		
CHAPTER 2.2.1.7: SCALLOPED HAMMERHEAD	AUTHORS: P. MILLER, R. FORSELLEDO AND F. MAS	LAST UPDATE: August 2022 (original: Spanish)

2.2.1.7 Description of Scalloped Hammerhead (SPL)

1. Names

1.a Classification and taxonomy

Species name: *Sphyrna lewini* (Griffith and Smith 1834)

Etymology *Sphyrna* comes from the Greek *sphyrá*, meaning hammer, referring to the shape of the head. In contrast, *lewini* is an unidentified patronymic, maybe honouring John Lewin (1770-1819), who illustrated the initial volumes of natural history of Australia (where this species was described for the first time) and it could be “Mr. Lewin” that illustrated the work of Griffin & Smith.

Synonyms: *Zygaena indica* (van Hasselt, 1823), *Zygaena lewini* (Griffith and Smith, 1834), *Cestracion leeuwenii* (Day, 1865), *Zygaena erythraea* (Hemprich & Ehrenberg, 1899), *Cestracion oceanica* (Garman, 1913), *Sphyrna diplana* (Springer, 1941).

ICCAT species code: SPL

ICCAT names: Scalloped hammerhead (English), Requin marteau halicorne (French), Cornuda común (Spanish).

According to the ITIS (Integrated Taxonomy Information System), the scalloped hammerhead is classified as follows:

- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Gnathostomata
- Class: Chondrichthyes
- Sub-class: Elasmobranchii
- Superorder: Euselachii
- Order: Carcharhiniformes
- Family: Sphyrnidae
- Genus: *Sphyrna*

1.b Common names

List of vernacular names used according to ICCAT, FAO, Fishbase (www.fishbase.org) and Compagno (1984). The list of countries is not exhaustive and some local names might not be included.

Australia: Hammerhead shark, Kidney-headed shark, Scalloped hammerhead, Scalloped hammerhead shark
Bahamas: Scalloped hammerhead
Brazil: Caçõ-cornudo, Cambeya, Cambeva-branca, Caçõ-martelo, Caçõ-rudela, Cambeva, Cambeva preta, Cornudo, Peixe-martelo, Rudela, Tubarão-martelo
Canary Islands: Cornuda
China: 双过仔, 双髻鲨, 牦头沙, 红肉双髻, 红肉丫髻鲨, 路氏双髻鲨, 路氏雙髻鲨, Dīng zì shā, Guān shā, Lù shì shuàng jì shā, Xiàng gōng yú
Chinese Taipei: 紅肉丫髻鯊
Colombia: Cachona, Pez martillo, Tiburón martillo
Cuba: Cornuda, Hammerhead, Scalloped Hammerhead
Denmark: Indo-pacifisk hammerhaj
Djibouti: Requin-marteau halicorne, Scalloped hammerhead
Dominican Republic: Cornúa
Ecuador: Tiburón martillo
Fiji: Hammerhead shark, Qio mataitalia, Qio ulu tu'I
Finland: Kampavasarahai
France: Requin-marteau halicorne
French Polynesia: Requin marteau
Greece: Κτενοζύγαινα, Ktenozygena
Hawaii: Mano kihikihi, Manō kihikihi
India: कानमुशी, मगळ, కజర, కొమసొర్రా, ചടയന് സൊറാവ്, Chadayan sravu, Kan mushi, Kanmushi, Kannar, Koma sorrah, Kombu sorrah, Magal, Magala, Scalloped hammerhead
Indonesia: Hiu bingkoh, Hiu capil, Hiu caping, Hiu martil, Yee rimbah, Scalloped hammerhead
Iran: Kooseh-e-sarchakoshi
Japan: Aka shumokuzame
Jordan: Qersh abu burnetta
Korea: 흥살귀상어, Hong-sal-gwi-sang-õ
Italy: Squalo martello smerlato
Madagascar: Akio viko, Viko, Viko palapalandoha
Malaysia: Yu bengkong, Yu jerung, Yu mata jauh, Yu palang, Yu parang, Yu sambaran, Yu sanggul, Yu sanggul lintang, Yu tanduk, Yu tukul, Yu-tukul sanggul
Maldives: Kalhigandu miyaru, Scalloped hammerhead
Mauritius: Requin marteau
Mexico: Cornuda, Cornuda común, Cornuda martillo, Tiburón martillo
Mozambique: Scalloped hammerhead shark
Netherlands: Geschulpte hamerhaai
New Zealand: Scalloped hammerhead
Nicaragua: Cornuda común
Oman: Abul-garn, Jarjur, Jarjur al graram
Panamá: Cornuda común, Gorrua, Tiburón martillo
Peru: Tiburón martillo festoneado
Philippines: Krusan, Pating, Scalloped hammerhead
Poland: Glowomlot tropikalny
Portugal: Tubarão-martelo-recortado, Tubarão-mona
Puerto Rico: Cornuda, Martillo, Morfillo, Scalloped hammerhead
Samoa: Mata'italiga
Solomon Islands: Bagea papala vohe, Scalloped hammerhead
Somalia: Manyaaso
South Africa: Scalloped hammerhead, Skulprand-hamerkop
Spain: Cornuda común, Cachona, Cornuda negra, Martell d'aleta negra
Sweden: Flerhornig hammarhaj
Tahiti: Ma'o taumata tamataroa, Ma'o tuamata
Tanzania: Papa mbingusi, Papa pingusi
Thailand: Chalarn Hua-kong, Scalloped hammerhead
Tonga: Hammerhead shark, Mātai
Trinidad and Tobago: Chapo, Hammerhead shark
Türkiye: Çekiç balığı
United Kingdom: Bronze hammerhead shark, gebuchteter Hammerhai, Scalloped hammerhead, Southern hammerhead shark
United States: Scalloped hammerhead

Uruguay: Martillo

Venezuela: Cornúa

Vietnam: Cá Nhám búa, Cá Nhám búa có rãnh, Scalloped hammerhead

2. Identification (Mainly based on Gilbert, 1967 and Compagno, 1984).

Characteristics of *Sphyrna lewini* (see Figure 1).



Figure 1. Scalloped hammerhead (*Sphyrna lewini*) (Griffith & Smith, 1834). Image taken by Domingo *et al.*, 2010. Photo credit: CSIRO Marine and Atmospheric Research, Australia.

Lengths

References to size throughout this document relate to total length (TL), unless otherwise specified (e.g., fork length: FL, and precaudal length: PCL).

According to Compagno (1984), *S. lewini* can reach sizes of 420 cm. Various studies from around the world have reported sizes of up to 313 cm (Northeast Atlantic, Piercy *et al.*, 2007), 317 cm (Indonesia, White *et al.*, 2008), 323 cm (Western Indian Ocean, de Bruyn *et al.*, 2005), 331 cm (northwest Pacific, Chen *et al.*, 1990), 363 cm (northeast Pacific, Torres-Huerta *et al.*, 2008), 346 cm (North of Australia, Stevens & Lyle, 1989), and 383 cm (southwest Atlantic, Vooren *et al.*, 2005). Within this literature review, the maximum length recorded for this species can be found in a 401 cm specimen caught to the southeast of India (Rajapacklam *et al.*, 1994).

Colour

Grey to brown back and white belly. The tips of the pectoral fins appear to darken with age, and they are black in large individuals (Gilbert, 1967).

External characteristics

Dorsally-ventrally compressed and laterally expanded head, giving the characteristic hammer shape that is unique to this family of sharks (*Sphyrnidae*). The anterior margin of the head is slightly arched (not as straight as in *S. mokarran*) with a prominent notch in the centre. No spiracles. The mouth is located on the ventral side and is very arched. The first dorsal fin has a curved trailing edge, with its origin at the same height or slightly behind the pectoral fin insertions. Free rear tip of the first dorsal fin in front of the pelvic fin insertion. The small second dorsal fin has a long free rear tip (almost twice the height of the second dorsal fin) that almost reaches the origin of the dorsal caudal-fin lobe. The trailing edge of the pelvic fins is relatively straight and has an accentuated curve in the case of the anal fin. Overlapping denticles, normally with three ridges in juvenile individuals and four or five in larger specimens.

Internal characteristics

Teeth with a relatively broad base and smooth or slightly serrated edges. Narrow and triangular upper teeth, the first three with erect cusps, which become progressively more slanted towards the sides of the mouth. Narrow and triangular lower teeth with erect cusps. The spinal column is made up of 174-209 vertebrae, although this large range could be due to the erroneous inclusion of a cryptic species that was recently described – *Sphyrna gilberti* (Abercrombie *et al.*, 2005; Quattro *et al.*, 2006; Quattro *et al.*, 2013; Barker *et al.*, 2019; see section 5.a), which has fewer vertebrae (Quattro *et al.*, 2006; Quattro *et al.*, 2013), and with which it can also be hybridized (Barker *et al.*, 2019). Only one of the nine specimens studied by Gilbert (1967) had fewer than 192 vertebrae. Quattro *et al.* (2013) pointed out that possibly this individual was the first record of *S. gilberti*.

3. Distribution and population ecology

3.a Geographic distribution

S. lewini is a coastal and oceanic shark, with circumglobal distribution in tropical and temperate waters (Compagno 1984). According to Rigby *et al.*, (2019), in the western Atlantic it can be found from New Jersey (United States) to Uruguay (Menni, 1976), including the Gulf of Mexico and the Caribbean. In the eastern Atlantic it is possibly found in the western Mediterranean and the Azores, and off the west coast of Africa at least down to Angola (Clavareau *et al.*, 2018). Serena (2005) mentions the presence of *S. lewini* in the western Mediterranean Sea as rare and occasional.

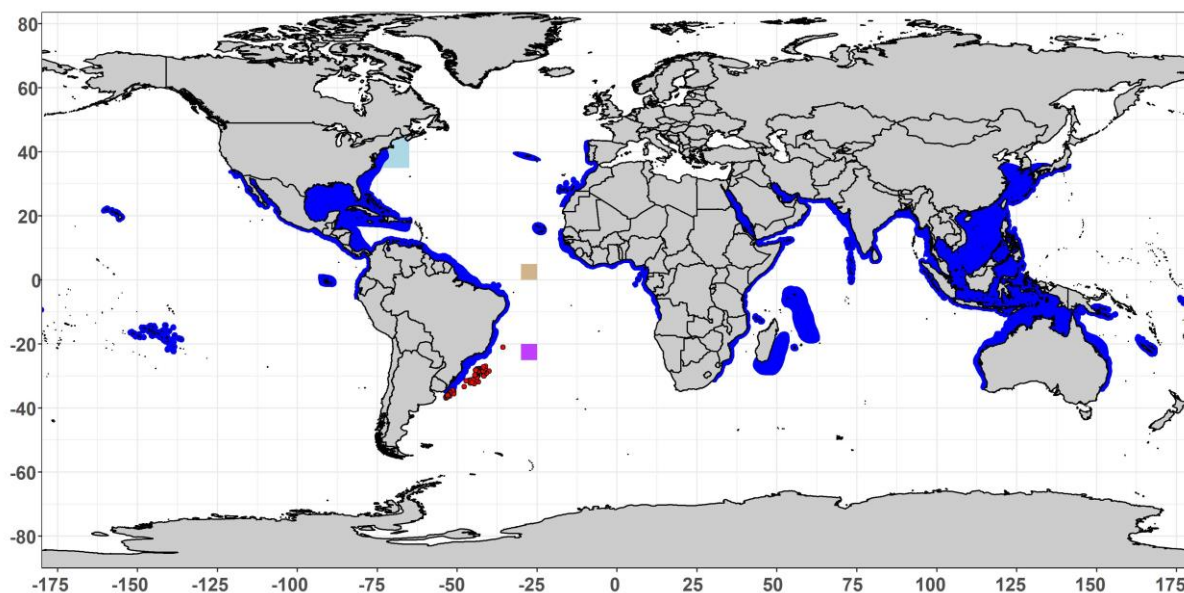


Figure 2. Geographic distribution of scalloped hammerhead *Sphyrna lewini* in the Atlantic. Taken and modified from IUCN (IUCN SSC Shark Specialist Group 2018. *Sphyrna lewini*. The IUCN Red List of Threatened Species. Version 2021-2). The red dots (DINARA, unpublished data) and blue (Kohler & Turner, 2019), brown (Bezerra *et al.*, 2020) and violet (Pinheiro *et al.*, 2015) polygons, refer to the records confirmed for the species in waters outside the distribution range suggested by IUCN. The revision of new records outside the IUCN distribution was conducted for the Atlantic Ocean only.

3.b Habitat preferences

S. lewini mainly lives in neritic environments and in the vicinity of oceanic islands and seamounts (Klimley & Nelson 1981, 1984; Arauz & Antoniou 2006; Sibaja-Cordero 2008; Vaske Júnior *et al.*, 2009; Hearn *et al.*, 2010; Bessudo *et al.*, 2011a,b; Pinheiro *et al.*, 2015; López *et al.*, 2022), although it can also be found in oceanic environments in areas far from any coastline (Ketchum *et al.*, 2009; Bessudo *et al.*, 2011b). Large aggregations of *S. lewini* were observed associated to extraction of hydrocarbon platforms (Hoffmayer *et al.*, 2013), as well as groups associated to choral schools (Childs 2001) in the Gulf of Mexico.

The environmental preferences of this species differ depending on age or stage of development. Neonates and small juveniles typically live close to the coast in shallow waters, including bays (Clarke 1971; Holland *et al.*, 1993; Gadig *et al.*, 2002; Vooren *et al.*, 2005; Adams & Paperno 2007; Doño 2008; Rasalato *et al.*, 2010; Harry *et al.*, 2011; Dolphine 2014; Horn 2014; Brown *et al.*, 2016; Marie *et al.*, 2017; Cuevas-Gómez *et al.*, 2020; Wargat, 2021). In Kaneohe Bay, Hawaii, Holland *et al.*, (1993) and Duncan & Holland (2006) established that neonates and juveniles remained in Kaneohe Bay, Hawaii, for several months or even one year. In a farming area in the central coast of Mexico in the Pacific (Jalisco), Rosendo-Pereiro and Corgos (2018) conducted acoustic monitoring for small juveniles, observing that the specimens showed a high site fidelity. Individuals generally remained at depths of less than 30m, and those recorded with sizes of less than 60cm were mainly observed at depths of less than 15m, whilst larger ones were mainly detected at depths of less than 15m. In the same study, the most extensive movements were carried out at dusk and dawn, whilst at night the individuals mostly remained near the mouth of the river. The extension of the main area of use was valued for each individual (n = 5), finding that it varied between 3 and 25 km². This observation was similarly observed by Marie *et al.*, (2017), who recorded

the regular occurrence of neonates and small juveniles for more than a year in a small area in a shallow habitat in the Rewa River delta (Fiji), finding evidence of site fidelity based on recapture rates of tagged samples that reached 12.7%, including some individuals that in many opportunities were caught again. Taking into account a total of 1,054 individuals caught, Marie *et al.*, (2017) determined that this habitat is exclusively used by individuals at initial stages, without recording the occurrence of large juveniles or adults, in a clear example of size segregation. In a study conducted in the southern Gulf of Mexico, the monitoring carried out throughout several years revealed the existence of a farming area of *S. lewini* in coastal waters of the states of Tabasco and Campeche, where the occurrence of juveniles was recorded throughout the year (Cuevas-Gómez *et al.*, 2020). Juveniles were mainly caught at depths between 10 and 30 metres, and the occurrence of neonates and small juveniles was recorded mainly between May and August, repetitively, throughout various years. Something similar was recorded in different areas of the southeast Atlantic, including the southeast of Brazil (Dolphine 2014), southern Brazil (Horn 2014) and Uruguay (Doño 2008), where the occurrence of neonates and small juveniles was recorded in coastal waters with depths of less than 30m between the end of spring and the beginning of the summer. Horn (2014) reported having recorded some fishing events with important catches of several hundreds of individuals, without adults or large juveniles, which shows a clear segregation by age and formation of large aggregations of neonates and small juveniles of *S. lewini* in shallow coastal waters of southern Brazil. The absence of large juveniles in catches observed during monitoring coincides with the observations made in other studies, indicating that after spending time in shallow coastal waters, juveniles abandon this area. In a study analysing catches of *S. lewini* by several fisheries operating in the SE and S of Brazil, Kotas *et al.*, (2012) observed that although the species was found at wide depth ranges (14 – 4,400 m), the majority of catches occurred above the continental platform, generally in coastal areas, and a total of 2,481 landed individuals, the average depth of the catch site was 133 m.

Larger juveniles are more frequently found in waters further away from the coast on the shelf (Vooren *et al.*, 2005; Kotas 2009; Harry *et al.*, 2011), and this transition appears to occur earlier in females than males (Klimley 1983, 1987). Adults occupy regions close to the slope and oceanic waters, although they may enter shelf waters and move closer to the coast during certain stages of the reproductive cycle (e.g., Clarke, 1971; Vooren *et al.*, 2005; López *et al.*, 2022, see section 4.d).

Regarding vertical movements of *S. lewini*, the first study conducted in the Atlantic obtained data from a female adult caught in the areas surrounding an oil platform located in the continental slope of the northern region of the Gulf of Mexico (Hoffmayer *et al.*, 2013). Throughout the 27 days that the specimen was monitored it was observed that it swam in relatively shallow waters during the day (0-228m), remaining between 20-80 m for 83.4% of the time. At night, it swam in deeper waters (0-946 m), remaining at depths between 0-60 m for 71.7 % of the time, and 16.4 % of the time at depths of more than 241 m. The shark carried out 76-night dives that reached at least 700 m in depth, 16 of which were deeper than 900 m. Each night, it carried out an average of 4.2 dives of around 41.6 minutes and reaching an average depth of 796 m. The average rate of dive descents was 1,31 m/s, whilst the ascent rate was 0.51 m/s. The time in which it remained at maximum depths was approximately 4 minutes in dives that exceeded 700 m in depth.

A later study analysing the movements of 33 specimens monitored in the northern Gulf of Mexico found that the habitat preferences of *S. lewini* appeared to be mainly determined by bathymetric aspects (depth, bottom type), more than by dynamic oceanic processes (SST and SSHA) (Wells *et al.*, 2018). The same study also indicates that the distance to structures that constitute artificial habitats was also a variable that influenced habit models, in particular, oil and gas platforms to which specimens were closely linked.

When analysing the vertical behaviour of 4 specimens equipped with archival electronic tags after being caught in the Saint Peter and Saint Paul Archipelago (East Equatorial Atlantic), Bezerra *et al.*, (2020) found that the specimens swam mainly in superficial and warm waters (< 22° C), eventually reaching up to 728 m in depth. Most of the time the specimens remained at depths of less than 150 m (98% during the day and 87% at night), in temperatures generally higher than 22°C (58% during the day and 63% at night). However, all the specimens carried out frequent deep dives each night, entering the meso-pelagic environment at night, where they found much colder waters with temperatures averaging 10.5° C, reaching a minimum of 5.6° C. In a later study that analysed the data of individuals, Afonso *et al.*, (2022) stated that there was preference during the day to carry out epi-pelagic dives focusing on depths of nearly 100 m but with frequent dives of depths up to approximately 400 m, contrasts with a more uniform distribution in the column of water up to approximately 750 m at night. During the deep dives, the descent rate found by Bezerra *et al.*, (2020), was always higher than the ascent rate (0.5 and 0.32 m/s, respectively), coinciding with the observations of Hoffmayer *et al.*, (2013) and Wells *et al.*, (2018) in a specimen monitored in the Gulf of Mexico. Andrzejczek *et al.*, (2022) analysed data obtained from 16 individuals monitored in different regions, and informed that even though the maximum depth recorded reached 973 m, individuals remained most of the time (54.8 %) at depths of less than 50 m, having also used the strata between 50-100 m in depth (35.9 % of the time), whilst the time spent at depths greater than 250 m merely

reached 2.6% of the total time monitored. Anderson *et al.*, (2022a) analysed the vertical behaviour of a male adult in the North of the Gulf of Mexico, finding contrasting results with previous studies. During the 90 day period, the individual remained practically on the continental platform, without carrying out dives at depths of more than 100 m.

It was observed that *S. lewini* was capable of swimming in deep waters of the Indian Ocean, where there exists an opportunistic record, where a sample of an estimated 150 cm in size was observed by a ROV camera operating at around 40 km off the coast of Tanzania. The specimen was observed for nearly a minute whilst it was swimming at one meter from the bottom of the sea at a depth of 1.042m, where the water temperature was 5.9° C (Moore & Gates, 2015).

A female of 240 cm FL caught in the Red Sea carried an electronic tag which was recovered, providing important time series including data on depth and temperature, corresponding to 182 monitoring days, with a very high time resolution (15 seconds). When analysing data, Spaet *et al.*, (2017) it was observed that the specimen remained >70% of the time at depths of less than 100 m, but less than 2.5 % of the time in the 10 m above. During the monitoring period the specimen carried out deep dives entering in the meso-pelagic environment, recording that out of the 182 days monitored, the shark carried out dives of more than 650 m in 174 days. The maximum depth recorded reached a maximum of 917 m, and the intervals between these deep dives are characterized by constant oscillatory dives in the 100 m above the column of water. Deeper dives (> 850 m) took place mainly between 19:00-03:00 hrs, whilst the less deep dives (<500 m) occurred throughout the entire daily cycle. Coinciding with what was observed in specimens monitored in other regions, the results of Spaet *et al.*, (2017) also indicates that during the dives the average descent rate was higher than the ascent rate.

According to telemetry studies carried out in the vicinity of oceanic islands and seamounts in the Pacific, *S. lewini* uses an extensive portion of the water column and experiences a wide range of temperatures during its vertical migrations. Bessudo *et al.*, (2011a) monitored 69 individuals with acoustic sensors and observed that they were generally found at depths associated with the location of the thermocline. Nonetheless, the implementation of satellite telemetry and archival tags have shown that this species is capable of large vertical migrations, even exceeding depths of 900 m and withstanding temperatures of up to 4° C (Jorgensen *et al.*, 2009; Bessudo *et al.*, 2011b). Jorgensen *et al.*, (2009) tracked the movements of a single individual in the Gulf of California over a period of 74 days and reported depths of up to 980 m and temperatures of between 4.8 and 27.8°C. The individual tagged by Jorgensen *et al.*, (2009) exceeded the depth of the oxygen minimum zone (~250 m) on several occasions during its vertical movements and came into contact with waters that had significantly low levels of dissolved oxygen. Based on their results, Jorgensen *et al.*, (2009) suggested that *S. lewini* could be extremely tolerant to high levels of hypoxia, which would allow it to expand its niche and exploit resources that may be inaccessible to other predators. A female monitored in Hawaii carried out the deepest dive recorded to date, reaching 1,240 m (Anderson *et al.*, 2022b). Furthermore, this study found that during the 180 days in which it was monitored, the individual reached 1,098 deep dives (greater than 500 m), of which only 14 took place during the day. The rates of descent during deep dives were greater than the rates of ascent, similar to previous studies (Hoffmayer *et al.*, 2013; Erguden *et al.*, 2017; Wells *et al.*, 2018; Bezerra *et al.*, 2020).

On Wolf Island in the Galapagos Islands, Hearn *et al.*, (2010) monitored 61 individuals with acoustic sensors and observed differences in the depths frequented during the day and at night. During the day, the individuals being monitored were mainly concentrated in the vicinity of the island at depths of under 50 m, while at night the same individuals moved into more oceanic waters and made frequent dives to depths of between 100 and 400 m. Working on Malpelo Island (northeast Pacific), Bessudo *et al.*, (2011a) also observed differences between use of the water column during the day and at night, with more extensive and frequent vertical movements during the latter. In the Gulf of California, Klimley & Nelson (1984) and Klimley *et al.*, (1988) observed large aggregations of individuals of this species on a seamount during the day, and they moved alone or in small groups towards open waters during the night. When studying these aggregations, Klimley & Nelson (1981) mentioned that they never saw individuals feed during the day. This observation has led to the consideration that *S. lewini* remains relatively inactive and forms schools during the day, and disperses into open waters at night to feed (Klimley & Nelson 1984).

In the Gulf of California, Klimley and Butler (1988) observed that the presence and return of individuals to a seamount was conditioned by the presence of different bodies of water, with a higher percentage of individuals returning during the influence of a warm body of water. On the Island of Malpelo, a specimen tracked via archival satellite telemetry made a more superficial use of the water column (0–10 m) during the cold-water season compared to the warm-water season (55 and 26% of the time, respectively) (Bessudo *et al.*, 2011b).

3.c. Migrations

There is relatively little information available on the migrations of *S. lewini*. As part of the *Cooperative Shark Tagging Program* carried out by the *National Marine and Fisheries Service*, 3,537 individuals of this species were tagged between 1962 and 2013 in the Atlantic, of which only 62 were recaptured. The maximum distance travelled was 902 nautical miles (~1,671 km) and the maximum time at liberty was 9.6 years (Kohler & Turner, 2019). The highest speed recorded for this species from conventional tags was 11.1 km per day (Kohler & Turner, 2001).

A total of 641 individuals were tagged on the South Africa coast between 1984 and 2009. A recapture rate of 1.9% from these was obtained (Diemer *et al.*, 2011). The average distance covered by the individuals was 147.8 ± 52.2 km, whilst the maximum distance attained 629 km. Average time at liberty was 224.6 ± 77.1 days. Four individuals were recaptured 1-100 km from the initial site after 29-832 days; two individuals were recaptured 101-200 km after 206 days; and four individuals were recaptured more than 200 km after 24-550 days. The minimal maximal travel per day was estimated at a rate of movement of 12.3 km a day. This corresponds to an individual of 107 cm PCL, which was recaptured at a distance of 629 km from the tagging site after 51 days.

Studies using satellite telemetry have in recent years enabled obtaining information on the movements of this species (Hoffmayer *et al.*, 2013; Spaet *et al.*, 2017; Wells *et al.*, 2018, Bezerra *et al.*, 2020). An adult female was monitored in the Gulf of Mexico with the use of an electronic archival tag, and after 27 days it was found a few kilometers from the initial tagging site (Hoffmayer *et al.*, 2013). The tag was found at 1.3km from the initial tagging site, 6hrs after having fallen off the monitored specimen.

A study conducted in an extensive region of the northern Gulf of Mexico, Wells *et al.*, (2018) analyzed the movements of 33 specimens that were equipped with satellite tags in waters over the continental platform of this region. The results indicated a limited dispersion of specimens that showed a residential behaviour in areas with cores that were relatively small and were exclusively found in neritic environments (over the continental platform). The size of the core areas did not present a significant relationship between sex and size of specimens. Females showed an association to areas near the breakage of the platform and the upper portion of the continental slope, whilst males mainly used the medium or interior platform.

The movements of 4 specimens with archival electronic tags in the Saint Peter and Saint Paul Archipelago (West Equatorial Atlantic) were studied by Bezerra *et al.*, (2020), who found that specimens remained near the Archipelago, without leaving the area. All the specimens, whose movements were monitored within 70-120 days (one and three specimens, respectively) showed fidelity to the area where they were caught, remaining all the time at a distance of less than 200km from the tagging site, except for a specimen that, although remained most of the time in the area, after four months when the monitoring was finished, it was located at approximately 380km of the initial site. The average speed for the specimens monitored was 17 ± 25 km/day, having reached a maximum of 65km/day.

A female of 240cm FL, monitored with an archival tag in the Red Sea, moved around 1,000 km away from the initial location and after 182 days its tag was recovered in the same initial location (Spaet *et al.*, 2017), which shows some fidelity to location and a likely residential behaviour, similar to that observed by studies conducted in other regions.

In the Pacific Ocean, studies have also been conducted by the implementation of acoustic devices in individuals and the installation of receiver stations at specific locations in the vicinity of oceanic islands (Galapagos, Malpelo, Cocos) revealed that *S. lewini* frequents specific locations within the same island, while it is also capable of migrating between different oceanic islands (Arauz & Antoniou, 2006; Hearn *et al.*, 2010; Bessudo *et al.*, 2011a). According to these studies, *S. lewini* clusters in the vicinity of islands at specific locations during the day and disperses at night to more distant oceanic waters, as observed with seamounts (Klimley & Nelson 1981, 1984; Klimley *et al.*, 1988; Klimley 1993). Bessudo *et al.*, (2011a) demonstrated the existence of migrations between oceanic islands. Notably, an individually tagged at the Island of Malpelo was detected in Cocos Island (~627 km) and later in the Galapagos Islands, covering a total estimated distance of approximately 1,941 km. Bessudo *et al.*, (2011a) observed that the majority of individuals spend extended periods of time in the vicinity of islands throughout the year. Individuals that abandon the island return after a few days or several months. Some of them even leave at the same time (within a range of a few days) and stay away for a similar period of time, which suggests that some type of oceanographic influence may be present in these movements (Bessudo *et al.*, 2011a). It was observed that also in Japan, *S. lewini* lives various months in reduced areas near a small oceanic island (Jacoby *et al.*, 2022).

Some studies have reported highly directional movements in this species (Klimley & Nelson 1984; Klimley 1993) and have suggested that *S. lewini* has a navigation system based on the ability to detect electromagnetic gradients and intensity differences in the topography of the ocean floor (Klimley 1993, see section 4.f).

4. Biology

4.a Growth

The information available on the age and growth of *S. lewini* corresponds to various studies carried out in different regions (**Table 1**).

In the Atlantic, the first age and growth study was performed by Schwartz (1983) on juvenile individuals (21 males and 14 females) caught in North Carolina (United States). According to the marginal increment analysis, Schwartz (1983) concluded that the formation of growth rings in vertebrae does not have annual periodicity, observing males and females of 8 and 5 years, respectively. All other studies carried out in the Atlantic Ocean have covered a more representative size spectrum for the species, and they generally all agree that *S. lewini* forms one growth ring in the vertebrae per year and has slow growth ($k=0.05-0.13$) that is not the same for both sexes, late maturity and extensive longevity (>30 years; Branstetter 1987; Mazzoleni *et al.*, 2004; Piercy *et al.*, 2007; Kotas *et al.*, 2011; Frazier *et al.*, 2021). Assuming a birth date of 1 June, in the Gulf of Mexico, Branstetter (1987) estimated a growth of 15 cm between birth and the first winter (approximately 6 months), 15-20 cm in the next 2 years of life, 10-15 cm between ages 3 and 5, and 10-12 cm to 5-7 cm between ages 6 and 17. Schwartz (1983) made similar estimations up to 5 years of age. Based on recaptures of 37 neonates and small juveniles with times at liberty varying from 1 to 5 months over a breeding area in the delta of River Rewa (Fiji), Marie *et al.*, (2017) managed to establish that the rates of monthly growth were $2.21 \text{ cm} \pm 1.45 \text{ cm}$ and $2.90 \text{ cm} \pm 2.85 \text{ cm}$ for males and females, respectively. The most long-lived individual by Branstetter (1987) was determined to be 17+ years of age but based on the growth curve obtained and the maximum sizes reported for the species, the author estimated a longevity of 30-35 years. A later study carried out in the northwest Atlantic and the Gulf of Mexico (Piercy *et al.*, 2007) supports the longevity estimations of Branstetter (1987), determining maximum ages of 30.5 years for both males (304 cm) and females (313 cm). In a recent study performed on individuals in the northwest Atlantic and Gulf of Mexico, Frazier *et al.*, (2021) informed that maximum ages observed attained 39.5 and 29.5 years for males and females, respectively. In the southwest Atlantic, Kotas *et al.*, (2011) reported maximum ages of 29.5 years (234 cm) for males and 31.5 years (217 cm) for females. The estimated longevity for this species in this study was 55 years. Although Piercy *et al.*, (2007) and Kotas *et al.*, (2011) recorded practically the same maximum ages in their respective studies, there is a notable difference between the sizes presented for both males and females of these ages comparing both regions. This could suggest that individuals in the southwest Atlantic grow significantly slower than their counterparts in the northwest Atlantic.

Table 1. Growth parameters for *Sphyrna lewini* According to the Von-Bertalanffy growth model. L_{∞} : Maximum asymptotic length (cm), k : growth coefficient (years⁻¹), t_0 : theoretical age to size 0 (years).

Growth Parameter			Area	Reference	Sex	Method
L_{∞}	k	t_0				
215 (FL)	0.13	-1.62	Northwest Atlantic	Piercy <i>et al.</i> , (2007)	Males	Vertebrae
233 (FL)	0.09	-2.22	Northwest Atlantic	Piercy <i>et al.</i> , (2007)	Females	Vertebrae
220 (FL)	0.12	-1.84	Northeast Atlantic	Piercy <i>et al.</i> , (2007)	Both	Vertebrae
329 (TL)	0.073	-2.22	Gulf of Mexico	Branstetter (1987)	Both	Vertebrae
266 (TL)	0.05	47 (TL)*	Southwest Atlantic	Kotas <i>et al.</i> , (2011)	Males	Vertebrae
300 (TL)	0.05	51 (TL)*	Southwest Atlantic	Kotas <i>et al.</i> , (2011)	Females	Vertebrae
329 (TL)	0.071	-2.370	Southwest Atlantic	Mazzoleni <i>et al.</i> , (2004)	Both	Vertebrae ¹
210.5 (LH)	0.122	-1.818	Gulf of Mexico	Frazier <i>et al.</i> , (2021)	Males	Vértebras
234.5 (LH)	0.084	-2.407	Gulf of Mexico	Frazier <i>et al.</i> , (2021)	Females	Vértebras
242.1 (LH)	0.081	-2.330	Northeast Atlantic	Frazier <i>et al.</i> , (2021) ^a	Males	Vértebras
225.8 (LH)	0.089	-2.290	Northeast Atlantic	Frazier <i>et al.</i> , (2021) ^a	Hembras	Vértebras
330 (TL)	0.077	58 (TL)	West Pacific	Harry <i>et al.</i> , (2011)	Both	Vertebrae
321 (TL)	0.222	-0.746	Northwest Pacific	Chen <i>et al.</i> , (1990)	Males	Vertebrae
320 (TL)	0.249	-0.413	Northwest Pacific	Chen <i>et al.</i> , (1990)	Females	Vertebrae
336 (TL)	0.131	-1.091	Northeast Pacific	Anislado & Robinson (2001)	Males	Vertebrae
353 (TL)	0.156	-0.633	Northeast Pacific	Anislado & Robinson (2001)	Females	Vertebrae
364 (TL)	0.123	-1.18	Northeast Pacific	Anislado <i>et al.</i> , (2008)	Males	Vertebrae
376 (TL)	0.10	-1.16	Northeast Pacific	Anislado <i>et al.</i> , (2008)	Females	Vertebrae
301 (TL)	0.13	-0.74	Northeast Pacific	Zarate-Rustrián (2010)	Males	Vertebrae
305 (TL)	0.13	-0.51	Northeast Pacific	Zarate-Rustrián (2010)	Females	Vertebrae
259.8 (TL)	0.155	56.8 (TL)	East Indian Ocean	Drew <i>et al.</i> , (2015) ^b	Male	Vertebrae
289.6 (TL)	0.161	-	East Indian Ocean	Drew <i>et al.</i> , (2015) ^c	Females	Vertebrae
289.6 (TL)	0.159	-	East Indian Ocean	Drew <i>et al.</i> , (2015) ^c	Both	Vertebrae

TL: total length; FL: fork length. * A modified version of the von Bertalanffy curve was used with a fixed size at birth. ¹ Estimated parameters using whole vertebrae. ^a Parametres for *Sphyrna lewini* and *S. gilberti* combined ^b Gompertz with 3 parametres. ^c Gompertz with 2 parametres.

Age and growth studies carried out in the Pacific suggest that *S. lewini* has a considerably higher growth rates than those reported for the Atlantic Ocean (Chen *et al.*, 1990; Anislado & Robinson, 2001; Anislado *et al.*, 2008; Zarate-Rustrián, 2010). Nonetheless, the difference found between the two oceans could be due to the interpretation of growth ring formation periodicity. Chen *et al.*, (1990) reported that two rings are formed per year in the northeast of Chinese Taipei. Anislado & Robinson (2001), Anislado *et al.*, (2008) and Zarate-Rustrián (2010) reported the same for the northeast Pacific.

In northeast Australia, Harry *et al.*, (2011) evaluated the periodicity of ring formation using Okamura & Semba's (2009) method, which considers three different models (annual periodicity, six-monthly periodicity or no periodicity). According to the results of this study, the most parsimonious model in terms of the AIC was annual periodicity, although the other models did have a certain level of empirical support. Assuming annual periodicity, these researchers determined maximum ages of 21 (262 cm) and 15 years (260 cm) for males and females, respectively. These researchers also reported a difference in the growth of males caught in the tropics compared to those caught in more temperate regions. However, they also pointed out that these results could be partly due to differences between the methodology and number of specimens in the different regions. Differences between studies in terms of ring growth formation periodicity have been discussed by various authors, and Chen *et al.*, (1990), Piercy *et al.*, (2007) and Harry *et al.*, (2011) recognised that the growth rates of individuals in different regions (including both oceans) would be very similar if the same periodicity were assumed in all of the studies. Nonetheless, even if annual periodicity is assumed, some studies have mentioned similar ages for individuals with big differences in size, which could suggest that there is a differential growth pattern between different regions. According to Piercy *et al.*, (2007), Harry *et al.*, (2011) and Kotas *et al.*, (2011), the sizes (and corresponding ages) reported for males were 304 cm (30.5 years), 262 cm (21 years) and 234 cm (29.5 years), respectively, while these were 313 cm (30.5 years), 260 cm (15 years) and 217 cm (31.5 years) for females.

The different periodicities mentioned in the various studies may reflect real differences between *S. lewini* populations or could be a result of the particular methodologies and data analysis in each study (Tanaka *et al.*, 1990; Harry *et al.*, 2011). In any case, the implementation of direct and more vigorous validation methods such as radiocarbon dating and tag and capture with chemical products (e.g., Campana, 2001) are necessary to determine the true nature of *S. lewini*'s growth. These methods have made it possible to validate annual periodicity in several shark species during the last decade (e.g., *Isurus oxyrinchus*, Natanson *et al.*, 2006, Ardizzone *et al.*, 2006; *Lamna nasus*, Campana *et al.*, 2002) and annual periodicity has recently been demonstrated in *S. mokarran* up to the age of 42 years (Passerotti *et al.*, 2011) based on radiocarbon dating.

4.b Length-weight relationship

There are few published length-weight relationships for *Sphyrna lewini* in the Atlantic Ocean, and the majority were developed considering neonate and small juvenile individuals. Those found in this literature review are presented in **Table 2** alongside relationships for other regions.

Table 2. Published length-weight relationships for *Sphyrna lewini*. W: total weight (kg); GW: gutted weight (without the head, guts or fins, kg); TL: total length (cm); PCL: precaudal length (cm); CL: carcass length (cm).

Equation	N	Length range (cm)	R ²	Area	Reference
$W = 1.26 \times 10^{-5} TL^{2.81}$	43	105-230*	-	Gulf of Mexico	Branstetter (1987)
$\log GW = -11.786 + 2.889 \log TL$	86	-	-	Northeast Brazil	Hazin (2001)
$GW = 8.00 \times 10^{-6} CL^{3.23}$	62	-	0.87	Southwest Atlantic	Amorim <i>et al.</i> , (2011)
$GW = 5.00 \times 10^{-6} CL^{3.34}$	29	-	0.93	Southwest Atlantic	Amorim <i>et al.</i> , (2011) ¹
$GW = 2.00 \times 10^{-6} CL^{3.08}$	33	-	0.84	Southwest Atlantic	Amorim <i>et al.</i> , (2011) ²
$W = 0,001945 \times (TL)^{3.19}$	796	41-127	0,924	Southeast Atlantic	Motta <i>et al.</i> , (2014) ¹
$W = 0,002555 \times (TL)^{3.13}$	1198	40,5-117	0,929	Southeast Atlantic	Motta <i>et al.</i> , (2014) ²
$W = 0.002257 TL^{3.16}$	1994	40,5-127	0.927	Southeast Atlantic	Motta <i>et al.</i> , (2014) ³
$W = 0,004 \times (TL)^{3,008}$	48	43,1-76	0,946	Southeast Atlantic	Dolphine (2014) ¹
$W = 0,002 \times (TL)^{3,128}$	47	46-79,5	0,951	Southeast Atlantic	Dolphine (2014) ²
$W = 0,003 \times (TL)^{3,07}$	95	43,1-79,5	0,948	Southeast Atlantic	Dolphine (2014) ³
$W = 3.99 \times 10^{-3} (TL)^{3.03}$	252	-	0,985	Northern Australia	Stevens & Lyle (1989)
$W = 1.35 \times 10^{-6} TL^{3.252}$	49	-	-	Northwest Pacific	Chen <i>et al.</i> , (1990) ¹
$W = 2.82 \times 10^{-6} TL^{3.129}$	276	-	-	Northwest Pacific	Chen <i>et al.</i> , (1990) ²
$W = 1.00 \times 10^{-5} TL^{2.82}$	67	45-250*	0.908	Northwest Pacific	Torres-Huerta <i>et al.</i> , (2008) ¹
$W = 3.00 \times 10^{-6} TL^{3.10}$	75	50-300*	0.979	Northwest Pacific	Torres-Huerta <i>et al.</i> , (2008) ²
$W = 4.00 \times 10^{-6} TL^{3.028}$	34	-	0.993	Indonesia	White <i>et al.</i> , (2008)
$W = 2.76 \times 10^{-6} TL^{3.07}$	87	47-84	-	Hawaii	Clarke (1971)
$W = 1.00 \times 10^{-5} PCL^{2.98}$	1,268	50-225*	-	Western Indian Ocean	De Bruyn <i>et al.</i> , (2005) ¹
$W = 8.00 \times 10^{-6} PCL^{3.10}$	353	70-240*	-	Western Indian Ocean	De Bruyn <i>et al.</i> , (2005) ²

*Approximate lengths based on study figures. ¹ and ² Conversion equations for males and females, respectively. ³ Equation for both sexes combined.

De Bruyn *et al.*, (2005) reported a large weight difference between males and females in the Indian Ocean. According to these authors, the largest recorded difference in length between females and males was 30 cm, but the female weighed more than double.

4.c Conversion factors

The length-length relationships published for different regions of the Atlantic are shown in **Table 4**.

Table 4. Published length-length relationships for *Sphyrna lewini*; TL: total length (cm); FL: fork length (cm); PCL: precaudal length (cm). DPI: Distance Posterior Insertion 1st dorsal to precaudal groove (cm); HW: head width (cm).

Equation	N	Length range (cm)	R ²	Area	Reference
TL = 1.31 (FL) - 0.64	55	-	0.997	Gulf of Mexico	Branstetter (1987)
TL = 1.296 (FL) + 0.516	1488	-	0.990	Northwest Atlantic	Piercy <i>et al.</i> , (2007)
PCL = 0.918 (FL) - 0.365	709	-	0.990	Northwest Atlantic	Piercy <i>et al.</i> , (2007)
TL = 2,76 x (DIP) + 9,13	92	-	0,99	Southwest Atlantic	Kotas <i>et al.</i> , (2012)
TL = 3,357 x (HW) + 60,49	75	-	0,894	Southwest Atlantic	Dolphine (2014)
TL = 1.30 (FL) -1.28	454	-	0.994	North Australia	Stevens & Lyle (1989)
TL = 1.30 (FL) + 15.38	-	-	0.990	Northeast Australia	Harry <i>et al.</i> , (2011)
TL = 1.43 (PCL) + 15.49	-	-	0.990	Northeast Australia	Harry <i>et al.</i> , (2011)
FL = 1.2 (TL) + 0.78	28	-	0.980	Hawaii	Holland <i>et al.</i> , (1993)**
FL = 0.771 (TL) + 0.589	260	50-340*	0.997	Gulf of California	Anislado (2000)
FL = 1.07 (PCL) + 2.27	722	53.7-243	0.970	Western Indian Ocean	De Bruyn <i>et al.</i> , (2005)
TL = 1.314 (PCL) + 3.816	1681	53.7-243	-	Western Indian Ocean	De Bruyn <i>et al.</i> , (2005)

* Estimated lengths based on the study figure. ** Length regression only in the case of neonates.

4.d Reproduction

Aspects related to the reproductive biology of *S. lewini* have been dealt with in numerous studies and several regions, and it is undoubtedly the most studied hammerhead shark species. Nonetheless, the most comprehensive and detailed work comes from studies carried out in the Indian and Pacific Oceans.

Gestation and pupping

S. lewini is a placental viviparous species and, as in other shark species, only the right ovary is functional (Wourms, 1977; Chen *et al.*, 1988). Fertilised eggs are encased in an embryonic membrane at the oviducal gland (Chen *et al.*, 1988; Bejarano 2007) and are subsequently deposited in the uterus. During gestation, the uterus compartmentalises and the embryos develop in individual chambers. In the initial stages of development embryos feed on a yolk sac. They subsequently develop a placenta connection and, once the yolk sac reserves are depleted, the embryos continue to develop at the expense of the placenta through an umbilical cord (Chen *et al.*, 1988). Hazin *et al.*, (2001) and Bejarano (2007) also observed that embryos were arranged in separate compartments within the uterus and specified that they were oriented longitudinally in the same direction as the mother. During birth, embryos are released in the posterior-anterior direction and the cephalic region is the last to leave the mother (Bejarano, 2007).

The gestation period appears to show certain variation between both regions and studies, but in all cases it lasts between 8 and 12 months, with parturition taking place in spring or summer.

In the Atlantic Ocean, and more specifically in southeast Brazil, Vooren *et al.*, (2005) estimated a gestation period of approximately 10 months, with parturition taking place in spring. Also in Southeast Brazil, Amorim *et al.*, (1994) studied embryo growth based on various litters over a period of time and concluded that parturition takes place between October and December (in Amorim *et al.*, 1998). In the same region, artisanal fishing operating between 5 and 19 miles off the coast and at depths of 8 to 15 metres caught neonates and juveniles with gillnets throughout the year, but more frequently between November and January (Gadig *et al.*, 2002). Even further south off the coast of Uruguay, Doño (2008) reported that neonates and juveniles were occasionally caught during spring and summer at depths of up to 20 m. In Northeast Brazil, Hazin *et al.*, (2001) studied the reproductive biology of *S. lewini* based on individuals caught over 150 km off the coast. Although gravid females were observed, none carried at-term embryos and, based on the presence of neonates close to the coast (Lessa *et al.*, 1998), suggested that the birth would take place in coastal waters midway or at the end of the summer. Kotas *et al.* (2012) analyzed 1,126 individuals landed in different ports of São Paulo and Santa Catarina (SE Brazil) between 2008-2009. They found a clear predominance of small juveniles, with an average size of 78.9 cm. Horn (2014) reported that the largest amounts of neonates in coastal waters from South Brazil were recorded between the end of spring and summer; with the largest proportions mainly in the months of November and December, which coincide with that observed a little further North by Gadig *et al.* (2002). Dolphine (2014) reported something similar based on the

analysis of individuals captured in shallow coastal waters from the central coast of São Paulo (southeast Brazil). It was notified that the largest amount of neonates were found in November and December, which significantly reduces in January and absent in subsequent months. In the Gulf of Mexico, the gestation period lasts for approximately 12 months and parturition takes place in spring over a 2- to 3-week period (Branstetter 1981, 1987). In the south of the gulf of Mexico, Cuevas-Gómez *et al.*, (2020) found that the largest amount of neonates were detected between spring and early summer (May to August). Similarly, based on the numbers of neonates with umbilical scar still open that were found during sample landings in Margarita Island (Venezuela, South Caribbean), Tagliafico *et al.*, (2021) indicated that the pupping in this region appears to be concentrated between May-June.

Off the east coast of Florida (United States), Adams & Paperno (2007) reported the presence of neonates measuring 38.5 to 50 cm in May and June. These authors observed the presence of partially healed umbilical scars in the majority of these specimens, which suggests that they had been born at the end of spring.

In the northeast Pacific, the gestation period is estimated to last between 10 and 11 months, with parturition taking place between May and July in the Gulf of California (Torres-Huerta *et al.*, 2008) and the coast of Michoacán, Mexico (Anislado, 2000), and between July and August on the Mexican coasts of Salina Cruz (Bejarano, 2007) and Oaxaca (Alejo-Plata *et al.*, 2007). In the northwest Pacific, parturition takes place between May and July and gestation lasts for approximately 10 months (Chen *et al.*, 1988).

In Northern Australia, parturition takes place between October and January after a 10- to 11-month gestation period (Stevens & Lyle 1989). Harry *et al.*, (2011) observed the presence of low numbers of neonates with unhealed umbilical scars in northeast Australia throughout the year, and reported higher abundance between the end of November and start of December. In Kaneohe Bay, Hawaii, parturition takes place throughout the year, but the intensity increases between April and October (Clarke 1971).

In KwaZulu-Natal, South Africa, De Bruyn *et al.*, (2005) reported the presence of pregnant females carrying at-term embryos between October and March, which suggests an extensive pupping season during spring and summer. According to Bass *et al.*, (1975), pupping takes place during the summer in the Western Indian Ocean. In Indonesia, White *et al.*, (2008) reported the presence of neonates in all seasons, but concluded that parturition mainly takes place between the end of October and start of November after an 8- to 9-month gestation period. The authors also suggested that mating may take place around March.

Apart from the studies of Clarke (1971), White *et al.*, (2008) and Harry *et al.*, (2011), *S. lewini* appears to have a well-defined pupping season, and even in the three aforementioned studies the authors report that there is a higher abundance of neonates, suggesting a higher number of births, at a specific time of year.

Although bites on the back of females is typically associated with the act of copulation (for example, Pratt, 1979), Klimley (1983) observed these bites in *S. lewini* in both immature (under 135 cm) and mature females, which suggests that they are not associated with reproduction, but rather with aggressive interactions between females of the same school.

According to reproductive biology studies, the size at birth of *S. lewini* is between 35.5 and 55 cm (Clarke, 1971; Bass *et al.*, 1975; Compagno, 1984; Branstetter, 1987; Stevens & Lyle, 1989; Anislado & Robinson, 2001; Vooren *et al.*, 2005; Alejo-Plata *et al.*, 2007; Bejarano, 2007; Torres-Huerta *et al.*, 2008; White *et al.*, 2008; Harry *et al.*, 2011; Horn, 2014; Cuevas-Gómez *et al.*, 2020). Nonetheless, the fact that White *et al.*, (2008) observed embryos of up to 55.6 cm and neonates of just 39 cm in the same region means that embryo growth and size at birth vary widely. Similarly, Moreno *et al.*, (1989) observed significant overlap in the size of embryos and neonates for *A. vulpinus* and suggested that birth may not be determined by the size of the embryos, but rather by key ontogenetic events. Furthermore, when studying 4 pregnant females off the coast of Senegal, Capapé *et al.*, (1998) observed size differences of up to 16 cm between embryos of the same litter. Assuming that once parturition begins all of the embryos are released within a short period of time, it is likely that size at birth varies considerably, which would explain White *et al.*,’s findings. (2008) in Indonesia. Branstetter (1987) mentioned that, given the large size of *S. lewini* litters, the variation in embryo size could occur if some develop at the expense of others. Big differences in embryo size within a single litter may not be a common occurrence, but it has been observed in other cases. De Bruyn *et al.*, (2005) reported the size range for 9 litters. The difference was no more than 5 cm in 8 of them, while in the remaining litter the difference was over 11 cm (24.7-36.2 cm PCL). Of the ten litters analysed by Hazin *et al.*, (2001), none presented differences of over 6 cm.

S. lewini has a complex reproductive cycle. Adults spend most of their time in oceanic waters, but female adults move closer to coasts, bays and estuaries for parturition (Clarke, 1971; Simpfendorfer & Milward, 1993; Stevens & Lyle, 1989; Gadig *et al.*, 2002; Vooren *et al.*, 2005; Adams & Paperno, 2007; Torres-Huerta *et al.*, 2008; Kotas 2009; Harry *et al.*, 2011). This behaviour or particularity of the reproductive cycle is generally associated with a strategy that aims to increase juvenile survival, giving them the opportunity to grow up in areas that are typically more productive and/or have a lower predation risk (Clarke 1971; Branstetter 1990; Duncan & Holland 2006; Heupel *et al.*, 2007). There are currently several studies reporting that *S. lewini* uses nursery areas, including Kaneohe Bay (Hawaii, Clarke 1971; Duncan & Holland 2006), Cleveland Bay (Australia, Simpfendorfer & Milward, 1993), northeast Australia (Harry *et al.*, 2011), coastal water including the delta of the Rewa River (Fiji, Rasalato *et al.*, 2010; Brown *et al.*, 2016; Marie *et al.*, 2017), the Gulf of California (Torres-Huerta *et al.*, 2008), the coast of Michoacán (Mexico, Anislado 2000), Salina Cruz (Mexico, Bejarano 2007), Jalisco (México, Rosende-Pereiro y Corgos, 2018), coasta of Tabasco and Campeche (southern Gulf of Mexico, Cuevas-Gómez *et al.*, 2020), Cape Canaveral (Florida, United States, Adams & Paperno 2007), Bulls Bay (South Carolina, United States, Castro 1993), and the coast of Southeast-South Brazil (Gadig *et al.*, 2002; Vooren *et al.*, 2005; Kotas, 2009; Dolphine, 2014; Horn, 2014).

Maturity

Compagno (1984) mentions general sizes at first maturity of 140-165 cm for males and 212 cm for females. Nonetheless, the sizes at first maturity reported by various researchers in several regions suggest that there are differences in the life history of different populations.

In the Atlantic Ocean, Bigelow & Schroeder (1984) and Castro (1993) suggested a common size at first maturity for both sexes of 180-185 cm. However, all other studies carried out on this species in the Atlantic and other oceans indicated that females reach reproductive maturity at a considerably larger size than males. According to Vooren *et al.*, (2005), in the Southeast-South region of Brazil males and females reach maturity at 192 and 204 cm, respectively, while in Northeast Brazil they reach maturity at 180-200 and 240 cm (Hazin *et al.*, 2001). In the Gulf of Mexico, Branstetter (1987) estimated that males reach maturity at 180 cm and 10 years of age, and females at 250 cm and 15 years of age.

In Northern Australia, males and females reach maturity at approximately 150 and 200 cm, respectively (Stevens & Lyle 1989). Also in Australia, Harry *et al.*, (2011) reported that males caught in tropical waters had lower sizes and ages at first maturity (147 cm and 5.7 years) than those caught in temperate waters (204 cm and 8.9 years). Based on the available data, Harry *et al.*, (2011) were unable to estimate the size at maturity for females; however, they did report an immature female of 198 cm and 12 years of age. According to Chen *et al.*, (1990), to the northeast of Chinese Taipei males reach maturity at 198 cm and 3.8 years of age, while females do so at approximately 210 cm and 4.1 years of age.

In the Gulf of California, the size at first maturity for males and females was estimated at 170 and 207 cm, respectively (Torres-Huerta *et al.*, 2008). Further south on the coast of Michoacán (Mexico), Anislado (2000) estimated a size at first maturity of 175 cm for males and 209 cm for females, although the author also reported the capture of a 190-cm gravid female. In Salina Cruz (Mexico), and according to Bejarano (2007), the size at maturity for females was 220 cm, while it was 178 cm for males. Surprisingly, and also in Mexico on the coast of Oaxaca, Alejo-Plata *et al.*, (2007) reported the capture of five gravid females of between 160 and 170 cm, meaning that the size at maturity is notably lower than figures reported by other researchers in nearby regions (Anislado 2000; Bejarano 2007; Torres-Huerta *et al.*, 2008).

In the Western Indian Ocean, De Bruyn *et al.*, (2005) reported a size at first maturity of 216 and 244 cm for males and females, respectively, while in Indonesia this was 176 and 228 cm (White *et al.*, 2008). A study carried out on part of the specimens considered by White *et al.*, (2008), Drew *et al.*, (2015) found that the ages of first maturity were 8 years (176 cm) for males and 11 years (221 cm) for females, as for maturity ages of 50% and 95% (A_{50} and A_{95}) they were 8.6 and 9.6 years for males and quite older for females (13.2 and 18.4 years).

As discussed in section 4.a, the differences in age at first maturity reported for the Atlantic and Pacific could be due to the assumption that a growth ring is formed every year or every six months, or due to real differences in the life history of different populations *S. lewini*.

Sex ratio

Although some studies on reproduction in *S. lewini* have documented an unequal proportion of males and females in the same litter (Chen *et al.*, 1988; Anislado 2000; Hazin *et al.*, 2001), more comprehensive work in terms of the gravid females examined agree that, considering all litters, the sex ratio does not differ significantly from 1:1 (Chen *et al.*, 1988; Bejarano 2007; Torres-Huerta *et al.*, 2008; White *et al.*, 2008).

S. lewini is a gregarious species capable of forming large schools of up to several hundreds of individuals; nonetheless, it also forms small groups (10-50) and is found alone (Clarke 1971; Klimley & Nelson 1981, 1984). These types of aggregations have also been reported in the vicinity of oceanic islands (Hearn *et al.*, 2010; Bessudo *et al.*, 2011a). Klimley & Nelson (1981) and Klimley (1983) studied aggregations associated with a seamount in the area of Baja California (Mexico), and observed that these groups included individuals of both sexes and of various sizes (88-371 cm), although females and immature individuals were the most abundant. Klimley (1987) observed that sizes were segregated within the same aggregations, with larger individuals located towards the lower part of the aggregations and smaller individuals above. Studying these associations in the Gulf of California, Klimley (1983) reported sex ratios in favour of females of between 1.6:1 and 34:1, which are due to the fact that females move to waters further from the coast earlier than males (Klimley 1983, 1987).

Owing to the characteristics of its reproductive cycle, *S. lewini* typically presents notable size segregation. Neonates and small juveniles concentrate in areas close to the coast or in shallow bays, where they remain for a variable period of time depending on the region (Clarke 1971; Simpfendorfer & Milward 1993; Adamas & Paperano 2007; Torres-Huerta *et al.*, 2008; Harry *et al.*, 2011; Horn, 2014). When they reach a certain size, juveniles move to waters further away from the coast and live in waters on the continental shelf and slope (Klimley 1987; Stevens & Lyle 1989; Vooren *et al.*, 2005; Kotas, 2009). Adults of both sexes mainly occupy oceanic waters, although females regularly migrate towards the coast to give birth, mainly during spring and/or summer (Clarke 1971; Vooren *et al.*, 2005; Kotas, 2009).

In northeast Australia, Harry *et al.*, (2011) observed that neonates of both sexes aggregated on the coast throughout the year. However, there were virtually no females of over approximately 100 cm TL, which suggests that they move towards deeper waters. According to Klimley (1987), juvenile females abandon the coast before males, change their diet to include mainly pelagic species and grow at a faster rate than males, reaching sexual maturity at a larger size.

Catch information from several fisheries operating in various regions also shows notable spatial segregation by size. According to Kotas (2004, 2009), bottom gillnet fishing in southeast Brazil, which operates in more coastal waters, catches neonates and juveniles of between 50 and 160 cm, with an average size of 80 cm. Surface gillnet fishing, which operates further off the coast on the slope, catches individuals of at least 70 cm but with an average of 180 cm. The longline fleet, which operates on the slope and in oceanic waters, mainly catches juveniles of over 140 cm and adults of up to 320 cm. White *et al.*, (2008) reported similar results for gillnet and longline fisheries in Indonesia. Horn (2014) analysed the catches of *S. lewini* in fisheries operating with set gill nets in very shallow coastal waters in south Brazil. He found that catches was comprised almost exclusively of neonates and small juveniles with a maximum size of 95 cm; the proportion of sexes detected was 1.1 males: 1 female for a sample of 422 individuals.

Fecundity

The litter size of *S. lewini* has been analysed by numerous researchers in several regions, and shows great variability among individuals and also great variability among regions (**Table 3**). As mentioned by White *et al.*, (2008), the uterine fecundity of *S. lewini* is similar to other large hammerhead sharks (*S. mokarran* and *S. zygaena*), but significantly greater than the majority of large placental viviparous Carcharhiniformes, except for the blue shark (*Prionace glauca*) (for example, Nakano & Stevens 2008).

Several studies have shown a positive correlation between litter size and the size of the female in this species, suggesting greater uterine fecundity in larger females (Chen *et al.*, 1988; Anislado, 2000; Bejarano, 2007; White *et al.*, 2008). In Northeast Brazil, Hazin *et al.*, (2001) did not observe this correlation, but this could be due to the low number of samples (n=10).

Table 3. Litter sizes reported for *S. lewini*.

Region	Litter size			Reference
	n	Range	Average	
Atlantic Ocean	10	2-21	14.3	Hazin (2001)
	4	2-22	14.5	Capapé <i>et al.</i> , (1998)
	2	24-28	-	Cadenat & Blache (1981)
	-	15-22	-	Vooren <i>et al.</i> , (2005)
Pacific Ocean	2	15-31	-	Clarke (1971)
	110	12-38	25.8	Chen <i>et al.</i> , (1988)
	4	13-23	16.5	Stevens & Lyle (1989)
	97	13-42	30	Anislado (2000)
	-	43	-	Campuzano (2002)*
	50	6-40	-	Bejarano (2007)
	5	18-24	21	Alejo-Plata <i>et al.</i> , (2007)
	24	19-32	25	Torres-Huerta <i>et al.</i> , (2008)
Indian Ocean	1	30	-	Bass <i>et al.</i> , (1975)
	11	2-19	10	De Bruyn <i>et al.</i> , (2005)
	25	15-41	25.4	White <i>et al.</i> , (2008)

* Cited in Torres-Huerta *et al.*, (2008).

According to some researchers, oocytes grow in the ovary at the same time as embryos develop during gestation, which means that copulation and fertilisation could occur a short time after parturition (Capapé *et al.*, 1998; White *et al.*, 2001; Bejarano, 2007; Torres-Huerta *et al.*, 2008). Clarke (1971) reported the capture of a 294 cm female that showed signs of having given birth recently, and also of having copulated judging from the presence of sperm in the uterus and fresh copulation wounds on the body.

Based on the literature, almost all gravid females recorded in the various investigations were at least 230 cm (294-304, Clarke, 1971; 230-320, Chen *et al.*, 1988; 251-263, Capapé *et al.*, 1998; 244-273, Hazin *et al.*, 2001; 245-323, de Bruyn *et al.*, 2005; 239-288, Bejarano 2007; 232-307, Torres-Huerta *et al.*, 2008). The only exceptions were observed by Anislado (2000), who recorded gravid females of between 190 and 336 cm on the coast of Michoacán (Mexico); and by Alejo-Plata *et al.*, (2007), who reported the capture of 5 gravid females of between 160 and 170 cm on the coast of Oaxaca (Mexico). Further south of these regions, Bejarano (2007) reported the capture of 50 gravid females in Salina Cruz (México), with a minimum size of 239 cm; while further north in the Gulf of California, the smallest gravid female of the 24 examined was 232 cm (Torres-Huerta *et al.*, 2008). The fact that the only 5 gravid females studied by Alejo-Plata *et al.*, (2007) were of 60-70 cm, lower than the values typically reported in other regions of Mexico and worldwide, could reflect a notable difference in the life strategy of individuals in that region compared to other areas, even within the Mexican coastal strip.

Some researchers reported on the depredation of neonates and small juveniles by other sharks, and even by specimens of the same species. In this sense, the large litter size of *S. lewini* could be a strategy to counteract high juvenile mortality and increase the probability of recruitment (Clarke 1971; Branstetter 1987).

4.e. Diet

The diet of *S. lewini* has mainly been studied in the Pacific Ocean off the coast of Mexico (Aguilar 2003, 2011; Torres-Rojas *et al.*, 2006, 2010), Costa Rica (Zanella *et al.*, 2010), Ecuador (Estupiñán-Montaña *et al.*, 2009), in Australia (Stevens 1984; Stevens & Lyle 1989; Simpfendorfer & Milward 1993), and in the vicinity of oceanic islands (Clarke 1971; Bush & Holland 2002; Bush 2003). In the Atlantic, there are few studies on aspects related to the diet of this species, including studies carried out in the Gulf of Mexico (Branstetter, 1987), as well as studies conducted in various regions throughout the coast of Brazil, including Northeast Brazil (Vaske Júnior *et al.*, (2009), southeast Brazil (Bornatowski *et al.*, 2014; Dolphine 2014), and southern Brazil (Horn 2014).

According to these studies, the diet of *S. lewini* is mainly composed of cephalopods, bony fish and, to a lesser extent, crustaceans, although other studies also mention the presence of chondrichthyans (Clarke 1971; Bigelow & Schroeder 1984; Compagno 1984; Stevens 1984; de Bruyn *et al.*, 2005, Bornatowski *et al.*, 2014) and, occasionally, birds and gasteropods (de Bruyn *et al.*, 2005). The relative importance of cephalopods and bony fish varies between studies. Some report that cephalopods are more important in the diet (Klimley 1983; Estupiñán-Montaño *et al.*, 2009; Vaske Júnior *et al.*, 2009; Zanella *et al.*, 2010) while others indicate greater consumption of bony fish (Clarke 1971; Bass *et al.*, 1975; Stevens & Lyle 1989; Cortés 1999; de Bruyn *et al.*, 2005; Torres-Rojas *et al.*, 2006, Bornatowski *et al.*, 2014, Dolphine 2014; Horn 2014).

Several studies have indicated differences between adults and juveniles in the dietary composition of the species *S. lewini* (Clarke 1971; Klimley 1983, 1987; Smale & Cliff 1998; de Bruyn *et al.*, 2005; Estupiñán-Montaño *et al.*, 2009; Aguilar 2011, Bornatowski *et al.*, 2014), and even between sexes (Klimley 1987; Estupiñán-Montaño *et al.*, 2009; Zanella *et al.*, 2010). Bornatowski *et al.*, (2014) found that for individuals caught in waters off the coast of SE Brazil, the Sciaenidae and crustaceans were the most important prey to discriminate between neonate and juvenile diets, and Sciaenidae, elasmobranchs and Carangids differentiated juveniles and adults. Differences in the diet of adults and juveniles are probably related to the fact that they live in different environments. Clarke (1971) observed that the diets of neonates in Kaneohe Bay (Hawaii), mainly consisted of crustaceans and benthic and reef fish, while the adults examined contained remains of cephalopods and bony fish. Vaske Júnior *et al.*, (2009) analysed the stomach contents of juvenile individuals in northeast Brazil and, based on the prey identified, suggested that these individuals frequently moved between shallow and deep waters to feed. The results obtained by Klimley (1983) in the Gulf of California coincide with those of Vaske Júnior *et al.*, (2009). Klimley (1983) observed that juvenile individuals mainly fed on neritic and benthic fish, intermediate-sized individuals feed on epipelagic cephalopods, and adults feed on neritic and epipelagic fish and mesopelagic and epipelagic cephalopods. Bornatowski *et al.*, (2014) found that for individuals caught in coastal waters in southeast Brazil, Sciaenids and crustaceans were the most significant prey to discriminate between neonate and juvenile diets, and Sciaenids, elasmobranchs and Carangids differentiated juveniles and adults. In shallow coastal waters in South Brazil (north coast of the Rio Grande do Sul), Horn (2014) found that teleost fish were the most significant prey group in accordance with their amount and frequency in regard to the occurrence in the stomachs of 107 neonates and small juveniles, followed by crustaceans, and to a lesser extent molluscs. For each group, the most common items were *Trichiurus lepturus*, unidentified shrimps, and *Lolliguncula brevis*. Similar results were found by Dolphine (2014) when analyzing the stomachs of 248 neonates and small juveniles (maximum size 80 cm, but most under 60 cm) captured in shallow coastal waters in southeast Brazil (central coast of Sao Paulo). It was detected that the most important items were fish (57% Index of Relative Importance, IRI), followed by crustaceans (25% IRI) and cephalopods (18%). Whilst it was not possible to identify most fish, Dolphine (2014) recorded the occurrence of at least 11 species, mainly from the families Scianidae, Engraulidae, Ophichtidae and Ariidae. Crustaceans were mainly represented by shrimp from the families Sergestidae and Penaeidae. Molluscs were represented by the species *L. brevis* and *Doryteuthis plei*. Crustaceans were relatively more significant in smaller individuals, which reveals a tendency that the consumption of cephalopods increased in larger individuals (Dolphine 2014). The importance of crustaceans in the diet of neonates and small juveniles has also been observed in an estuary area in Fiji (Rio Rewa), where Brown *et al.*, (2016) analyzed the stomachs of 50 individuals with sizes under 80 cm. It was found that predominant diet was crustaceans (decapods and stomatopods), with a relative importance as a whole of 81.04 %

The preference for crustaceans and benthic fish and mollusc species in the diet of neonate and juvenile *S. lewini* has been mentioned in several studies (Clarke 1971; Simpfendorfer & Milward 1993; Aguilar 2003; Torres-Rojas *et al.*, 2006; Estupiñán-Montaño *et al.*, 2009, Bornatowski *et al.*, 2014), but as they grow and move further away from the coast, their diet is mainly composed of epipelagic species of squid and bony fish (Clarke 1971; Klimley 1983, 1987), although benthic cephalopods have also been mentioned as a significant prey (Estupiñán-Montaño *et al.*, 2009; Aguilar 2011). Horn (2014) found that while crustaceans comprise a secondary fish group in South Brazil, they are more significant in neonates than in small juveniles captured in the same area. De Bruyn *et al.*, (2005) observed that the presence of chondrichthyan species in the diet of *S. lewini* was more frequent in larger individuals. In Ecuador, Estupiñán-Montaño *et al.*, (2009) reported a notable difference between the diet of female and male adults, where females preferably consume benthic cephalopods and males mesopelagic cephalopods. A recent study focused on adult females in the Galapagos Islands found that by analyzing of stable isotopes, *S. lewini* shows a response to climate variations in terms of its nutritional behaviour (Arnés-Urgellés *et al.*, 2021). According to the authors, the data obtained suggest that during the warm years *S. lewini*'s nutritional efficiency may reduce in the region, whereby the trophic niche of individuals could be extended when adopting a more generalist nutritional behaviour, which could involve an increased use of areas far removed from the coast for nutrition.

The dietary habits of *S. lewini* seem to be highly dependent on the different stages of the species' lifecycle and the various geographical regions where it has been studied. Some researchers have characterised this species as a general and opportunistic predator that is not very selective, with a diet that is mainly determined by which prey is the most abundant and accessible in the region (Klimley 1983; Torres-Rojas *et al.*, 2006; Aguilar 2011). Some researchers reported that *S. lewini* does not feed during the day (Klimley & Nelson 1981, 1984; Hearn *et al.*, 2010) and is more active at night (Holland *et al.*, 1992, 1993; Lowe 2002), which suggests that this species feeds at night-time.

4.f Physiology

The various sensory advantages related to the shape of hammerhead sharks' head have been described, but none are specific to *S. lewini* to date. These sensory advantages include the hypothesis of increased olfactory capacity; it has been demonstrated that the width of their head allows them to explore a larger proportion of waters tracking smells. In addition, the distance between their nostrils helps them identify where smells come from, although it has not been confirmed whether they have greater olfactory acuity. In any case, these olfactory advantages, together with a larger number of electroreceptors over the width of the head, increase the probability of finding prey (Kajiura *et al.*, 2005). Moreover, it has also been proposed that the form of the head lends hydrodynamic stability to the curves. This facilitates more manoeuvrability that may be important for efficacy when catching prey (Kajiura *et al.*, 2003; Gaylord *et al.*, 2020).

Some studies have indicated that *S. lewini* makes highly directional movements, which suggests that this species is able to guide itself or navigate using environmental variables or characteristics (for example, temperature, topography of the ocean floor, electromagnetic gradients) (Klimley & Nelson 1984; Klimley *et al.*, 1988). One of the hypotheses proposed to explain *S. lewini*'s orientation capacities is based on the ability to detect small changes in geomagnetic intensity associated with the topography of the ocean floor via the ampullae of Lorenzini. In this sense, the peculiar shape of the hammerhead sharks could imply greater acuity in the detection of intensity changes, as it can better distinguish between the intensities detected by the groups of electroreceptors located at each end of the head (Klimley 1993). However, this hypothesis has not yet been proven and other possible hypotheses have been proposed (Klimley 1993), such as the orientation of magnetite minerals (Fe_3O_4) in the skin and the differential pumping of chemical components between the eyes.

Mercury is a highly toxic contaminant that is found in the environment as a result of human and volcanic activity. This and other components bioaccumulate along the trophic chain, and higher concentrations therefore tend to be found in the tissues of large predators. Consequently, knowledge of the potential impact on human health is important, as these species are caught for consumption in some countries. In the Gulf of California, García-Hernández *et al.*, (2007) observed significant differences between the mercury concentrations found in 11 shark species belonging to 8 genera. *Sphyrna* spp. was the genus with the highest values. A significant correlation between TL and mercury concentration was found for *S. lewini* in this study, but no relationship was discovered in the case of *S. zygaena*.

5. Fisheries biology

5.a Populations/Stock structure

Duncan *et al.*, (2006) studied the phylogeography of *S. lewini* based on mitochondrial DNA and found a coherent populational structure between the considered regions, both within and between the Atlantic, Pacific and Indian Oceans. In addition, various coastal nursery areas that are connected by continental or insular shelves showed greater genetic homogeneity. In accordance with these results, Duncan *et al.*, (2006) suggested that *S. lewini* has little dispersal capacity between areas separated by vast oceanic regions and a low degree of philopatry according to the little population structure between nursery areas connected by the neritic environment. However, a more recent global study that considered both mitochondrial and nuclear genetic markers (Daly-Engel 2012) successfully demonstrated a notable bias in the dispersal capacity and behaviour of males and females. Daly-Engel *et al.*, (2012) observed restricted gene flow through the maternal lineage (mitochondrial DNA) between regions not connected by coastline, in addition to extensive nuclear DNA gene flow, even showing low levels of population structure across regions in different ocean basins. By way of example, the researchers detected a highly significant mitochondrial DNA structure, in contrast with a lack of structure in nuclear DNA, between the Seychelles and the Western Indian Ocean and Western Australia, and between Hawaii and the east Pacific. This discovery means that connectivity on large spatial scales is maintained by the greater dispersal capacity of males, while on smaller scales the close link between females and nursery areas, together with the annual periodicity of

the reproductive cycle, could reduce their dispersal capacity and strengthen genetic structure on the local scale (Daly-Engel *et al.*, 2012). The connectivity of *S. lewini* between different regions has been mentioned in other genetic studies. Ovenden *et al.*, (2011) reported that there is a single stock along the east coast of Australia (~2,000 km) and detected that there is no population structure between this region and Indonesia. The only regions considered in the study of Daly-Engel *et al.*, (2012) in the Atlantic Ocean were the Gulf of Mexico, South Carolina (United States) and West Africa, and all showed significant levels of population structure. According to these authors, the degree of genetic differentiation between the Gulf of Mexico and South Carolina is surprisingly high considering the geographic proximity, but there appears to be a one-way gene flow towards South Carolina.

A later study conducted by Pinhal *et al.*, (2020) analysed an important quantity of samples from the different regions throughout the West Atlantic, including the Gulf of Mexico, Caribbean Sea, and different states throughout the North, Northeast, southeast and South of Brazil, aiming at covering most of the latitudinal distribution range of this species in the West Atlantic. Sequence analysis of the control region of the ADNmt and nuclear microsatellites both indicated genetic structuring among the populations of the Gulf of Mexico, Caribbean Sea and Brazil. Furthermore, population structuring was also found within the areas sampled in Brazil, with a significant differentiation among individuals of the N and NE and those samples of the SE and S of this country. Contrary to this proposal that the large-scale genetic flux is mediated through males (Daly-Engel *et al.*, 2012), analysis at population levels conducted by Pinhal *et al.*, (2020) indicate that there could be ecological, oceanic or behavioural barriers that sufficiently affect the dispersion of males, restricting this connectivity. The link between the movements of the species and the structure of the population are related to a philantropical behaviour associated to reproduction, where males and females probably migrate to different locations of the Atlantic, later returning to the same area to give birth. In this way, the specimens with high ancestry coefficient pertaining to the Gulf of Mexico and the Caribbean that were found in Brazil have probably migrated between these regions, later returning to the original area to copulate and give birth. The connectivity among areas sampled in Brazil was substantially higher than the connectivity with the Gulf of Mexico and Caribbean.

As well as a restricted genetic connectivity among populations of *S. lewini* in the Atlantic, Pinhal *et al.*, (2020) also obtained results that suggest that specimens are not disperse in long distances, which coincides with what was determined by different studies which analysed the movements and dispersion patterns by means of tag-recapture (Kohler & Turner 2019) as well as also electronic tags (Wells *et al.*, 2018; Bezerra *et al.*, 2020). Pinhal *et al.*, (2020) support that the philantropic behavior associated to reproduction is the main factor contributing to the population structure in the Atlantic and, based on the peculiarity of long-distance migrations and the extent and regional location of genetic structure found in their study, suggests that there are at least 3 populations of *S. lewini* in the West Atlantic (Gulf of Mexico, Caribbean Sea and Brazil), each with their own particular farming area and different annual and ontogenetic cycles of migration from these farming areas towards oceanic environments.

Some genetic studies on *S. lewini* have detected a mysterious and undescribed species of hammerhead shark in the Atlantic Ocean (Abercrombie *et al.*, 2005; Quattro *et al.*, 2006; Pinhal *et al.*, 2012, Quattro *et al.*, 2013). This species is morphologically similar to *S. lewini* but has recently been recognised as a new species (*S. gilberti*) based on genetic analyses and differences in the number of vertebrae in the column (Quattro *et al.*, 2006, Quattro *et al.*, 2013). It was initially detected in the United States, coastal waters of South Carolina (NW Atlantic) and considered endemic to that region (Quattro *et al.*, 2006), but Pinhal *et al.*, (2012) recently confirmed its presence in the southwest Atlantic. Subsequent studies also highlight the occurrence of this new species in coastal waters from other states (including Georgia, Florida and North Carolina). This covers a broad portion of the United States east coast with the highest relative abundance found in North and South Carolina (Barker *et al.*, 2019; Barker *et al.*, 2021). Aside from presenting overlap with the distribution of *S. lewini*, hybrid individuals have also been found between both species (Barker *et al.*, 2019).

In the locations where it has been detected, it is probably wrongly identified as *S. lewini*, which could cause potential problems in population studies and demographic parameter estimations for *S. lewini*. Barker *et al.*, (2021) found that 25% of individuals captured in the northwest Atlantic (mainly small juveniles) were identified as *S. gilberti*, and indicated that, if adults were found in a similar proportion, they may include an important portion of what is currently deemed the *S. lewini* population on the United States coast. In the same study, the authors suggest that while past evaluations include data from a second species with different biological parameters, there may be important implications for the management of the complex of hammerhead shark species, similar to that recently declared by Barker *et al.*, (2019) and Pinhal *et al.*, (2020).

Some studies have reported a notable decrease in hammerhead shark populations (mainly *S. lewini*) in the northwest Atlantic (Baum *et al.*, 2003; Myers *et al.*, 2007), but these trends could be even more serious if the existence of this cryptic species is recognised. Both the abundance and total distribution of this new species are not clearly defined, meaning that it is not possible to know what effect this could have on demographic studies and stock assessments of *S. lewini*. Consequently, efforts must focus on improving the identification and characterisation of this species and better defining its range and the collection of data on its life history.

5.b Description of the fisheries

Given the difficulties for the correct identification of hammerhead shark species, in general, these are recorded in aggregated form to logbooks, reducing the availability of records on smooth hammerhead shark catches (Camhi *et al.*, 2009; Miller *et al.*, 2014; Bezerra *et al.*, 2016, Gallagher & Klimley 2018). This limitation is also present in some analyses on catch data obtained by means of on-board observer programmes. In the specific case of the northwest Atlantic the recent determination that there is a recently reported cryptic species there (Quattro *et al.*, 2006; Quattro *et al.*, 2013 Barker *et al.*, 2021), very similar to the not very studied smooth hammerhead shark, implies that the existing data on catch of the latter possibly includes individuals from both species.

S. lewini is caught throughout its distribution area by various fisheries (artisanal, industrial and recreational), including pelagic and bottom longline, set and drift gillnets, trawl nets, purse-seine, and rod and reel (Compagno 1984; Fowler *et al.*, 2005; Baum *et al.*, 2007, Cortés & Baertlein 2021, Martinazzo *et al.*, 2022). Close to the coast and in waters on the continental shelf, neonates and juveniles are caught by artisanal fisheries, while larger juveniles and adults are more frequently caught on the slope and in oceanic waters by industrial fisheries, mainly pelagic longline and gillnets (Kotas 2004; Baum *et al.*, 2007; Amorim *et al.*, 2011, Kotas *et al.*, 2012; Horn, 2014). Although some fisheries have targeted this species (for example, Kotas, 2004; Alejo-Plata *et al.*, 2007; Bejarano, 2007; Torres-Huerta *et al.*, 2008; Torres-Huerta *et al.*, 2008, Horn, 2014), it is generally as by-catch, and the carcass and fins or just the fins may be retained (Baum *et al.*, 2007).

S. lewini fins are extremely coveted on some Asian markets and can reach very high values (Kotas 2004; Amorim *et al.*, 2011). By means of samples taken during commercial operations, it was determined that this species, along with *S. mokarran* and *S. zygaena*, has reached a 6% share of the Hong Kong market (Clarke *et al.*, 2006). The meat, skin and liver oil are also traded, but have a lower economic value (Compagno 1984).

In the Atlantic Ocean, *S. lewini* catches vary by fishing gear and region. According to Kotas (2004), between 1989 and 2002, 78.4% of the hammerhead sharks caught by fisheries operating out of the Port of Santa Catarina (southeast Brazil) were caught by gillnet fisheries (bottom and surface), 14.5% by pelagic longline and 4.9% by pair trawl. Kotas *et al.* (2012) observed that for the fleet operating in S and SE Brazil with bottom set gillnet targeted at capturing sea bass (*Micropogonias furnieri*) from the two main ports of Santa Catarina, *S. lewini* represented 80.4% of total hammerhead sharks landed over the period 2008-2009; and *S. zygaena* comprised the remaining 19.6%. In Northeast Brazil, *S. lewini* is the most frequently caught shark species in gillnet fisheries, together with *Carcharhinus signatus* (Vaske Júnior *et al.*, 2009), while in the South of Brazil it is targeted by surface gillnet fisheries, alongside *S. zygaena* (Kotas 2004; Kotas *et al.*, 2008, Horn, 2014). Significant catches (various events between 550 and more than 1000 individuals including neonates and small juveniles) have been recorded with bottom set gill nets (both bottom and surface) in south Brazil coastal waters, which reveals that *S. lewini* forms large aggregations in this region (Horn, 2014).

According to Amorim *et al.*, (2011) hammerhead sharks (*S. lewini* and *S. zygaena*) represented 6.3% of the total shark catch of longline fleets in the South of Brazil between 2007 and 2008. Kotas (2004) reported a higher value (8.3%) between 2000 and 2002 for longline vessels operating out of the Port of Santa Catalina. Bezerra *et al.*, (2016) analysed catch and effort data of national and chartered longline fleets of Brazil for the 2004-2011 period, observing that hammerhead shark catches (*S. lewini*, *S. mokarran* and *S. zygaena* in conjunction), reached a total of 6,172 specimens in 29,418 fishing sets, representing 0.40% of the total specimens caught. This study also indicates that the average catch per unit effort for all surface longline sets was nearly double than that of deep longline. In the exclusive economic zone (EEZ) of Uruguay, *S. lewini* and *S. zygaena* jointly represent 3.8% of the total shark catch of the Uruguayan longline fleet between 1998 and 2009, while *S. lewini* alone accounted for just 0.2% (Mas 2012). In the southeast of the United States, *S. lewini* represented 4.3% of the total shark catch of longline fleets between 1992 and 2000 (Beerkircher *et al.*, 2002). Between January 2004 and April 2005, scientific observers on a vessel operating with bottom longline targeting sharks in coastal waters of the United States (Gulf of Mexico and the NW Atlantic), recorded catches of at least 455 *S. lewini* specimens, with sizes between 56-287 cm FL (Morgan & Burgess 2007). Mortality reached 91.4% of the total specimens observed, being higher for juveniles (95.2%) than for adults (90.9%). In Venezuela, Arocha *et al.*, (2002) reported that 4.1% of the Venezuelan longline fleets' total shark catch was accounted for by *S. lewini*.

Purse seine fleets targeting tropical tunas in the East Atlantic caught various species of elasmobranches as bycatch, including *S. lewini* (Clavareau *et al.*, 2018, Lezama-Ochoa *et al.*, 2018). Between 2005-2017, the total catch of 929 specimens (6.0% of all elasmobranches) was recorded by observers onboard the French fleet (Clavareau *et al.*, 2018). In this study, the authors determined that 70.3% were juvenile specimens, and the mortality rate reached 41.7%. Lezama-Ochoa *et al.*, (2018) reported that between 2003-2011 the catch of 217 individuals was observed in a total of 1,591 sets performed by Spanish and French fleets operating in the East tropical Atlantic.

Using an ecological risk evaluation, *S. lewini* was classified as low-medium vulnerability for fleets operating with industrial pelagic longline in the Atlantic Ocean (Cortés *et al.*, 2015), in part because of the low susceptibility to these fisheries and their relatively medium-high productivity.

However, seeing as this species is caught by several fishing modalities and over the whole range of age and size classes (Gadig *et al.*, 2002; Vooren *et al.*, 2005; Adams & Paperno 2007; Doño 2008; Kotas *et al.*, 2008; Kotas 2009; Mas 2012, Kotas *et al.*, 2012; Miller *et al.*, 2013; Gallagher y Klimley, 2018), it is likely that *S. lewini* is at a higher risk level than estimated when just the industrial longline fleet is considered.

Unlike other shark species, *S. lewini* is particularly susceptible to some fishing gears such as gillnets and pelagic longlines. Clarke (1971) mentioned that the characteristic shape of this shark's head made it easier for it to get caught in gillnets. For pelagic longline, some studies indicated a high percentage of dead individuals at haulback. Beerkircher *et al.*, (2002) reported that 61% (n=77) of specimens were dead at haulback in the southeast of the United States, while Coelho *et al.*, (2012) calculated a mortality of 57% (n=21) in a wider area of the Atlantic.

Data obtained from 1998 to 2005 by observers in South Africa longline fisheries targeting large pelagics, indicate that hammerhead sharks represented 0.6% of the total shark catches (Petersen *et al.*, 2009). The authors indicate that this value corresponds to the set of *S. zygaena*, *S. lewini* and *S. mokarran*. No values for each species are provided.

Globally, *S. lewini* is classified as *Critically Endangered* in the International Union for Conservation of Nature's red lists (IUCN; Rigby *et al.*, 2019). More local assessments classified the species as *Vulnerable* (central-east Atlantic, southwest Atlantic) and *Endangered* (southeast and central-east Pacific, northwest and central-west Atlantic, Western Indian Ocean). *S. mokarran* and *S. zygaena*, *S. lewini* were included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2013, having entered into force in September 2014. In the Atlantic Ocean, and in accordance with ICCAT Recommendation 10-08, it is prohibited to retain onboard, transship, land, store, sell, or offer for sale any part or whole carcass of hammerhead sharks of the family Sphyrnidae (except for *S. tiburo*) (ICCAT, 2010).

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