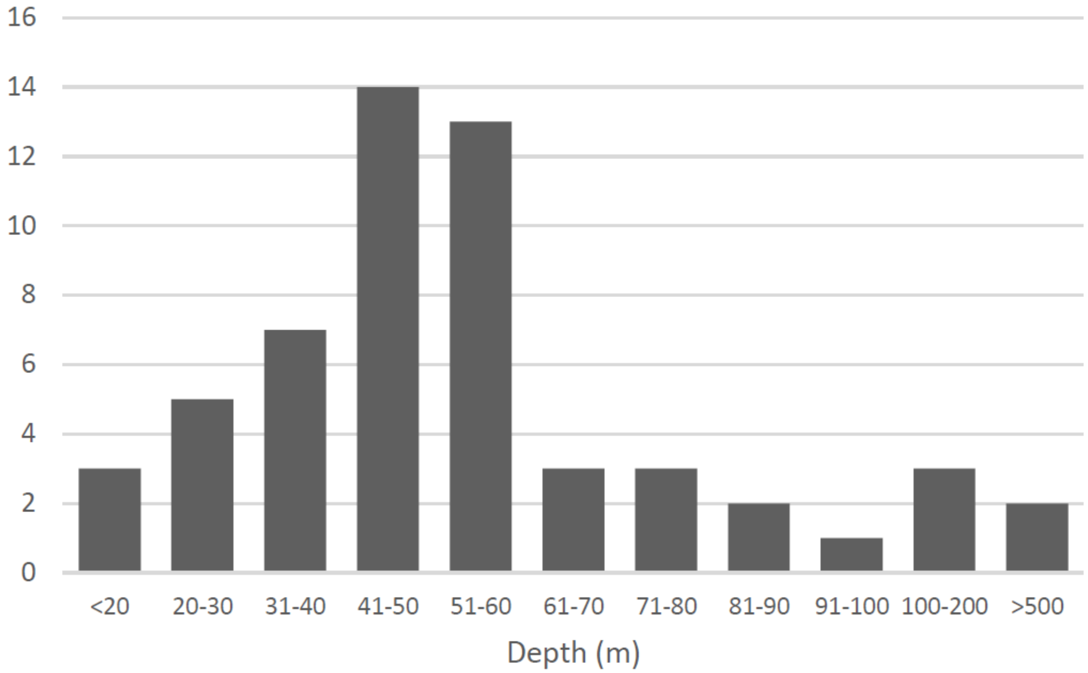

Figure 10. Frequency distribution of records of SAG in Ecuador according to depth (n=56).

Group size of SAG in central Ecuador varied widely from 3 to 500 (mean 121.22, SD=129.62, n= 52). (Figure 11). Most groups had 100 or fewer individuals. Large aggregations appeared to be integrated by several smaller units (50-100 individuals) that likely joined temporarily for feeding or social activities. High variability in group size has also been reported in other coastal areas in the Eastern Pacific (e.g. García and Dawson, 2003; Palacios & Salazar, 2002). Herrera et al. (2011b) reported significantly smaller group sizes around Malpelo Island (mean = 17.3, SD = 7.3, range = 8–30, n=6) compared to those recorded along the crossing route to the mainland (mean = 42.1, SD = 33.6, range = 3–100, n=14), suggesting spatial variation in social aggregation patterns consistent with niche separation.

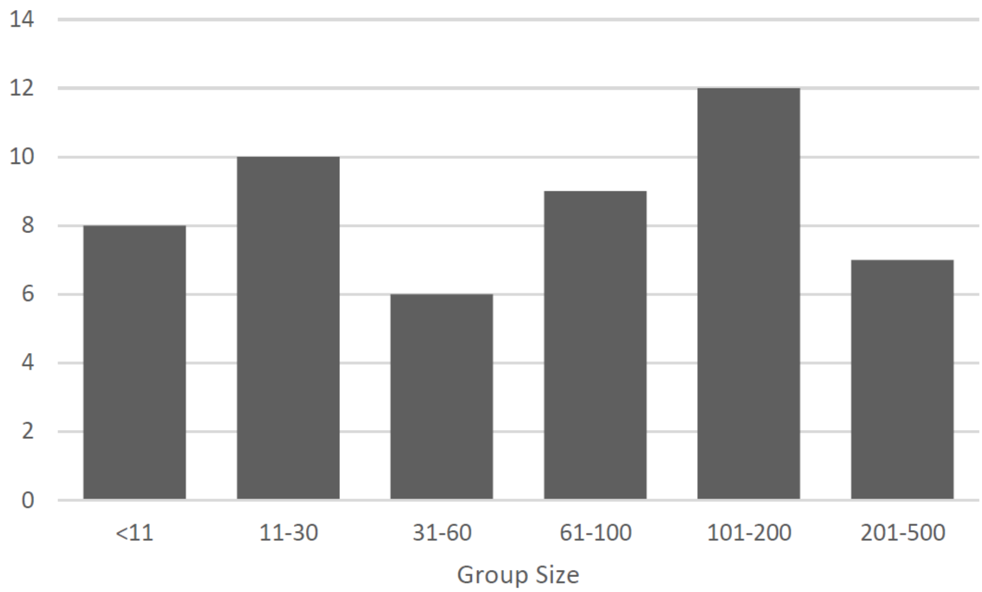

Figure 11. Frequency distribution of SAG group size (n=52).

SAG groups were also seen to be associated with other cetacean species in Ecuador on 14 occasions (Table 2): nine times with humpback whales (15.2 %), four with Bryde's whales (6.78%), and on one occasion with both humpback whales and offshore bottlenose dolphins (1.69%). Interactions with humpback whales appeared to be social, while Bryde's whales were typically linked to feeding activities. Interspecific associations between spotted dolphins and other species of cetaceans have been reported in Brazil (Rossi-Santos et al., 2009), Hawaii (Psarakos et al., 2003) and Galápagos (Palacios and Salazar, 2002). Further pelagic surveys could shed more light on SAG ecology, and in particular document interspecific relations.

Genetic Diversity and Population Structure

Two of the 29 samples from the coast of Ecuador did not amplify for mtDNA CR (Table S1). Haplotype diversity (*h*) was estimated at 0.8746 ± 0.0473, and nucleotide diversity (π) at 0.230550 ± 0.126309, showing that the population has high genetic diversity concordant with a large population. Tajima's D (-0.40581, $p = 0.327$) and Fu's Fs (-2.12380, $p = 0.2033$) provide no strong evidence of a recent evolutionary event in the population. Among the 27 sequences of the 405 bp mtDNA CR, 26 polymorphic sites were identified, revealing 14 haplotypes (Table 5). The nucleotide sequences were deposited in GenBank under accession numbers OQ867166–OQ867185 and PV131008–PV131014.

Table 5. Nucleotide and haplotype frequencies of the control region of *S. a. graffmani* from central Ecuador. Polymorphic sites and haplotype frequencies of the 405 bp mtDNA CR are shown. Sequence identity was assessed relative to the reference haplotype (HR; GenBank accession number NC_012051.1). Numbers in the first three rows indicate the positions of polymorphic sites. Dots (.) denote identity with HR.

Haplotype	**Polymorphic sites**																										**Haplotype frequency**
	1	2	5	7	8	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	
	6	6	1	9	8	0	3	3	4	6	7	2	3	4	4	5	5	6	6	7	1	5	5	7	7	9	
						4	4	6	9	5	5	7	0	1	7	1	9	4	5	2	1	2	5	2	3	3	
Hap_R	**C**	**T**	**T**	**T**	**G**	**T**	**G**	**A**	**T**	**T**	**A**	**T**	**A**	**T**	**A**	**C**	**T**	**T**	**T**	**A**	**C**	**C**	**T**	**A**	**C**	**A**	
Hap_1	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	.	.	G	8
Hap_2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	T	.	2

Hap_3	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	.	.	1
Hap_4	.	.	.	.	.	C	.	.	.	.	.	C	.	.	.	T	.	.	C	.	T	T	.	G	T	.	1
Hap_5	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	T	.	.	C	.	.	T	.	.	T	G	1
Hap_6	.	.	.	.	A	.	.	C	.	.	.	.	.	.	.	.	.	.	C	.	.	.	C	.	.	G	1
Hap_7	.	.	.	.	A	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	T	.	.	.	G	6
Hap_8	T	C	.	.	.	.	A	.	.	.	.	.	G	.	T	.	C	.	.	G	.	.	.	.	T	.	1
Hap_9	.	C	.	.	.	.	A	.	.	.	G	.	.	.	.	.	.	C	C	.	.	T	.	.	T	.	1
Hap_10	.	.	.	.	.	C	.	.	C	.	.	C	.	.	.	T	.	C	C	.	T	T	.	G	T	.	1
Hap_11	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	C	.	.	.	.	.	.	.	1
Hap_12	.	C	.	.	.	.	A	.	.	C	.	C	G	.	.	.	.	C	C	.	.	T	.	.	T	.	1
Hap_13	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	.	T	.	.	.	.	1
Hap_14	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	T	.	1

Of the 14 distinct haplotypes, six were unique (H1, H3, H4, H6, H11, and H13). Most of them (H3, H4, H6, H11, and H13) were identified in only one individual. The most common haplotypes were H1 and H7, found in 8 and 6 specimens, respectively. Eight haplotypes (H2, H5, H7, H8, H9, H10, H12, and H14) were previously reported in more than one location within the Eastern Tropical Pacific (ETP), Ecuador + Panama, California, and Costa Rica, indicating slight maternal genetic flow between these locations. However, as it was indicated earlier, it was not possible to distinguish between Ecuadorian and Panamanian sequences used for comparison. Haplotype H8 showed six mutational steps from H16, a haplotype from California, and H28 was identified as an offshore haplotype. H15 networked with distant localities, including Hawaii, ETP coastal regions, the Solomon Islands, and offshore stocks (Figure 12), suggesting it is one of the most ancestral haplotypes. Ecuadorian haplotypes are shared with at least one or two localities in the ETP and are primarily located at the periphery of the haplotype network, suggesting they are likely recent haplotypes. The haplotype network reveals the presence of unique haplotypes along the central coast of Ecuador and non-differentiated groups, indicating low genetic flow with other localities in the ETP and even lower connectivity with populations in the central and western Pacific (Figure 12).

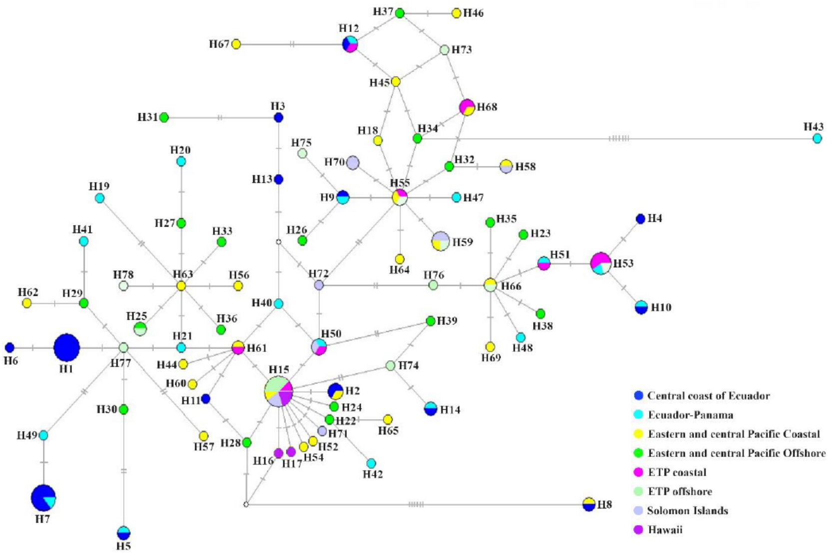

Figure 12. Median-joining network of *Stenella attenuata* mtDNA CR. Circle size represents the number of individuals sharing the same haplotype. Circles are colored based on the geographic regions indicated in the legend. The white circle represents a missing or intermediate haplotype. Branch length is proportional to the

number of mutational steps between haplotypes, with hatch marks indicating the total number of mutations. ETP: Eastern Tropical Pacific.

According to the phylogenetic analysis, the Ecuadorian dolphins were distributed across seven different clades, with most belonging to the three largest clades, while only one haplotype was found in each of the remaining four (Figure 13). The Ecuadorian sequences primarily group with those previously identified by Escorza-Treviño et al. (2005) and labelled Ecuador-Panama (all labelled as ECU in the phylogenetic tree). This pattern suggests a complex evolutionary history, possibly indicating substructures within the population or an ongoing evolutionary process. The presence of haplotypes in multiple clades may reflect high genetic diversity, likely influenced by dolphin migration between nearby geographic areas, facilitating haplotype exchange and contributing to the observed distribution.

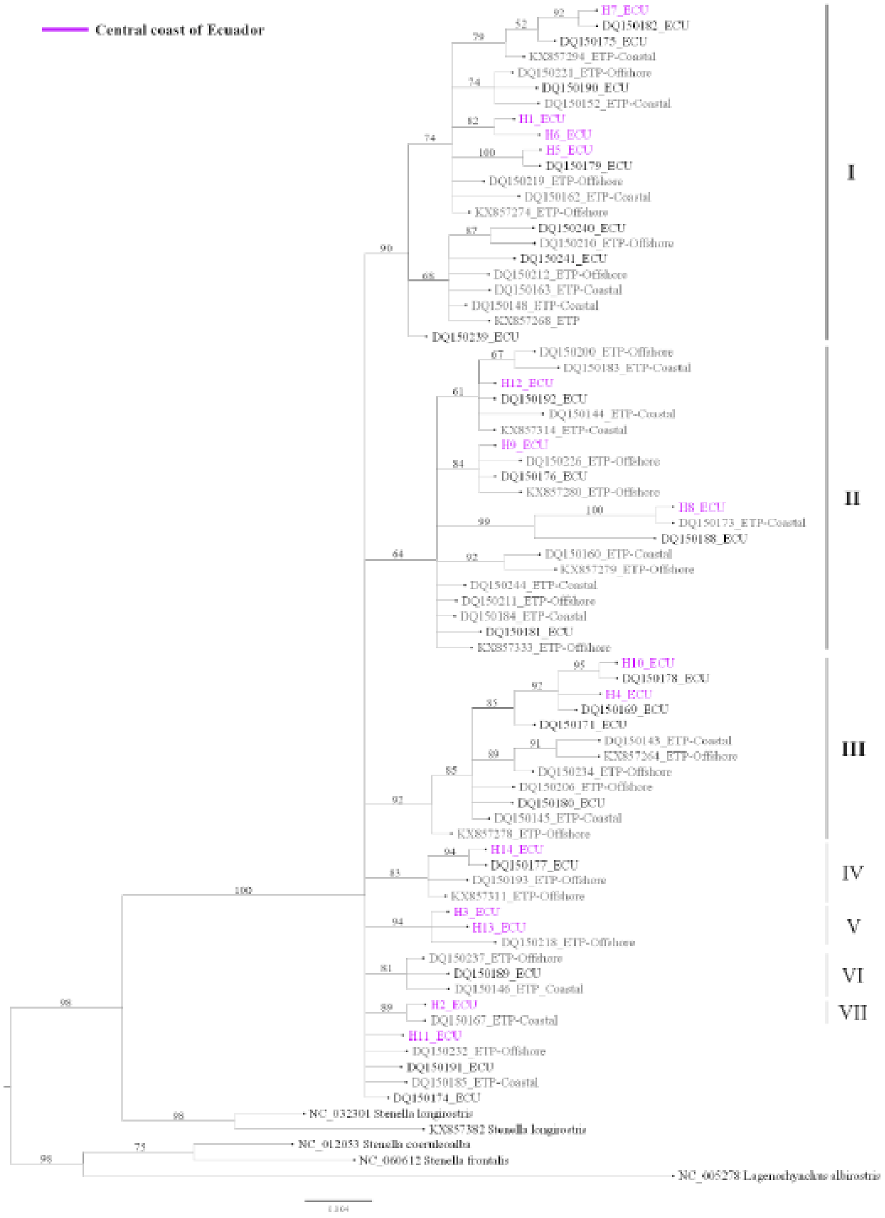

Figure 13. Bayesian phylogenetic tree of spotted dolphins mtDNA CR. Bayesian phylogenetic tree inferred from a 405 bp segment of mtDNA CR. Posterior probability values are shown above the main branches. Sequences

obtained from GenBank are labeled with accession numbers. The outgroup includes *Lagenorhynchus albirostris* (accession number NC_005278.1). Haplotypes representing sequences identified in the central coast of Ecuador (this study) are shown in violet. Ecuadorian sequences previously identified by Escorza-Treviño et al. (2005) are shown in black. ECU: Ecuador; ETP: Eastern Tropical Pacific.

Fisheries Interactions and Other Threats

Bycatches of SAG are well-documented in coastal fisheries, mainly in artisanal gillnet fisheries in Ecuador and Peru (Van Waerebeek and Reyes, 1994; Castro and Van Waerebeek, 2019; Félix and Samaniego, 1994; this paper), in the bottom-trawl fishery for shrimp off Panama (Justines, 1997; García et al., 2008), and by harpooning for bait in artisanal fisheries in Chocó, Colombia (Avila *et al.*, 2008; García et al., 2008). Of four Peruvian specimens, at least three had been killed in fisheries, one by harpooning. Of seven SAG specimens found stranded in Ecuador in 2009-2016, six (86%) bore evidence of net entanglement (Figure 14), underscoring the taxon's high vulnerability to fisheries pressure (Castro and Van Waerebeek, 2019). In Ecuador, Castro and Rosero (2010) documented two additional cases of bycatch in Machalilla National Park, on the central coast, and Félix et al. (2011) reported that two of eleven stranding records found in Ecuador were probably a product of bycatch and three were suspected collisions with boats. Data on bycatches in Colombia are lacking. However, a study on the interaction between cetaceans and purse-seine fisheries targeting small pelagic fish found no evidence of interaction in 18 fishing sets conducted along the 1,300 km of the Colombian Pacific coast (Herrera and Flórez-González, 2018). No other threats have been identified, but dedicated field research is needed. For instance, potentially high contaminant loads in SAG, linked to neritic habitats, have not been studied.

Figure 14. Large-bodied, heavily spotted coastal form *Stenella attenuata graffmani* found stranded at Barbasquillo, Manta, Ecuador, on 07/12/2016. Tail flukes were necrotized from net entanglement. Photo MAE- PWF.

Conclusions

Available evidence demonstrates that the spotted dolphins documented either free-ranging, taken in small-scale fisheries or stranded along the coasts of western South America, belong to *S. a. graffmani,* bar one dubious case from Puerto López, Ecuador.

We determine the known austral range of *S. a. graffmani* to the southern border of the Lima Department, at 13°02'S 76°29'W, which is 1,870 km and 1,360 km farther southeast than previously reported austral ranges, *i.e.* respectively the southern Colombia border (Perrin, 2018) and Playas, Ecuador (Chiluiza *et al*., 1998). We argued that the Peruvian southern range extension into the Lima Department was temporally related to a strong *El Niño* warm water intrusion into the coastal Humboldt Current Ecosystem which is concordant with recent records in northern Peru (Cortez-Casamayor et al., 2024). Abundant data from sighting surveys, strandings and bycatches support the notion that SAG is absent from southern Peru and Chile. The habitual southern range in non-El Niño years includes neritic waters off Ecuador's Guayas and Manabí provinces (01°-02°S), perhaps including also Tumbes and Piura departments of northern Peru, in the months with higher SST. North of Ecuador, indications are of a continuous coastal distribution throughout the tropical waters of Colombia and Central America, into Baja California. Habitat of *S. a. graffmani* is thought to be largely limited to neritic waters and in Peru may be sympatric with the coastal ecotype of common bottlenose dolphin (Van Waerebeek et al., 1990, 2017), while off central Ecuador sympatry occurs with the offshore *T. truncatus*.

Phylogenetic analysis of mt-DNA control region (602 and 727 bp) of 29 Ecuadorian SAG samples confirms the presence of population structure, consistent with previous findings (Escorza-Treviño et al., 2005) and indicate limited gene flow with adjacent (northern) stocks. The SAG southern stock currently exhibits high genetic diversity and represents the most abundant neritic cetacean along the Ecuadorian coast and likely along the Colombian coast as well. Nevertheless, small-scale gillnet fisheries pose a persistent bycatch threat to the subspecies across its entire distribution range.

It is recommended that any spotted dolphin specimens becoming available in the study region be fully necropsied and sampled as to increase the currently unusually scarce life history record. All skeletal material, including postcranials, should also be collected.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

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Conflicts of Interest: The authors declare that no conflict of interest exists.

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