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Recurrent juvenile stranding of the porbeagle shark *Lamna nasus* along the South West Atlantic coast

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Abstract: Strandings of juvenile porbeagles are recurrent in the South West Atlantic (SWA). We provide new biological information and explore to which haplogroups the juveniles may belong. Fourteen stranding events occurred between May 2009 and May 2022 on porbeagle in the beaches of the SWA Argentine coast were identified. Based on a 2019 beached specimen, total length, 83 morphometric measures, and the parasites diversity were provided, as well as the COI gene sequences, derived from DNA extraction from muscle tissue, followed by PCR. The sequence matched *Lamna nasus* (98.76% – 100.00%; n=100), using the Barcode of Life Data System identification. Molecular data show a great genetic diversity in COI sequences, especially between northern and southern hemisphere samples, in accordance with previous studies. In addition, juveniles recorded in northern Argentine coastal waters differ in COI nucleotide sequences and are located in different clusters in the maximum likelihood (ML) analysis. The haplotype network built showed a star-shaped topology and, as the ML tree, revealed the existence of three genetically distinct clusters. A partition of the genetic variation into Southern Hemisphere and Northern Hemisphere groups was observed.

Key words: Beaching, genetic differentiation, Lamnidae, parasites

Resumen: Varamiento recurrente de juveniles de marrajo sardinero *Lamna nasus* en la costa del Océano Atlántico Sudoccidental. Los varamientos de juveniles de marrajo sardinero son recurrentes en el Atlántico Sudoccidental (ASO). Aportamos nueva información biológica y exploramos a qué haplogrupos pueden pertenecer los juveniles. Se identificaron 14 eventos de varamiento de marrajo sardinero ocurridos entre mayo de 2009 y mayo de 2022 en las playas de la costa argentina del ASO. A partir de un ejemplar varado en 2019, se proporcionó la longitud total, 83 medidas morfométricas, y la diversidad de parásitos, así como secuencias del gen COI provenientes de la extracción de ADN del tejido muscular, seguida de PCR. La secuencia coincidió con *Lamna nasus* (98,76% - 100,00%; n=100), utilizando la identificación del Barcode of Life Data System. Los datos moleculares muestran una gran diversidad genética en las secuencias COI, especialmente entre las muestras del hemisferio norte y las del hemisferio sur, de acuerdo con estudios anteriores. Además, los juveniles registrados en aguas costeras del norte de Argentina difieren en las secuencias nucleotídicas COI y se localizan en clusters diferentes en el análisis de máxima verosimilitud (ML). La red de haplotipos construida mostró una topología en forma de estrella y, al igual que el árbol ML, reveló la existencia de tres clusters genéticamente distintos. Se observó una partición de la variación genética en grupos del hemisferio sur y del hemisferio norte.

Palabras clave: Varamiento, diferenciación genética, Lamnidae, parásitos

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INTRODUCTION

There is agreement that the family Lamnidae comprises three recognised genera, *Isurus* Rafinesque, 1810, *Lamna* Cuvier, 1817, and *Carcharodon* Smith, 1838, all of which encompass large sharks with pointed snouts and spindle-shaped bodies, long mouths –with large blade-like teeth– and long gill slits. The pectoral fins of these sharks are long and the dorsal fins are high, whereas the second dorsal fins as well as their small anal fins, are pivoting. The presence of large lateral keels and prominent precaudal pits in the caudal peduncle are characteristic, as well as their caudal fins' lunar shape (Compagno, 2002).

Sharks of the genus *Lamna* are oceanic sharks, abundant in the cold areas of the North and South Pacific and Atlantic Oceans. Towards the end of the 20th century, the specific composition of the genus *Lamna* was reduced to only two species, the salmon shark *Lamna ditropis* Hubbs & Follett, 1947, and the porbeagle shark *Lamna nasus* (Bonnaterre, 1788), while *L. philippi* (which is found off the coast of Chile) and *L. whitleyi* (found off the waters of New Zealand and Australia), were considered synonyms for *L. nasus* (Compagno, 2002; Stevens *et al.,* 1983).

The porbeagle shark, listed as Vulnerable by the IUCN (Rigby *et al*., 2019), is a top predator with amphi-temperate, coastal, and oceanic distribution. This shark inhabits the cold temperate pelagic zones of the North Atlantic, and a wide circum-global band of temperate and cold waters in the Southern Hemisphere formed by the Atlantic, Indian and Pacific Oceans, as well as subantarctic waters off the South Georgia and Kerguelen Islands (Compagno, 2002). This wide geographical distribution is the result of its ability to maintain body temperature above sea temperature, which allows it to inhabit cold waters (Camhi *et al*., 2008), maintaining a body temperature of up to 16 °C higher than the temperature of the sea (Goldman *et al*., 2004). It is frequently caught in cold and temperate waters, with a preferred temperature range between 5 °C and 10 °C. The species is mainly found in the open ocean and on continental shelves, from the surface to depths of 200 m. Although there are reports of its presence between 305 and 700 m and a maximum of up to 1360 m, it has also been recorded in coastal areas (Lucifora & Menni, 1998; Compagno, 2002; Francis *et al*., 2008; Campana *et al*., 2010).

The study of the occurrence of stranding in Lamnidae is not very balanced. In the first global assessment of shark stranding, Wosnick *et al*. (2022) reported that, of the 3150 individual reports analysed, only 412 were Lamnidae, with 403 *L. ditropis* and only 10 *L. nasus*. In the literature, only isolated records exist for porbeagle sharks (Quigley & Carney, 2013; van der Vyver *et al*., 2015; O'Reilly & Hantke, 2020), whereas for salmon sharks, attempts have been made to address the problem more comprehensively given their proportions. Carlisle *et al*. (2015) associated the recurrence of salmon shark stranding –which has been documented since the 19th century– with abrupt temperature changes in the environment due to coastal upwelling events: these events cause stress in juvenile salmon sharks, leading to bacterial infections that would be the cause of stranding (Schaffer *et al*., 2013; Carlisle *et al*., 2015; Martinez-Steele *et al*., 2018).

In the South West Atlantic (SWA), porbeagle distribution ranges from southern Brazil (26°45´S; Nakaya, 1971; Sadowsky *et al*., 1985; Waessle, 2007) to southern Argentina (57 °S; Nakaya, 1971; Waessle, 2007). Brazilian and Uruguayan reports refer that *L. nasus* is captured by the longline fleet with a low frequency (Montealegre-Quijano *et al*., 2007; Soto & Montealegre-Quijano, 2012) and captures have decreased in the last 12 years (Domingo, 2000; Domingo *et al*., 2002; Pons & Domingo, 2010). In another study, Forselledo (2012) recorded a higher occurrence and a higher catch per unit effort (CPUE) of *L. nasus* between 20–45 °S during the winter and spring months, with a bimodal size structure made up of juvenile and adult individuals. The sex ratio (male:female) throughout the study period was 1.95:1, but autumn and winter were the seasons where the sex ratio was statistically significant. Finally, in the southern extreme of the SWA, the highest abundances of *L. nasus* were observed during summer and autumn, coinciding with the time when females greater than 180 cm fork length predominate in the area (Waessle & Cortés, 2011; Cortés & Waessle, 2017), many of which carried embryos in different development stages (Waessle, unpublished data). The seasonal distribution of *L. nasus* is characterised by marked latitudinal migration, with aggregations observed in high latitudes during the summer and autumn months, and aggregations in low latitudes during winter (Yatsu, 1995; Francis & Stevens, 2000). In the SWA, studies with longline fleets off Rio Grande (33 °S – 35 °W), southern Brazil, have shown a higher occurrence during spring, associated with the convergence of the subtropical current, with high CPUE values for juveniles of *L. nasus*. The area has been reported as a breeding ground for the species in the SWA (Montealegre-Quijano *et al.*, 2007; Soto & Montealegre-Quijano, 2012).

In the SWA, there are two different kinds of sources for the reports of parasitological studies of porbeagle, both scarce. One source bases its data on opportunistic sampling of accidental captures from strandings of these large sharks (Arquez *et al.*, 1986; Lucifora & Menni, 1998), while the other obtains information from bycatch of longline and trawl fisheries in the SWA (Randhawa & Brickle, 2011). These latter authors investigated the trophic relationships of the porbeagle involved in the transmission of marine tapeworms in the SWA.

From the molecular analysis carried out by Mabragaña *et al.* (2015) on a specimen of *L. nasus* found dead on the beach of Chapadmalal (Buenos Aires province, Argentina) and its subsequent comparison with sequences available in the Barcode of Life Data System (BOLD) library, structuring in COI sequences was detected. These authors recognised three main clusters of closely related haplotypes. One of these clusters contains specimens exclusively from the Northern Hemisphere (NH), while the other two correspond to specimens from the Southern Hemisphere (SH) and both contain specimens from South Africa, New Zealand, Chile and Islas Malvinas. They were able to verify that there are no shared haplotypes between specimens from both hemispheres. Finally, the authors mentioned above assigned the haplotype studied to one of these two clusters of SH (Mabragaña *et al.*, 2015). Two well-defined clusters in the SH were also suggested by González *et al.* (2020), analysing the population genetic structure of *L. nasus* in the South East Pacific (SEP) and at a global scale.

In this paper, we review the historical records of local stranding of *L. nasus*, as well as reports on a series of recent beaching events of juvenile porbeagle sharks. Finally, we provide new insights about the parasites of this species in the SWA and its variability at COI level.

MATERIAL AND METHODS

The collection and verification of information on stranding in *Lamna nasus* was heterogeneous. In some cases, various sources of written and online media were consulted, as well as reports from fishermen who provided information and photographs. In others, it was possible to review the body and/or recover it for study.

For the estimation of sexual maturity, the fork lengths (FL) in Table 1 were obtained by retrocalculation, according to Francis & Duffy (2005; $FL = -6.943 + 0.893\ TL_{nat}$). Then, the values of FL obtained were contrasted with the ranges of sexual maturity presented by Francis *et al.* (2008).

In a female beached near Necochea in May 2019, total length (TL) and 83 other morphometric characters were measured (Table 2). During the necropsy, the body surface, including the nasal *fossae*, buccal cavity and fins, as well as the branchial chambers, and body cavity were visually inspected for ectoparasites. The viscera (stomach, spiral valve, heart, liver, gonads and mesenteries) were removed and examined with the aid of a Leica WILD MZ 8 stereomicroscope binocular. Metazoan parasites were collected and preserved according to a standardised protocol (Pritchard & Kruse, 1982; Berland, 1984). Temporary mounts of each specimen were prepared to ensure an accurate identification of the parasites. Since the *L. nasus* specimen had been frozen, the structures that allow the correct identification were deteriorated, particularly in tapeworms. Nevertheless, all parasites were identified at the lowest possible taxa, following the works of Schmidt (1986) and Palm (2004) for Cestodes, and Gibbons (2010) for Nematodes.

A sample of muscle tissue was excised from the specimen for genetic analysis and preserved in 96% ethanol at -20 °C. DNA extraction, polymerase chain reaction (PCR), and sequencing of cytochrome oxidase subunit I (COI) genes were performed following standard DNA barcoding protocols (Ivanova *et al.*, 2006) coupled with primers and primer cocktails developed for fishes (Ward *et al.*, 2005; Ivanova *et al.*, 2007). DNA extraction and amplification were performed at the Argentine International Barcode of Life Laboratory (IIMyC, CONICET, Mar del Plata, Argentina). A 652-base pair amplicon from the 5´ region of the mitochondrial COI gene was bidirectionally sequenced in MACROGEN (Seoul, Korea) (GenBank accession number in process).

Using the library of sequences available in BOLD (Barcode of Life Data Systems), the closest matches to our DNA sequences were obtained. In addition, the relative placement of our sequence in the lineage cluster, or Barcode Index Number (BIN) assigned in BOLD, was assessed. BIN analysis clusters barcode sequences algorithmically to create Operational Taxonomic

Table 1. *Lamna nasus* juvenile stranding events in the Southwest Atlantic Ocean between 2009 and 2022. Asterisk indicates that the TL is over the range of TL50% of maturity. Full videos of the strandings are available for: 1. https://www.youtube.com/watch?v=goTvNx8u6Fs; 2. https://www.youtube.com/watch?v=t2h0EDrE9o4; 3. https://www.facebook.com/watch/?v=350469655823209; 4. https://www.youtube.com/watch?v=57V_Jj87p1I

Year	Date	Locality	Lat	Long	Find	Condition	TL (m)	Sex
2009	29 May	Chapadmalal	-38.196	-57.672	Beached	Dead	~1.30	M
2009	15 June	Necochea	-38.350	-58.430	Beached	Dead	1.00	?
2012	06 September	Mar del Plata	-38.007	-57.333	Beached	Alive	–	?
2015	20 July	South of Puerto Visser	-45.433	-67.149	Beached	Dead	1.10	?
2016	16 May	Playa Unión	-43.263	-64.986	Beached	Dead	1.66*	M
2016	16 November	Mar del Plata	-38.034	-57.728	Beached	Alive 1	1.50–2.00*	M
2017	22 January	North of Puerto Visser	-45.382	-67.095	Beached	Dead	1.70	F
2018	29 May	Bajo de los Huesos	-43.183	-64.834	Beached	Dead	1.85*	M
2019	13 January	Santa Clara del Mar	-37.845	-57.503	Sight	Alive 2	~2.00*	?
2019	14 May	Necochea	-38.656	-58.944	Beached	Dead	1.28	F
2019	17 May	Pinamar	-37.122	-56.858	Captured	Alive 3	–	F
2019	16 December	Cabo Domingo	-53.688	-67.847	Beached	Dead 4	~1.50	M
2020	07 July	Claromecó	-38.874	-60.172	Beached	Dead	~1.00	?
2022	14 May	Balneario Marisol	-38.550	-60.320	Beached	Dead	~1.10	F

Units (OTUs) that closely reflect species groupings (see boldsystems.org and Ratnasingham & Hebert, 2013 for further details). Finally, the publicly available COI sequences of *L. nasus* (Wong *et al.*, 2009) were downloaded and compared with the sequence of our specimen. Sequence divergences were calculated using the Kimura two-parameter (K2P) distance model (Kimura, 1980). A best-fit model of nucleotide evolution was estimated using Akaike information criterion in MEGA X and was determined to be Kimura two-parameter (K2P). A Maximum Likelihood (ML) approach was carried out for cluster analyses using K2P, and 500 bootstrap pseudoreplicates were conducted to estimate node support values. A sequence of *L. ditropis* was used as the outgroup. Finally, we examined the COI sequences of the two records of *L. nasus* from northern Argentina for diagnostic characters using MEGA v6.0 (Tamura *et al.*, 2013). Given that Mabragaña *et al.* (2015) showed evidence of three distinct clusters within *L. nasus* using COI sequences, samples were grouped by the mtDNA cluster to which the COI haplotype belongs. Basic sequence properties and polymorphisms such as nucleotide (π) and haplotype diversity (h) were examined with DNASP 5.10 (Librado & Rozas, 2009). A phylogenetic network based on differences in nucleotide sequences was built according to the median joining method using the Network software (Bandelt *et al.*, 1999).

RESULTS

The collection of porbeagle stranding data dates back to 2009. Since then, a total of 14 specimens have been positively identified as *Lamna nasus* by us or by shark specialists' colleagues. Table 1 and Figure 1 report on all recent recognised events recorded in beaches of the Argentine coast between 2009–2022.

The specimen beached near Necochea in May 2019 is a juvenile female of 1280 mm Total Length (TL), without evident gonadal development. Some morphometric measurements (in mm and as a proportion of the TL) are provided in Table 2.

In the specimen beached near Necochea in May 2019, the following metazoan parasites were recorded: anisakid nematode larvae belonging to the genera *Anisakis* Dujardin, 1845 (n=72) and *Contracaecum* Railliet & Henry, 1913 (n=2). Moreover, individuals of nematodes belonging to the Family Spiruridae Oerley, 1885 (n=13), were found in the stomach wall. Furthermore, adult cestodes belonging to the genus *Dinobothrium* van Beneden, 1889 (Tetraphyllidea: Gastrolecithidae) (n=10) and *Clistobothrium* cf. *montaukensis* Rhunke, 1993 (Phyllobothriidea: Phyllobothriidae) (n=3) were recorded within the spiral valve, while *Hepatoxylum* cf. *trichiuri* (Holten, 1802) Dollfus, 1942 (Trypanorhyncha: Sphyriocephalidae) (n=3) was found in both the stomach content and the spiral valve.

Table 2. Eighty-four morphometric measurements (in mm) and as a proportion (%) of Total Length taken on the specimen of *Lamna nasus* from Punta Florida beach (Quequén, Argentina).

Measurements	Value	%	Measurements	Value	%
Total length	1.280	100.0	First dorsal-fin base	151	11.8
Fork length	1.112	86.9	First dorsal-fin height	170	13.3
Precaudal-fin length	990	77.3	First dorsal-fin inner margin	53	4.1
Pre-second dorsal-fin length	871	68.0	First dorsal-fin posterior margin	181	14.1
Pre-first dorsal-fin length	416	32.5	Second dorsal-fin length	62	4.8
Head length	363	28.4	Second dorsal-fin anterior margin	34	2.7
Prebranchial length	235	18.4	Second dorsal-fin base	23	1.8
Preorbital length	74	5.8	Second dorsal-fin height	20	1.6
Prepectoral-fin length	315	24.6	Second dorsal-fin inner margin	39	3.0
Prepelvic-fin length	675	52.7	Second dorsal-fin posterior margin	29	2.3
Preanal-fin length	854	66.7	Pelvic fin length	97	7.6
Interdorsal space	342	26.7	Pelvic fin anterior margin	71	5.5
Dorsal caudal-fin space	94	7.3	Pelvic fin base	71	5.5
Pectoral-fin pelvic-fin space	293	22.9	Pelvic fin height	60	4.7
Pelvic-fin anal-fin space	131	10.2	Pelvic fin inner margin	42	3.3
Anal-fin caudal-fin space	108	8.4	Pelvic fin posterior margin	73	5.7
Pelvic-fin caudal-fin space	252	19.7	Anal-fin length	66	5.2
Vent caudal fin length	427	33.4	Anal-fin anterior margin	45	3.5
Prenarial length	89	7.0	Anal-fin base	29	2.3
Preoral length	101	7.9	Anal-fin height	25	2.0
Eye length	31	2.4	Anal-fin inner margin	47	3.7
Eye height	34	2.7	Anal-fin Posterior margin	33	2.6
Intergill length	106	8.3	Head height	220	17.2
First gill height	100	7.8	Trunk height	231	18.0
Fifth gill height	119	9.3	Abdomen height	212	16.6
Pectoral-fin anterior margin	271	21.2	Tail height	136	10.6
Pectoral-fin base	91	7.1	Caudal-fin peduncule height	37	2.9
Pectoral-fin inner margin	72	5.6	First dorsal-fin midpoint pectoral-fin insert.	110	8.6
Pectoral-fin posterior margin	217	17.0	First dorsal-fin midpoint pelvic-fin origin	191	14.9
Pectoral-fin height	230	18.0	Pelvic-fin midpoint first dorsal-fin insertion	172	13.4
Pectoral-fin length	148	11.6	Pelvic-fin midpoint second dorsal-fin origin	169	13.2
Dorsal caudal-fin margin	344	26.9	Mouth length	69	5.4
Preventral caudal-fin margin	255	19.9	Mouth width	111	8.7
Upper postventral caudal-fin margin	198	15.5	Nostril width	15	1.2
Lower postventral caudal-fin margin	194	15.2	Internarial space	48	3.8
Caudal-fin fork width	115	9.0	Anterior nasal-flap length	4	0.3
Caudal-fin fork length	141	11.0	Interorbital space	78	6.1
Subterminal caudal-fin margin	11	0.9	Head width	223	17.4
Terminal-fin margin	72	5.6	Trunk width	263	20.5
Terminal-fin lobe	75	5.9	Abdomen width	241	18.8
First dorsal-fin length	200	15.6	Tail width	148	11.6
First dorsal-fin anterior margin	205	16.0	Caudal-fin peduncle width	80	6.3

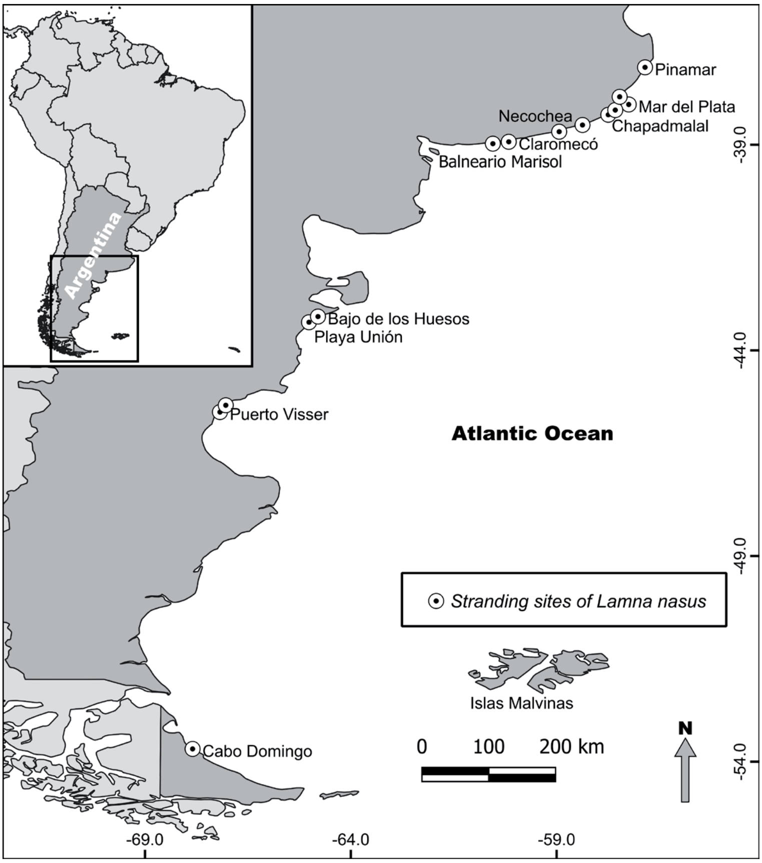

Fig. 1. Recent stranding sites (dots) in the SWA of porbeagle *Lamna nasus* from 2009 to 2022.

The analysis using the BOLD identification system showed that the sequences obtained from the specimen of *L. nasus* beached near Necochea matched *L. nasus* with a similarity range of 98.76%–100% (n=100) within the BIN BOLD:AAA3577, where all *L. nasus* are included. Interestingly, two specimens of *L. nasus* from northern Argentina (LNQ519 and FARG 664-09) are located in different clusters (Fig. 2A). The specimen LNQ519 showed a much lower genetic distance (GD) from specimens collected in the SH that belong to the same cluster (GD = 0–0.16%), than from those from the other SH clusters (GD = 0.94–1.41%) or the NH cluster (GD = 0.94–1.41%).

The GD between the two specimens collected in the coastal waters of Argentina was relatively high (1.094%). Both sequences differed in several nucleotic diagnostic characters (Table 3). The 85 sequences of *L. nasus* analysed contained 23 segregating sites. Genetic variability was high for the pooled samples, displaying an overall haplotype (h) and nucleotic (π) diversity of 0.836 and 0.00749, respectively. The h ranged between 0.8366 in NH and 0.641 in SH, while π ranged from 0.00763 (NH) to 0.00567 (SH) (Table 4).

The haplotype network showed a star-shaped topology and revealed a similar pattern as the ML tree (Fig. 2B). In total, 23 haplotypes (Hp) were identified as Hp1 to Hp23. The most frequent haplotypes were H17 (SH, represented by 31 individuals), H1 (NH, represented by 9 individuals) and H10 (SH, represented by 8 individuals). The number of private haplotypes was high in each hemisphere (H1 to H9 in NH, H10 to H23 in SH). The SH haplotypes exhibited two main haplogroups, which corresponded to two distinct clusters of the ML tree (Figs. 2A and 2B).

DISCUSSION

The first record of the porbeagle shark *Lamna nasus* in the Argentine SWA is attributable to Lahille (1928) as *Lamia nasus*. Since then, there have been two major types of records, some associated with fishing surveys and fisheries that

Table 3. Nucleotide position for each diagnostic character of sequences of the two specimens of *Lamna nasus* collected in coastal waters of Buenos Aires province, Argentina.

	#79	#85	#169	#214	#313	#385	#625
LNQ519	G	C	G	C	A	A	A
FARG664-09	A	T	A	T	G	G	G

Table 4. Genetic diversity of *Lamna nasus* based on a 594 base pair long fragment of the cytochrome oxidase I mitochondrial DNA locus per species and population; h: haplotype diversity, π: nucleotide diversity. SH = southern hemisphere, NH = northern hemisphere.

Area	**Sequences**	**Haplotypes**	**Private haplotypes**	***H***	π
	85	23	-	0.84	0.00752
NH	31	9	9	0.8366 +/-0.0369	0.00763 +/- 0.0497
SH	54	14	14	0.641 +/-0.071	0.00563 +/- 0.0007

occur in the area (Gneri *et al.*, 1967; Nakaya, 1971; Menni & Gosztonyi, 1977; Arquez *et al.*, 1986; Figueroa, 1997; Forselledo, 2012; Cortés & Waessle, 2017), and others associated with the presence of porbeagle sharks caught or found dead on the coast (Lahille, 1928; Lucifora & Menni, 1998; Mabragaña *et al.*, 2015; present work). In another record from Puerto Quequén, we were unable to establish if its origin was fishing or stranding (Siccardi in Springer & Garrick, 1964).

Five potential causes are analysed by Wosnick *et al.* (2022) as possible factors that trigger shark stranding:

1. Infectious disease. While several informal records of porbeagle stranding can be found online (Supporting Information, Appendix A), only a few have been reported in the scientific literature. Quigley & Carney (2013) suggested the hypothesis that the specimen found beached at Crookhaven Harbour (Ireland) may have been chased on the beach by a herd of Bottlenose Dolphins (*Tursiops truncatus* Montagu, 1821). However, in a recent work, Retallack *et al.* (2019) state that they found the ciliated protozoan pathogen *Miamiensis avidus* Thompson & Moewus, 1964 in the nervous central system in a sample of hundreds of leopard sharks (*Triakis semifasciata* Girard, 1854) stranded off the coast of San Francisco Bay, California, giving as a hypothesis for the massive stranding of sharks an infection by this parasite. Furthermore, for *L. ditropis* it has been postulated that stranding could be associated with infection by *Carnobacterium maltaromaticum*-like bacteria (Schaffer *et al.*, 2013; Carlisle *et al.*, 2015; Martinez-Steele *et al.*, 2018). Given this evidence, the possible infection of the central nervous system of SWA porbeagle sharks should be taken into account as a hypothesis in future work.

2. Abrupt environmental alterations. The seasonality and size structure observed by different authors in *L. nasus* in the SWA (Waessle, 2007; Forselledo, 2012; Cortés & Waessle, 2017) would indicate that the distribution pattern of this species in the SWA seems to respond to that observed for the same species in the North Atlantic (Campana *et al.*, 2010). There the breeding areas would be found in the more temperate zones, while the adult feeding areas would be found in the colder zones. However, the offshore circulation off the coast of Argentina is dominated by an opposing flow of two currents: the Brazil (subtropical) current further east of the coast and the Malvinas (subantarctic) current close to the coast. Both currents converge around 36 °S in an area known as the Brazil/Malvinas Confluence, where the two flows turn offshore in a series of wide meanders (Acha *et al.*, 2004). Thus, it is interesting to note that although the strandings of juveniles reported in this work were found along the coast from southern Patagonia (Magellan Zoogeographic Province) to the southern limit of the zoogeographic area known as the Bonaerense District of the Argentine Zoogeographic Province (Balech, 1964; López, 1964; Boltovskoy, 1981; Cousseau *et al.*, 2020; Sabadin *et al.*, 2020), the area covered by these strandings would be more influenced by the cold Malvinas current than by the warm Brazilian current —the current with which the species' breeding areas would be more associated—, suggesting that the stranded specimens would be in waters outside their comfort zone.

3. Negative interaction with fisheries and 4. Other traumata. Other possible cause of the stranding to examine is the negative interaction

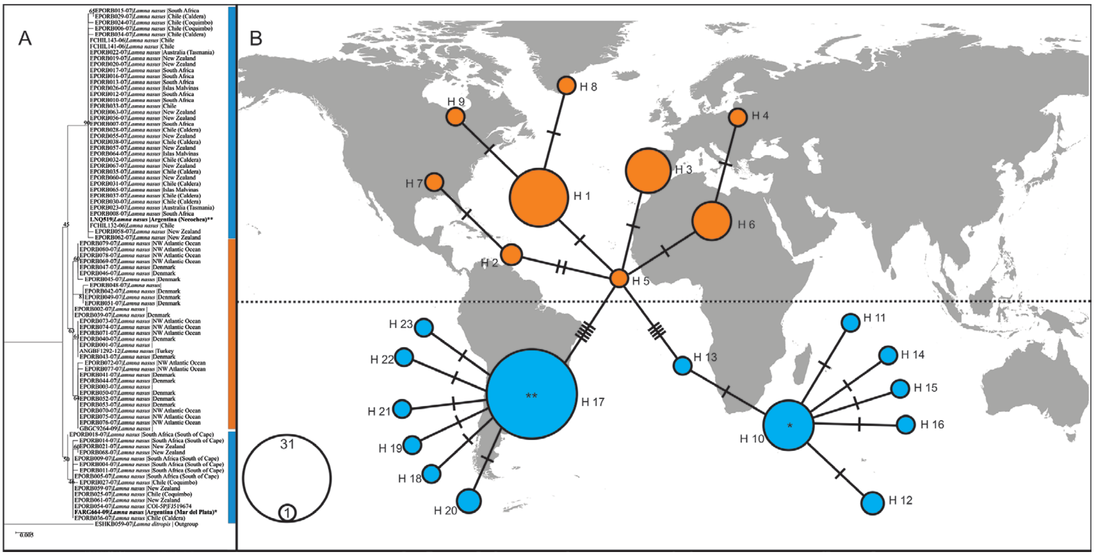

Fig. 2. (A) Maximum likelihood tree based on K2P distances of public barcode records of *Lamna nasus* from BOLD. Number at nodes represent bootstrap values. SH = southern hemisphere, NH = northern hemisphere. In bold, specimens collected in coastal Argentine waters. Samples from SH (light blue) and NH (orange). (B) Median-joining network of COI haplotypes for *Lamna nasus*. Haplotypes are represented by circles with size proportional to frequency in the total sample. Specimens collected in coastal Argentine waters (*: FARG664-09 and **: LNQ519).

with fisheries, and that the specimens have been discarded by fishing vessels. Given that *L. nasus* is included in the Appendix II of the Convention on International Trade in Endangered Species (CITES), the specimens may be dropped into the water to avoid fines. The fishing fleet operating in one of the areas of occurrence of this species in the SWA has observers on board to record these catches. Although in the study of porbeagle bycatch in the surimi fleet, Cortés & Waessle (2017) do not mention whether they are landed and marketed, they did record and estimate 426 t and 489 t respectively of porbeagle bycatch between 2006 and 2012. Their results show that the species was an important part of the bycatch of that fleet prior to the listing of the species in CITES Appendix II. However, the species reported in Argentina's exports between 2014 and 2021 do not include *L. nasus* (https://www.magyp.gob.ar/sitio/areas/pesca_maritima/informes/economia/index.php; 03/04/2023).

On the other hand, approximately 28.6% (4 of 14, Table 1) of the stranded porbeagles that we recorded came to shore alive, with no signs of entanglement or injury. Moreover, in the specimens examined that were in a good state of conservation, no signs of manipulation by fishermen were detected (neither signs of entanglement nor of hooks). It is also difficult to establish whether the succession of strandings here exposed can be explained by chasing by marine mammals.

5. Foraging sandbanks and tide pools. In some of the cases analysed, where the animal reached the coast alive, it cannot be ruled out that it had done so in pursuit of a shoal (the specimen reported by Lucifora & Menni (1998) had bitten a hook at the mouth of the Mar Chiquita lagoon), although this cannot be assumed to be the cause of stranding either. In the few cases where necropsy could be performed on the specimens, the stomachs were found to be empty.

Morphometric measurements published in works on the species of SWA are based on individual specimens (Lahille, 1928; Nakaya, 1971; Arquez *et al.*, 1986; Menni & Gosztonyi, 1977). Nakaya (1971) compares the proportional morphometric measurements of a single specimen of *L. nasus* from SWA with the mean measurements of three specimens of *L. ditropis* from the North Pacific Ocean, arguing that the specimens of *L. nasus* with which he could compare are too small. In the present work, although the proportional values of the morphometric measurements collected were consistent with the values published in the cited literature, being all single specimens, they do not allow us to perform any statistical comparison between specimens that would allow us to draw conclusions from them. Furthermore, for the same reason argued by Nakaya, we are reluctant to make any comparison between the measurements presented by Nakaya (1971) of a 2190 mm male specimen with those of the 1280 mm immature female specimen measured here, because we do not know the allometry patterns for the species, or even whether secondary sexual dimorphism exists for any of the measurements given here.

In population studies, using parasites as biological markers is valuable, but it is largely unexplored in elasmobranchs (Caira, 1990), particularly in pelagic sharks. Two main limitations are obtaining suitable population sample sizes and the unsuitability of these top predators as hosts for long-lived larval parasites, which are more reliable markers (Pawson & Ellis, 2005; Lester & MacKenzie, 2009; MacKenzie & Hemmingsen, 2014).

Previous studies on porbeagle sharks often had small sample sizes and limited quantitative data on helminths (parasitic worms) (Knoff et al., 2007; O'Reilly & Hantke, 2020). However, there is evidence of trophic interactions between porbeagles and squid involving tapeworm transmission (Randhawa & Brickle, 2011). In the Southwestern Atlantic (SWA) waters, this study contributes valuable information on porbeagle shark parasite fauna.

Some parasites found, like the tapeworm *H. trichiuri* and *C. montaukensis*, were previously documented (Lucifora & Menni, 1998; Randhawa & Brickle, 2011), while others, such as *Anisakis* sp., *Contracaecum* sp. and nematodes belonging to the Family Spiruridae, are new records for this host in SWA. Notably, *Anisakis* sp. larvae were found alive in the shark's stomach wall, surviving freezing temperatures of -15 °C for 20 days, likely acquired from the shark's prey, which includes pelagic fish and squid (Compagno, 2002), susceptible to *Anisakis* infection (Mattiucci *et al*., 1997; Brickle *et a*l., 2001). This suggests porbeagles might not be the endpoint in the life cycle of these parasites but also a potential alternative pathway for their transmission.

On the other hand, in a porbeagle captured in Patagonian waters off Cabo Blanco (Santa Cruz province, Argentina) and studied by Arquez *et al*. (1986), numerous specimens of the copepod *Anthosoma crassum* (Abilgaard, 1794) were found attached in the buccal cavity. This copepod species was not found in the porbeagle beached near Necochea.

Regarding tapeworms, the presence of plerocerci of *H. trichiuri* has been reported in teleost fishes *Cynoscion guatucupa* (Cuvier 1830) (Sciaenidae) and *Merluccius hubbsi* Marini 1933 (Merlucciidae) as intermediate hosts for this parasite species in the Argentine Sea (Menoret, 2012). Therefore, the finding of adult specimens of *H. trichiuri* in the spiral valve confirms the porbeagle as a definitive host for this parasite in SWA waters. In summary, large marine predators like porbeagle provide a valuable opportunity to study marine helminth life cycles.

Molecular data presented in this paper show a great genetic diversity in COI sequences, especially between NH and SH samples, which is in accordance with previous studies (Kitamura & Matsunaga, 2010; Testerman, 2014; Rigby *et al.*, 2019). In addition, juveniles recorded in northern Argentine coastal waters differ in COI nucleotide sequences, which are located in different clusters in the ML analysis, and correspond to two different haplogroups.

Currently, two separate subpopulations, one in the North Atlantic and another in the SH, are recognized (Rigby *et al.*, 2019). Kitamura & Matsunaga (2010) analysed the genetic population structure of the porbeagle shark using nucleotide sequences of the control region. They found that North and South Atlantic populations are subdivided, indicating a restriction of gene flow between both populations. Even though with low support, their results also suggested the presence of two subpopulations in the South Atlantic. On the other hand, Testerman (2014) investigated the porbeagle global genetic structure using the complete mitochondrial control region, nuclear ITS2 and published mitochondrial COI sequences. He found a strong geographic subdivision between the North Atlantic and the SH, with no genetic connectivity between the two hemispheres and no genetic structure within either hemisphere. More recently, González *et al.* (2020) described the population genetics of *L. nasus* at a regional (SEP) and global scale by using COI and control region (CR). The authors reported two genetic clusters co-occurring in the SEP (Chile). Their global analyses also demonstrated genetic differences between populations from the NH and SH, but not among populations in the SH. However, the aforementioned authors also registered two well-defined haplotype groups that inhabit all ocean basins in the SH. Although the authors did not discount the possibility of two genetically dissimilar populations, they suggested that these two haplotype groups "could reflect a historical scenario of reproductive isolation and a more recent mixture among previously isolated populations in the SH". Differences in the results of those studies are probably due to the use of different molecular markers. The amount of evidence presented here suggests that porbeagle *L. nasus* strandings occur regularly in the SWA, and that porbeagles from Argentine waters belong to two different haplogroups. Further studies are needed to establish the causes of the stranding phenomenon as well to fill the gaps concerning population issues.

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Appendix A

Porbeagle shark (*Lamna nasus*) information for recent stranding events (2011–2020). Cases found within the first 300 search online results for each keyword worldwide, both in English and Spanish languages by Google search (https://www.google.com). Key words utilized in the search includes “porbeagle”, “beached”, “stranding”, “washed up”, “cailón”, “tiburón sardinero”, “varamiento”, “playa”. Most of events were confirmed trough two or more related posts, and the date is as close as possible to the record. We assume that the published photo corresponds to the event and other details such as TL and sex are right.

Year	Date	Country	Locality	Photo	Find	Condition	TL (m)	Sex	Link
2011	03 January	Spain	Playa Santa Cristina, Oleiros, A Coruña	Yes	Beached	Dead	~2.10	M	https://tiburonesengalicia.blogspot.com/2013/01/cailon-lamna-nasus-primera-parte.html
2013	09 September	England	Redcar Beach, Yorkshire	Yes	Beached	Dead	~1.20	M	https://www.bbc.com/news/uk-england-tees-24021163
2013	02 November	USA	New Castle Commons, New Hampshire	Yes	Beached	Dead	~2.20	M	https://www.seacoastonline.com/article/20131103/news/311030359
2014	11 March	Ireland	Aughacasla Beach, Castlegregory, Kerry	Yes	Beached	Dead	~1.80	F	https://www.mirror.co.uk/news/uk-news/kerry-great-white-shark-huge-3228612
2015	26 March	Chile	Pucatrihue, Osorno	Yes	Beached	Dead	+1.00	?	https://www.soychile.cl/Osorno/Sociedad/2015/03/25/312406/Mira-los-tiburones-que-aparecieron-en-el-litoral-de-Pucatrihue.aspx
2015	17 June	New Zealand	Kaikoura Beach	Yes	Beached	Dead	~1.95	F	https://www.stuff.co.nz/marlborough-express/news/69464032/large-shark-washes-up-on-kaikoura-beach
2015	09 November	Scotland	Cullen Bay, Moray	Yes	Beached	Dead	~2.20	F	https://www.pressandjournal.co.uk/fp/news/moray/745880/cullen-shark/
2016	30 March	New Zealand	Warrington Beach, Otago	Yes	Beached	Dead	?	?	https://www.odt.co.nz/news/dunedin/missing-jaw-unusual-shark-sought-video
2017	20 May	USA	Ryder’s Cove Boatyard, Chatham, Massachusetts	Yes	Beached	Alive	~2.00	?	https://patch.com/massachusetts/barnstable-hyannis/7-foot-shark-found-stranded-cape-cod
2017	01 September	USA	Revere Beach, Massachusetts	Yes	Beached	Dead	~1.90	?	https://www.boston.com/news/animals/2017/09/01/a-dead-shark-washed-ashore-on-a-beach-in-revere
2017	30 October	Canada	Inverness Beach, Nova Scotia	Yes	Beached	Dead	~3.00	?	https://www.cbc.ca/news/canada/nova-scotia/shark-beached-cape-breton-1.4378654
2019	25 July	Chile	Playa de Cobquecura, Ñuble	Yes	Beached	Dead	?	?	https://orbitanoticias.cl/tiburon-fue-encontrado-muerto-playa-cobquecura/
2019	02 December	USA	Marconi Beach, Wellfleet, Massachusetts	Yes	Beached	Dead	~1.80	?	https://whdh.com/news/dead-shark-found-washed-up-on-cape-cod-beach/

2019	15 April	England	Pakefield Beach, Lowestoft, Suffolk	Yes	Beached	Dead	~1.00	?	https://www.thelondoneconomic.com/must-reads/dog-walker-stumbles-across-shark-washed-up-local-british-beach/15/04/
2019	21 April	Chile	Balneario Las Cruces, El Tabo, Valparaiso	Yes	Beached	Dead	~1.40	F	https://www.algarrobodigital.cl/2019/04/tiburones-en-las-costas-de-el-litoral.html
2020	25 February	Chile	Playa Lechagua, Chiloé	Yes	Beached	Dead	?	?	https://www.centralnoticia.cl/2020/02/26/alerta-presencia-de-tiburones-en-chiloe-genera-temor-en-los-habitantes/
2020	07 May	Ireland	Derrymore Beach, Kerry	Yes	Beached	Dead	~3.00	F	https://www.independent.ie/regionals/kerryman/news/beached-shark-at-derrymore-39201716.html
2020	25 February	Chile	Playa La Herradura, Coquimbo	Yes	Beached	Alive	~1.50	M	https://www.lavozdelnorte.cl/2020/02/tiburon-de-especie-en-peligro-de-extincion-fue-encontrado-varado-en-playa-la-herradura-de-coquimbo/
2020	20 December	USA	Marblehead Beach, Massachusetts	No	Beached	Dead	?	?	https://www.fisheries.noaa.gov/feature-story/citizen-science-participation-shark-tagging-program-grows-during-pandemic?utm_medium=email&utm_source=govdelivery